## **Géominpal Belgica**

Découvertes géologiques, minéralogiques et paléontologiques

en Belgique.

6

Observations concerning the Evolution and the Parasystematics of all the living and fossil Chlamydoselachiformes, Squatiniformes, Orectolobiformes, and Pristiophoriformes, based on both biological and odontological data. Suggestion of a possible origin of the Order Pristiophoriformes, of the Order Ganopristiformes and a global Synthesis of the previous Systematics proposals. (Last Data integrated: These published before 05.03.2014)

By

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Chlamydoselachus anguineus GARMAN, 1884. Caught off the North Hebrides, the North East Atlantic, between 680-720 metres depth. Female of 131 centimetres of total length. Longitude: 08° 55' West, Latitude: 59° 10' North. Gift of the senior-author to the I.R.S.N.B., Brussels, Belgium Collections of the Recent Vertebrates. Registration Numbers: P. 24860 Photograph Jacques Herman.

**HERMAN Jacques Editor** 

### **Dedication:**

This work is dedicated

to the memory of

Dr. Lev Semonovich Berg, (1876 - 1950)

to the memory of

Dr. Wilhem Heinrich Waagen (1841 - 1900)

and to the memory of

Dr. Alfred Sherwood Romer, (1894 - 1973)

who wrote the principal Systematic conceptions utilised by the Senior-Author

> Respectfully, Dr. Jacques Herman and his Wife, at Beigem, 30 June 2013\*

> > Jacques Herman and Hilde Van Waes,

\*Such as for the preceding issues of *Géominpal Belgica*, the date of the Dedication is the date of the beginning of its redaction and not this of its Publication.

## **TABLE OF CONTENTS**

- 1. Summary Résumé Samenvatting Kurzfassung Resumo
- Резюме: р.: 10
- 2. Introduction: p.: 15
- 3. Introduction: p.: 16
- 4. Introductie: p.: 17

## 5. Euselachii and Neoselachii: p.: 18

- -5.1. Euselachii: p.: 18
- -5.2. Neoselachii: p.: 18
- -5.3. Suggestion: p.: 19

### 6. Additional recent and fossil materials: p.: 19

-6.1. Additional recent material: p.: 19

-6.2. Additional fossil material: p.: 19

### 7. Super Order Chlamydoselachiformes nov.: p.: 19

- -Order Chlamydoselachiformes HERMAN & VAN WAES, 2012: p.: 20 -Family Chlamydoselachidae GARMAN, 1884: p.: 20 -Family Phoebodontidae WILLIAMS, 1985: p.: 20
- -7.1. Living representatives of the Order Chlamydoselachiformes: p.: 20

-Generalities: p.: 20

-Distribution of the two extant species: p.: 20

- -7.2. Odontological characteristics of the Order Chlamydoselachiformes: p.: 22
- -7.3. Principal Biological characteristics of the Order Chlamydoselachiformes: p.: 22
- -7.4. Biological data detectable on fossil skeletons of the Order Chlamydoselachiformes: p.: 22
- -7.5. Fossil representatives of the Order Chlamydoselachiformes: p.: 23
- -7.6. Natural History of the Order Chlamydoselachiformes and Conclusion: p.: 23
- -7.7. Ontogeny of the teeth of the Super Order Chlamydoselachomorphii: p.: 25

### 8. Order Squatiniformes de BUEN, 1926: p.: 26

-8.1. Living representatives: p.: 26

-Anatomical singularities of the extant representatives of the Genus Squatina: p.: 27

-Anatomical singularities of the extant representatives of the three Genera: Orectolobus,

Sutorectus and Eucrossorhinus (Family Orectolobidae): p.: 28

- -Logical reflections applied to the research of possible ancestors of extant taxa: p.: 28
- -A review of the successive taxonomic propositions: p.: 31
- -8.2. Odontological characteristics of the Genus Squatina: p.: 37
- -8.3. Principal Biological data of the Genus Squatina: p.: 37
  - -Reflections concerning the distribution of the Genus Squatina: p.: 39
  - -Searching an explanation for its absence in the northern Indian Ocean: p.: 39
- -8.4. Biological data detectable on fossil skeletons attributed to the Genus Squatina: p.: 40
- -8.5. Fossil representatives of the Order Squatiniformes: p.: 40
  - -Odontological characteristics of the fossil taxa attributed to the Order Squatiniformes: p.: 41
  - -Re-examination of the other fossil taxa of the Genus Squatina: p.: 44
- -8.6. Conclusion and Natural History of the Order Squatiniformes: p.: 47

### 9. Order Orectolobiformes sensu APPLEGATE, 1974: p.: 47

-9.1. Living representatives of the Order Orectolobiformes (*sensu* APPLEGATE, 1974), with adjustments to 2012: p.: 47

-9.2.: Systematics: p.: 47

-Extant Families included in this Order: p.: 47

-Extant Genera included in these Families: p.: 48

-9.3. Family Orectolobidae GILL, 1896: p.: 49

-Genus Orectolobus BONAPARTE, 1834: p.: 49

- -Genus Eucrossorhinus REGAN, 1908: p.: 53
- -Genus Sutorectus REGAN, 1908: p.: 54

-9.4. Family Stegostomatidae GILL, 1862: p.: 55

-9.5. Family Ginglymostomatidae GILL, 1862: p.: 56 -Genus Ginglymostoma Müller & Henle, 1837: p.: 56 -Genus Nebrius RÜPPEL, 1837: p.: 57 -9.6. Family Hemiscylliidae GILL, 1862: p.: 58 -Genus Hemiscyllium Müller & Henle, 1838: p.: 58 -Natural History of the Genus Hemiscyllium: p.: 63 -Possible ancestor of the Genus Hemiscyllium: p.: 63 -Genus Chiloscyllium Müller & Henle, 1837: p.: 63 -Natural History of the Genus Chiloscyllium: p.: 68 -Possible ancestor of the Genus Chiloscyllium: p.: 68 -9.7. Family Brachaeluridae APPLEGATE, 1974: p.: 68 -Genus Brachaelurus OGILBY, 1908: p.: 69 -Spatio-temporal distribution of the Genus Brachaelurus: p.: 70 -Validity of their attribution to the Genus Brachaelurus: p.: 70 -Genus Cirrhoscyllium OGILBY, 1908: p.: 70 -Genus Heteroscyllium REGAN, 1906: p.: 71 -9.8. Family Parascylliidae GILL, 1862: p.: 71 -Genus Parascyllium GILL, 1862: p.: 71 -Geological range of the Genus Parascyllium: p.: 72 -Genus Cirrhoscyllium SMITH & RADCLIFFE, 1913: p.: 74

### 10. Re-examination of the Order Orectolobiformes (sensu APPLEGATE, 1974): p.: 76

-10.1. Odontological data of the Order Orectolobiformes (sensu APPLEGATE, 1974): p.: 76

-10.2. Principal Biological data of the Order Orectolobiformes (sensu APPLEGATE, 1974): p.: 76

-General morphology: p.: 76

-Reflection concerning the risk-perception capacity of some Orectolobiformes: p.: 76

-Reflection concerning the performances of some Orectolobiformes: p.: 77

-Ecological data furnished by extant representatives: p.: 77

- 1. Respiratory performances: p.: 77
- 2. Moving performances: p.: 77
- 3. New risk: p.: 77
- -Paleontological data: p.: 77

-10.3. Biological data detectable on fossil skeletons of the Order Orectolobiformes (*sensu* APPLEGATE, 1972): p.: 77

-10.4. Fossil representatives of the Order Orectolobiformes (*sensu* CAPPETTA, 2002) and Orectolobiformes considered as *incertae sedis*: p.: 78

-Genus Orectolobus BONAPARTE, 1834: p.: 78

-Genus Ginglymostoma Müller & Henle, 1837: p.: 78

- 1. Paleogeographical and stratigraphical distribution of the Genus Ginglymostoma: p.: 79
- 2. Paleoecological distribution of the Genus *Ginglymostoma*: p.: 79
- 3. Natural History of the Genus Ginglymostoma: p.: 79
  - 1. Distribution of its extant representatives: p.: 79
  - 2. Distribution of its extinct representatives: p.: 79
  - 3. Conclusion: p.: 80

-Genus Nebrius RÜPPEL, 1837: p.: 80

- 1. Fossil representatives of this Genus: p.: 80
- 2. Geological range: p.: 80
- 3. Natural History of the Genus Nebrius: p.: 80

-Genus Chiloscyllium Müller & Henle, 1837: p.: 81

-Reflection concerning the American fossil taxa attributed to the Genus Chiloscyllium: p.: 82

- -Genus Hemiscyllium MÜLLER & HENLE, 1838: p.: 82
- -Genus Phorcynis THIOLLIERE, 1854: p.: 83

-Genus Parascyllium GILL, 1862: p.: 84

-Genus Plicodus WINKLER, 1874: p.: 84

-Genus Acrodobatis LEIDY, 1877: p.: 84

-Genus Cantioscyllium WOODWARD, 1889: p.: 84

-Genus Brachaelurus OGILBY, 1907: p.: 86

-Genus Crossorhinus WOODWARD, 1918: p.: 87

-Genus Corysodon de SAINT-SEINE, 1949: p.: 87

-Genus Eostegostoma HERMAN, 1977 in NOLF & TAVERNE, 1977: p.: 88

-Genus Protoginglymostoma HERMAN, 1977: p.: 89 -Genus Cretorectolobus CASE, 1978: p.: 90 -Genus Orectoloboides CAPPETTA, 1979: p.: 92 -Genus Squatiscyllium CAPPETTA, 1980: p.: 94 -Genus Almascyllium CAPPETTA, 1980: p.: 95 -Genus Paraginglymostoma HERMAN, 1982: p.: 96 -Genus Palaeobrachaelurus THIES, 1983: p.: 96 -Genus Annea THIES, 1983: p.: 98 -Genus Pseudoginglymostoma DINGERKUS, 1986: p.: 98 -Genus Cederstroemia SIVERSON, 1995: p.: 99 -Genus Delpitoscyllium NHOUBANI & CAPPETTA, 1997: p.: 100 -Genus Ganntouria NHOUBANI & CAPPETTA, 1997: p.: 101 -Genus Hologinglymostoma NHOUBANI & CAPPETTA, 1997: p.: 102 -Genus Plicatoscyllium CASE & CAPPETTA, 1997: p.: 102 -Genus Columbusia CASE, SCHWIMMER, BORODIN & LEGGETT, 2001: p.: 105 -Genus Navia BERNARDEZ, 2002: p.: 106 -Genus Eometlaouia NOUBHANI & CAPPETTA, 2002: p.: 107 -Genus Microtoxodus DELSATE, 2003: p.: 108 -Genus Folipistrix KRIWET, 2003: p.: 109 -Genus Dorsetoscyllium UNDERWOOD & WARD, 2004: p.: 110 -Genus Heterophorcynus UNDERWOOD & WARD, 2004: p.: 110 -Genus Palaeorectolobus KRIWET, 2008: p.: 111 -Genus Rhincodon SMITH, 1829: p.: 112 -10.5.: Conclusion and Natural History of the Order Orectolobiformes sensu Cappetta 2012: p.: 112 1. General conclusions of the re-examination of all the data concerning the fossil taxa of the Order Orectolobiformes (sensu Applegate 1972): p.: 112 2. Convexity and ornamentation of their dental crown: p.: 113 - Objective data: p.: 113 -Interpretation of this evidence: p.: 113 -Geological data of the appearance of this phenomenon and its cessation: p.: 113 -Lineages affected by this phenomenon: p.: 113 3. Fossil Genera included in the Order Orectolobiformes before the proposal of its emendation and reconsideration of their Family attribution: p.: 114 4. Reconsideration of their attribution and proposal of one new Family: p.: 114 1. General conclusion: p.: 114 2. Detailed review: p.: 114 -Family Agaleidae REES, 2000: p.: 114 -Family Phorcynidae nov.: p.: 114 -Family Orectolobidae JORDAN & FOWLER, 1903: p.: 114 -Family Orectolobidae emend .: p.: 114 -Family Brachaeluridae APPLEGATE, 1974: p.: 115 -Family Ginglymostomatidae GILL, 1862: p.: 115 -Systematics: p.: 115 -Reproduction: p.: 115 -Genus Ginglymostoma Müller & Henle, 1837: p.: 115 1. Fossil representatives of this Genus: p.: 115 2. Material examined: p.: 116 3. Conclusions: p.: 116 1. Paleogeographical and stratigraphical distribution of the Genus Ginglymostoma: p.: 116 2. Paleoecological distribution of the Genus Ginglymostoma: p.: 116 4. Natural History of the Genus Ginglymostoma: p.: 116 1. Distribution of its extant representatives: p.: 116 2. Distribution of its extinct representatives: p.: 117 3. Conclusion: p.: 117 -Genus Nebrius RÜPPEL, 1837: p.: 117 1. Fossil representatives of this Genus: p.: 117 2. Geological range: p.: 117 3. Natural History of the Genus Nebrius: p.: 117 -Distribution of its extant representatives: p.: 117 -Distribution of its extinct representatives: p.: 117

-Conclusion: p.: 118

-Family Stegostomatidae GILL, 1862: p.: 118

-Family Pseudoginglymostomatidae DINGERKUS, 1986: p.: 118

-Family Hemiscylliidae GILL, 1862: p.: 118

-Family Parascylliidae GILL, 1862: p.: 118

-Family Rhincodontidae GARMAN, 1913: p.: 118

-Genus Rhincodon SMITH, 1829: p.: 119

-Genus Pararhincodon HERMAN, 1976 in CAPPETTA, 1976: p.: 119

-10.6. Systematic problems: the Orectolobiformes incertae Family sensu CAPPETTA, 2012: p.: 120

1. List of the taxa: p.: 120

2. Partial Solution: p.: 120

3. Morphological observations: p.: 120

## 11. Problem of the systematic position of the Genus Squatirhina CASIER, 1947: p.: 121

-11.1. Ancient data concerning the Genus Squatirhina: p.: 121

-Odontological characteristics of the Genus Squatirhina: p.: 121

-Biological characteristics of the Genus Squatirhina: p.: 121

-Spatio-temporal distribution of the Genus Squatirhina: p.: 121

-11.2. Additional reflection: p.: 122

-11.3. Systematic readjustment and conclusion: p.: 122

### 12. Order Pristiophoriformes BERG, 1958: p.: 123

-12.1. Living representatives of the Order Pristiophoriformes: p.: 123

-Family Pristiophoridae BLEEKER, 1859: p.: 123

-Genus Pristiophorus MÜLLER & HENLE, 1837: p.: 123

-Genus Pliotrema REGAN, 1906: p.: 123

-12.2. Odontological characteristics of the Order Pristiophoriformes: p.: 129

-12.3. Biological characteristics of the Order Pristiophoriformes: p.: 129

-12.4. Biological data detectable on fossil skeletons of the Order Pristiophoriformes: p.: 129

-12.5. Fossil representatives of the Order Pristiophoriformes: p.: 129

-Family Pristiophoridae BLEEKER, 1859: p.: 129

-Genus Pristiophorus MÜLLER & HENLE, 1837: p.: 129

-Genus Propristiophorus WOODWARD, 1932: p.: 129

-12.6. Conclusion and Natural History of the Order Pristiophoriformes: p.: 131

-The Natural History of the Genus Pristiophorus: p.: 131

-The Natural History of the Genus *Pliotrema*: p.: 132

-12.7. Similarities and differences existing between the members of the Order Ganopristiformes and the

members of the Order Pristiophoriformes: p.: 132

1. General morphology of their body: p.: 132

2. Constitution of their rostral teeth: p.: 132

3. Mode of implantation of the rostral teeth: p.: 132

4. Oral teeth: p.: 132

- 5. Vertebral column: p.: 132
- 6. Mode of reproduction: p.: 133

7. Zone of apparition and Epoch: p.: 133

8. Odontological conclusion: p.: 133

9. Differences presented by the specific taxa of the Orders Ganopristiformes and the Order Pristiophoriformes: p.: 133

13. New Parasystematic proposals: p.: 133

-13.1. Super Order Chlamydoselachomorphii nov.: p.: 133 -Odontological characteristics of the Chlamydoselachomorphii: p.: 133 -Biological characteristics of the Chlamydoselachomorphii: p.: 134

-13.2. Super Order Orectolobomorphii HERMAN & VAN WAES, 2012: p.: 134 -Odontological characteristics of this Super Order: p.: 134

-Biological characteristics of this Super Order: p.: 1 -Biological characteristics of this Super Order: p.: 134

-13.3. Super Order Pristiophoromorphii nov.: p.: 134

-13.4. Order Hemiscylliiformes nov.: p.: 134

-Odontological characteristics of the Order Hemiscylliiformes: p.: 134

-Biological characteristics of the Order Hemiscylliiformes: p.: 135

-Spatio-temporal distribution of the Order Hemiscylliiformes: p.: 135 -Family Phorcynidae nov. Fam.: p.: 135 -Odontological characteristics of the Family Phorcynidae: p.: 135 -Biological characteristics of the Family Phorcynidae: p.: 135 -Spatio-temporal distribution of each of its Genera: p.: 135 -Conclusion: p.: 136 -Remark: p.: 136 -Family Agaleidae DUFFIN & WARD, 1983: p.: 137 -Family Hemiscylliidae GILL, 1862: p.: 137 -Family Brachaeluridae APPLEGATE, 1974: p.: 137 -Family Ginglymostomatidae GILL, 1862: p.: 138 -Final conclusions concerning spatio-temporal distribution of the Order Hemiscylliiformes: p.: 139 -13.5. Order Stegostomatiformes nov. : p.: 140 -Family Stegostomatidae GILL, 1862: p.: 140 -Odontological characteristics and their progressive modifications: p.: 140 -Biological characteristics of the Family Stegostomatidae: p.: 140 -Family Parascylliidae GILL, 1862: p.: 140 -Family Rhincodontidae GARMAN, 1913: p.: 141

### 14. The Hemiscylliidae as possible ancestors of the Order Pristiophoriformes: p.: 143

-14.1. Principles of the *modus operandi* utilised for searching a possible ancestor of one taxon: p.: 143

- 1. Biological arguments: p.: 143
- 2. Anatomical criteria: p.: 143
- 3. Odontological data furnished by one isolated tooth of the Genus Squatina: p.: 143
- 4. Odontological data furnished by other isolated teeth: p.: 143
  - -Presence of a radicular notch: p.: 143
  - -Presence of lateral cusplets: p.: 144
  - -Presence of an ornamentation: p.: 144
  - -Presence of ancestral teeth without function: p.: 144
- 5. Data furnished by Ontogeny: p.: 144
- 6. Data furnished by Taphonomy: p.: 144
- 7. Distribution of their extant and extinct representatives: p.: 145
- -14.2. Geophysical arguments: p.: 145

-14.3. Astrophysical arguments: p.: 145

- 1. Solar loss of highly ionized particles: p.: 145
- 2. Influence of the solar winds on the terrestrial biosphere: p.: 145
- 3. Inversions of the Earth's magnetic poles and their possible influence on the Evolution: p.: 145

### 15. Reflection concerning the Eggs of the Chondrichthyes: p.: 146

- -15.1. Eggs of Holocephali: p.: 146
- -15.2. Eggs of Neoselachii: p.: 146
  - -Eggs of the different species of the Genus Heterodontus: p.: 146
  - -Eggs attributed to the Genus Cephaloscyllium: p.: 146
- -15.3. Eggs of Batoidei: p.: 146

## 16. Proposals for a global Parasystematics of the Selachii (2010-2014) A critical

## Synthesis: p.: 146

-Reminder: p.: 146

- -16.1. Respect of the bi-nominal Nomenclature of Linné and Artedi: p.: 147
  - 1. Origin of the bi-nominal Nomenclature of all the living forms: p.: 147
  - 2. The intentions of Pierre Artedi and Karl von Linné: p.: 147
  - 3. Remark: p.: 148
  - 4. The tri-nominal nomenclature: p.: 148
- -16.2. Criteria used by the Senior-Author of Géominpal Belgica: p.: 148
  - 1. Odontological Criteria: p.: 148
  - 2. Biological Criteria: p.: 151
  - 3. Surprising results: p.: 153
  - 4. Other sources of information: p.: 153
    - -4.1. The growth of the teeth of Selachii and Batoidei: p.: 153
    - -4.2. Evolution of the neurological system of the Elasmobranchii: p.: 155

-16.3. Synthesis of the proposals concerning the higher Taxa of the extant Selachii: p.: 155 1. Preliminary remark concerning the extant Elasmobranchii: p.: 156 2. Biodiversity of the extant Families of Chondrichthyes: p.: 157 3. Generic taxa proposed after the publication of the new Parasystematics proposals presented in the Series Géominpal Belgica 2.1. to Addition to Géominpal Belgica 4. : p.: 157 -Systematics remark: p.: 157 -New Families: p.: 158 -New Genera: p.: 158 4. Systematic Inventory: p.: 159 -Class Chondrichthyes HUXLEY, 1880: p.: 159 -Euselachii HAY, 1902: p.: 159 -Super Order Hybodontomorphii nov.: p.: 160 -Order Hybodontiformes OWEN, 1846: p.: 160 -Family Hybodontidae OWEN, 1846: p.: 160 -Order Acrodontiformes nov. : p.: 160 -Family Acrodontidae CASIER, 1959: p.: 160 -Family Polyacrodontidae GLYCKMAN, 1964: p.: 161 -Order Ptychodontiformes rev.: p.: 161 -Family Ptychodontidae JAEKEL, 1898: p.: 161 -Family Hylaeobatidae HERMAN & VAN WAES, 2012: p.: 161 -Super Order Chlamydoselachomorphii HERMAN & VAN WAES, 2012: p.: 161 -Super Order Echinorhinomorphii HERMAN & VAN WAES, 2012: p.: 162 -Order Echinorhiniformes de BUEN, 1926: p.: 162 -Family Echinorhinidae GILL, 1862: p.: 164 -Family Pseudoechinorhinidae nov.: p.: 166 -Family Orthechinorhinidae nov.: p.: 167 -Order Hexanchiformes de BUEN, 1926 rev.: p.: 169 -Family Hexanchidae GRAY, 1851: p.: 169 -Order Heptranchiformes nov.: p.: 170 -Family Heptranchidae BARNARD, 1925: p.: 170 -Family Pseudonotidanidae UNDERWOOD & WARD, 2004: p.: 170 -Super Order Heterodontomorphii: p.: 171 -Order Heterodontiformes BERG, 1937: p.: 171 -Order Paracestracioniformes HERMAN & VAN WAES, 2012: p.: 171 -Super Order Squatinomorphii rev.: p.: 172 -Order Squatiniformes de BUEN, 1926: p.: 172 -Order Orectolobiformes HERMAN & VAN WAES, 2012 rev.: p.: 172 -Super Order Hemiscylliiomorphii nov.: p.: 172 -Order Hemiscylliiformes nov.: p.: 172 -Order Stegostomatiformes nov.: p.: 174 -Super Order Squalomorphii HERMAN & VAN WAES, 2012: p.: 176 -Order Squaliformes sensu HERMAN & VAN WAES, 2012: p.: 176 -Order Etmopteriformes HERMAN & VAN WAES, 2012: p.: 176 -Order Oxynotiformes HERMAN & VAN WAES, 2012: p.: 176 -Order Aculeoliformes HERMAN & VAN WAES, 2012: p.: 176 -Order Centrophoriformes HERMAN & VAN WAES, 2012: p.: 177 -Order Dalatiiformes HERMAN & VAN WAES, 2012: p.: 177 -Order Somniosiformes HERMAN & VAN WAES, 2012: p.: 177 -Super Order Scyliorhinomorphii HERMAN & VAN WAES, 2012: p.: 177 -Order Scyliorhiniformes HERMAN & VAN WAES, 2012: p.: 177 -Order Atelomycteriformes HERMAN & VAN WAES, 2012: p.: 178 -Order Halaeluriformes HERMAN & VAN WAES, 2012: p.: 178 -Order Pentanchiformes HERMAN & VAN WAES, 2012: p.: 178 -Order Triaenodoniformes HERMAN & VAN WAES, 2012: p.: 178 -Order Triakiformes nov.: p.: 179 -Family Triakidae GRAY, 1851: p.: 179

-Family Pseudotriakidae GILL, 1893: p.: 181 -Family Proscylliidae sensu COMPAGNO, 1973: p.: 183 -Family Leptochariidae GRAY, 1851: p.: 183 -Super Order Anacoracomorphii nov.: p.: 184 -Order Anacoraciformes HERMAN & VAN WAES, 2012: p.: 184 -Family Anacoracidae CASIER, 1947: p.: 185 -Family Galeocerdidae HERMAN & VAN DEN EECKHAUT, 2010: p.: 185 -Family Ptychocoracidae HERMAN & VAN WAES, 2012: p.: 185 -Family Paracoracidae CAPPETTA, 2012: p.: 186 -Super Order Isuromorphii nov.: p.: 186 -Order Isuriformes HERMAN & VAN WAES, 2012: p.: 186 -Family Isuridae HERMAN & VAN WAES, 2012 rev.: p.: 186 -Family Cretoxyrhinidae GLYCKMAN, 1958: p.: 187 -Family Paraisuridae HERMAN & VAN WAES, 2012: p.: 188 -Order Alopiiformes HERMAN & VAN WAES, 2012: p.: 188 -Family Alopiidae BONAPARTE, 1838: p.: 188 -Order Cetorhiniformes HERMAN & VAN WAES, 2012: p.: 192 -Family Cetorhinidae GILL, 1862: p.: 192 -Family Ostenoselachidae DUFFIN, 1998: p.: 192 -Super Order Odontaspididomorphii nov.: p.: 192 -Order Odontaspididiformes HERMAN & VAN WAES, 2012: p.: 192 -Family Odontaspididae rev.: p.: 192 -Family Mitsukurinidae JORDAN, 1898 rev.: p.: 193 -Family Pseudocarchariidae COMPAGNO, 1973: p.: 193 -Super Order Lamnomorphii nov.: p.: 194 -Order Lamniformes sensu HERMAN & VAN WAES, 2012: p.: 194 -Family Lamnidae rev.: p.: 194 -Family Archaeolamnidae UNDERWOOOD & CUMBAA, 2010: p.: 194 -Family Otodontidae GLYCKMAN, 1964: p.: 195 -Family Megachasmidae TAYLOR, COMPAGNO & STRUHSAKER, 1983: p.: 195 -Super Order Carcharhinomorphii rev.: p.: 195 -Order Carcharhiniformes sensu HERMAN & VAN WAES, 2012: p.: 196 -Super Order Scapanorhynchomorphii nov.: p.: 196 -Order Odontaspididiformes HERMAN & VAN WAES, 2012: p.: 196 -Super Order Pristiophoromorphii nov.: p.: 196 -Order Ptychotrygoniformes rev.: p.: 196 -Family Ptychotrygonidae KRIWET, NUNN & KLUG, 2009: p.: 196 -Super Order Ganopristomorphii nov.: p.: 198 -Order Ganopristiformes HERMAN & VAN WAES, 2012: p.: 199 -Family Ganopristidae HERMAN, 1977: p.: 200 -Family Sclerorhynchidae CAPPETTA, 1974: p.: 200 -Selachii: Enigmatic taxa: p.: 204 17. Batoidei (Sensu Compagno, 1973): p.: 204 -Super Order Rajomorphii HERMAN & VAN WAES, 2012: p.: 205 -Order Rajiformes BERG, 1940: p.: 205 -Family Rajidae BONAPARTE, 1831: p.: 205 -Family Parapalaeobatidae CAPPETTA, 1992: p.: 206 -Family Hypsobatidae CAPPETTA, 1992: p.: 206 -Family Cyclobatidae CAPPETTA, 1980: p.: 206 -Order Rhinobatiformes COMPAGNO, 1977 rev.: p.: 206 -Family Rhinobatidae Müller & Henle, 1838 rev.: p.: 207 -Conclusion concerning the Rhinobatidae incertae sedis CAPPETTA, 2012: p.: 209 -Other incertae sedis Genus of the Super Order Squatinomorphii: p.: 210 -Remark concerning the odontology of the Genus Rhinobatos LINCK, 1790: p.: 210 -Family Platyrhinidae JORDAN, 1923: p.: 210

-8-

-Order Dasyatiformes nov.: p.: 211 -Family Dasyatidae JORDAN, 1888: p.: 211 -Dasyatoid Incertae Family: p.: 211 -Family Rhynchobatidae GARMAN, 1913: p.: 211 -Family Rhinidae Müller & Henle, 1838: p.: 212 -Family Mobulidae GILL, 1862: p.: 212 -Family Pastinachidae nov.: p.: 214 -Family Hexatrygonidae HEEMSTRA & SMITH, 1980: p.: 217 -Order Rhiniformes HERMAN & VAN WAES, 2012: p.: 218 -Order Torpediniformes de BUEN, 1926: p.: 218 -Family Torpedinidae BONAPARTE, 1838: p.: 218 -Family Narcinidae GILL, 1862: p.: 218 -Order Pristiformes nov.: p.: 218 -Family Pristidae BONAPARTE, 1838: p.: 220 -Super Order Myliobatomorphii HERMAN & VAN WAES, 2012: p.: 220 -Order Myliobatiformes COMPAGNO, 1973: p.: 220 -Family Brachyrhizodontidae HERMAN & VAN WAES, 2012: p.: 221 -Family Myliobatidae BONAPARTE, 1838 rev.: p.: 221 -Family Rhinopteridae JORDAN & EVERMANN, 1896: p.: 221 -Family Rhombodontidae CAPPETTA, 1987: p.: 221

18. Chondrichthyes' constant trials for the domination of the Seas: p.: 222

19. Convergent evolution and Parallel evolution: p.: 222

- -19.1. Convergent evolution: p.: 222
- -19.2. Parallel evolution: p.: 223

### 20. Hot vents and Origin of Life: p.: 223

- -20. 1. Traditional conception of the Origin of Life: p.: 223
- -20. 2. Discovery of the hot vents and their biodiversity: p.: 224
- -20. 3. New suggestions and additional reflections: p.: 224
  - 1. Suggestion of Dr. Wächtershäuser: p.: 224
  - 2. Suggestion of the senior-author: p.: 224
  - 3. Additional reflections: p.: 224

-20.4. Settlement of the continents and return to a marine environment: p.: 225

### 21. Implications of the evolution of the Oceans and the Plate Tectonics: p.: 228

- 1. Geographical definition of the extant Atlantic Ocean: p.: 228
- 2. Formation of the North Atlantic Ocean: p.: 229
- 3. Formation of the South Atlantic Ocean: p.: 229
- 4. Implications for the paleodistribution of all the benthic Chondrichthyes: p.: 229
- 5. Summary of the History of the formation of the Indo-Pacific Oceans: p.: 229
- 6. Data concerning the Arctic Ocean: p.: 230
- 7. Impact of the Plate Tectonics on benthic coastal fauna: p.: 230

## 22. List and pagination of the new taxa and taxa revised proposed in *Géominpal Belgica* 6: p.: 230

- 23. Acknowledgements: p.: 232
- 24. Bibliography: p.: 233
- -24.1. Philosophy, Plate Tectonics and Radioactivity: p.: 233
- -24.2. Extremophyly: p.: 233
- -24.3. Parthenogenesis, Amphimixis and Automixis: p.: 234
- -24.4. Hot vents: p.: 234
- -24.5. Oldest Fossil records: p.: 235
- -24.6. Systematics Anatomy Ecology: p.: 236
- -24.7. Locomotion of marine vertebrates: p.: 266
- 25. Plates: p.: 268
- 26. Comments to the Plates: p.: 334

## 1. Summary - Résumé - Samenvatting - Kurzfassung - Resumen – Russia

### Summary (Hilde Van Waes)

A thorough examination of the root structure and of the morphology of the dental crown of the teeth of all the extant generic taxa of the four Orders mentioned in the title of this Publication, as well as the majority of the same data concerning the fossil taxa, which were attributed to these Orders, allows reconsidering the systematic rank of each of these and to redistribute their generic taxa into the five Super Orders: Chlamydoselachomorphii nov., Echinorhinomorphii rev., Orectolobomorphii rev., Hemiscylliomorphii nov., and Pristiophoromorphii rev.

The Orectolobomorphii rev. are subdivided into two Orders: Orectolobiformes\* rev., and Squatiniformes.

\*Orectolobiformes rev.: Family Orectolobidae GILL, 1896.

The Hemiscylliomorphii are subdivided into two Orders: Hemiscylliiformes\* and Stegostomatiformes\*\*.

\*Order Hemiscylliiformes: Family Hemiscylliidae, Family Agaleidae, Family Phorcynidae, Family Ginglymostomatidae, Family Bracheluridae and Family Parascylliidae. \*\*Order Stegostomatiformes: Family Stegostomatidae and Family Rhincodontidae.

A reconstitution of the Natural History of each of these Super Orders of Chondrichthyes is proposed.

Some odontological and anatomical characteristics allow suggesting which orectolobid generic taxon could have been the ancestor of the Super Order Pristiophoromorphii.

A critical synthesis of the principal suggestions concerning the revision of the Systematics\* of the post-Triassic Elasmobranchii is presented and commented.

\*Published between 2010 and 2013 in the electronic Series Géominpal Belgica.

Nine new Super Orders: Hybodontomorphii, Hemiscylliomorphii, Anacoracomorphii, Isuromorphii, Odontaspididomorphii, Lamnomorphii, Scapanorhynchomorphii, Pristiophoromorphii and Ganopristomorphii are proposed.

Seven new Orders: Acrodontiformes\*, Heptranchiformes, Hemiscylliiformes, Stegostomiformes, Triakiformes, Dasyatiformes and Pristiformes are proposed.

\*Acrodontiformes nov. replaces Polyacrodontiformes HERMAN & VAN WAES, 2012.

Four new Families are proposed: Orthechinorhinidae, Pseudoechinorhinidae, Phorcynidae and Pastinachidae.

Two Families: Anotodontidae and Parotodontidae are suppressed.

Keywords: Zoology, Palaeontology, Anatomy, Odontology, Systematics, Evolution, Chondrichthyes, Euselachii, Neoselachii, Hybodontomorphii, Acrodontiformes, Chlamydoselachomorphii, Echinorhinomorphii, Orthechinorhinidae, Parechinorhinidae, Heptranchiformes, Orectolobomorphii, Squatiniformes, Squatinidae, Orectolobidae, Hemiscylliomorphii, Hemiscylliiformes, Phorcynidae, Hemiscylliidae, Ginglymostomatidae, Stegostomatidae, Pristiophoromorphii, Pristiophoriformes, Pristiophoridae, Propristiophorus, Pristiophorus, Ganopristomorphii, Triakiformes, Triakidae, Isuromorphii, Lamnomorphii, Odontaspididomorphii, Anacoracomorphii, Ptychotrygoniformes, Pristiformes, Dasyiatiformes, Pastinachidae.

## Résumé

### (Jacques Herman)

Un examen approfondi de la structure radiculaire et de la morphologie de la couronne dentaire des dents de l'ensemble des taxa génériques existants des quatre Ordres cités dans le titre de cette Publication, ainsi que de la majorité de ces mêmes données concernant les taxa fossiles qui leur ont été attribués, permet de reconsidérer le rang systématique de chacun d'entre eux et de redistribuer leurs taxa génériques en cinq Super Ordres: les Chlamydoselachomorphii, les Echinorhinomorphii rev., les Orectolobomorphii rev., les Hemiscylliomorphii nov., et les Pristiophoromorphii rev..

Les Orectolobomorphii rev. sont subdivisés en deux Ordres: Orectolobiformes\* et Squatiniformes.

\*Orectolobiformes sensu stricto: Family Orectolobidae GILL, 1896.

Les Hemiscylliomorphi sont subdivisés en deux Ordres: Hemiscylliformes\* et Stegostomatiformes\*\*.

\*Ordre Hemiscylliiformes: Famille Hemiscylliidae, Famille Agaleidae, Famille Phorcynidae, Famille Ginglymostomatidae, Famille Bracheluridae et Famille Parascylliidae.

\*\*Ordre Stegostomatiformes: Famille Stegostomatidae et Famille Rhincodontidae.

Une reconstitution de l'Histoire Naturelle de chacun de ces Super Ordres de Chondrichthyes est proposée.

Certaines caractéristiques odontologiques et anatomiques permettent de suggérer quel taxon générique pourrait avoir été l'ancêtre du Super Ordre des Pristiophoromorphii.

Une synthèse des principales suggestions\* concernant la révision de la Systématique des Elasmobranches post Triassiques est présentée et commentée.

\*Publiées, entre 2010 et 2013, dans la Série électronique Géominpal Belgica.

Neuf nouveaux Super Ordres: Hybodontomorphii, Hemiscylliomorphii, Anacoracomorphii, Isuromorphii, Odontaspididomorphii, Lamnomorphii, Scapanorhynchomorphii, Pristiophoromorphii et Ganopristomorphii sont proposés.

Sept nouveaux Ordres: Acrodontiformes\*, Heptranchiformes, Hemiscylliiformes, Stegostomiformes, Triakiformes, Dasyatiformes et Pristiformes sont proposés.

\*Acrodontiformes nov. remplace Polyacrodontiformes HERMAN & VAN WAES, 2012.

Quatre nouvelles Familles: Orthechinorhinidae, Pseudoechinorhinidae, Phorcynidae, et Pastinachidae sont proposées.

Deux Familles: Anotodontidae et Parotodontidae sont supprimées.

Mots-clés: Zoologie, Paléontologie, Anatomie, Odontologie, Systématique, Evolution, Chondrichthyes, Euselachii, Neoselachii, Hybodontomorphii, Acrodontiformes, Chlamydoselachomorphii, Echinorhinomorphii, Orthechinorhinidae, Parechinorhinidae, Heptranchiformes, Orectolobomorphii, Orectolobiformes, Orectolobidae, Squatiniformes, Squatinidae, Hemiscylliomorphii, Hemiscylliiformes, Phorcynidae, Hemiscylliidae, Ginglymostomatidae, Stegostomatidae, Pristiophoromorphii, Pristiophoriformes, Pristiophoridae, Propristiophorus, Pristiorus, Ganopristomorphii, Ganopristidae, Sclerorhynchidae, Triakiformes, Triakidae, Isuromorphii, Lamnomorphii, Odontaspididomorphii, Anacoracomorphii, Batoidei, Ptychodontiformes, Ptychotrygoniformes, Pristiforformes, Dasyiatiformes, Pastinachidae.

## Samenvatting (Hilde Van Waes)

Een grondig nieuw onderzoek van de structuur van de wortel en de morfologie van de kroon van de tanden van al de bestaande generieke taxa van de vier Orden geciteerd in de titel van deze Publicatie, alsook van het merendeel van dezelfde elementen van de fossiele taxa die aan deze Orden toegewezen waren, maakt het mogelijk hun systematieke rang te herzien en hun generieke taxa te herverdelen over vijf Super Orden: Chlamydoselachomorphii nov., Echinorhinomorphii rev., Orectolobomorphii rev., Hemiscylliomorphii nov. en Pristiophoromorphii rev.

De Orectolobomorphii rev. zijn onderverdeeld in drie Orden: Orectolobiformes rev., Squatiniformes rev., en Hemiscylliiformes nov.

Een reconstitutie van de Natuurlijke Historie van elk van deze Super Orden van de Chondrichthyes wordt voorgesteld.

Enkele odontologische en anatomische karakteristieken maken het mogelijk te suggereren welk generiek taxon de voorouder zou kunnen geweest zijn van de Super Orde Pristiophoromorphii.

De Orectolobomorphii rev. zijn onderverdeeld in twee Orden: Orectolobiformes\* en Squatiniformes.

\*Orectolobiformes sensu stricto: Family Orectolobidae GILL, 1896.

De Hemiscylliomorphii zijn onderverdeeld in twee Orden: Hemiscylliiformes\* en Stegostomatiformes\*\*.

\*Orde Hemiscylliiformes: Familie Hemiscylliidae, Familie Agaleidae, Familie Phorcynidae, Familie Ginglymostomatidae, Familie Bracheluridae en Familie Parascylliidae.

\*\*Orde Stegostomatiformes: Familie Stegostomatidae en Familie Rhincodontidae.

Een kritische synthese van de voornaamste suggesties\* betreffende de revisie van de Systematiek van de post-Triassic Selachii wordt voorgesteld en becommentarieerd.

\*Gepubliceerd tussen 2010 en 2013 in de elektronische Reeks Géominpal Belgica.

Negen nieuwe Super Orden: Hybodontomorphii, Hemiscylliomorphii, Anacoracomorphii, Isuromorphii, Odontaspididomorphii, Lamnomorphii, Scapanorhynchomorphii, Pristiophoromorphii en Ganopristomorphii worden voorgesteld.

Zeven nieuwe Orden: Acrodontiformes\*, Heptranchiformes, Hemiscylliiformes, Stegostomiformes, Triakiformes, Dasyatiformes en Pristiformes worden voorgesteld.

\*Acrodontiformes nov. vervangt Polyacrodontiformes HERMAN & VAN WAES, 2012.

Vier nieuwe Families worden voorgesteld: Orthechinorhinidae, Pseudoechinorhinidae, Phorcynidae en Pastinachidae.

Twee Families: Anotodontidae en Parotodontidae worden gesupprimeerd.

Sleutelwoorden: Zoölogie, Paleontologie, Anatomie, Odontologie, Systematiek, Evolutie, Chondrichthyes, Euselachii, Neoselachii, Hybodontomorphii, Acrodontiformes, Chlamydoselachomorphii, Echinorhinomorphii, Orthechinorhinidae, Parechinorhinidae, Heptranchiformes, Orectolobomorphii, Orectolobiformes, Orectolobidae Squatiniformes, Squatinidae, Hemiscylliomorphii, Hemiscylliiformes, Phorcynidae, Hemiscylliidae, Ginglymostomatidae, Stegostomatidae, Pristiophoromorphii, Pristiophoriformes, Pristiophoridae, Propristiophorus, Pristiophorus, Ganopristomorphii, Ganopristidae, Sclerorhynchidae, Triakiformes, Triakidae, Isuromorphii, Lamnomorphii, Odontaspididomorphii, Anacoracomorphii, Batoidei, Ptychodontiformes, Ptychotrygoniformes, Pristiformes, Dasyiatiformes, Pastinachidae.

## **Kurzfassung**

### (Jacques Herman & Fritz Pfeil)

Eine gründliche Untersuchung der Struktur der Wurzeln und der Morphologie der Zahnkronen der Zähne aller lebenden Gattungen der vier Ordnungen von Haien, die im Titel dieser Publikation erwähnt sind, sowie die Mehrzahl gleicher Daten fossiler Taxa, die diesen Ordnungen zugeordnet wurden, ermöglicht es, die systematische Stellung all dieser Taxa neu zu überdenken und sie in Über Ordnungen aufzuteilen: die Chlamydoselachomorphii nov., die Orectolobomorphii rev. und die Pristiophoromorphii rev.

Die Orectolobomorphii werden in drei Ordnungen unterteilt: Orectolobiformes rev., die Squatiniformes rev., und Hemiscylliiformes nov.

Der Hemiscylliomorphii werden in zwei Ordnungen unterteilt: Hemiscylliiformes\* nov. und Stegostomatiforformes\*\*.

\*Ordnung Hemiscylliiformes: Familie Hemiscylliidae, Familie Agaleidae, Familie Phorcynidae, Familie Ginglymostomatidae, Familie Bracheluridae und Familie Parascylliidae. \*\*Ordnung Stegostomatiformes: Familie Stegostomatidae und Familie Rhincodontidae.

Eine Rekonstruktion der Entwicklungsgeschichte jeder dieser neuen Über-Ordnungen der Chondrichthyes wird vorgeschlagen.

Einige zahnmorphologische und anatomische Merkmale ermöglichen Hinweise darauf, welche orectolobide Gattung der Vorläufer der Über-Ordnung Pristiophoromorphii sein könnte.

Es wird hier eine Zusammenfassung der wichtigsten Vorschläge\* zur Änderung der Systematik der post-Triadischen Selachii vorgestellt und kommentiert.

\*Erschienen im Zeitraum von 2010 bis 2013 in der digitalen Serie Géominpal Belgica.

Neun neue Super Ordnungen: Hybodontomorphii, Hemiscylliomorphii, Anacoracomorphii, Isuromorphii, Odon-

taspididomorphii, Lamnomorphii, Scapanorhynchomorphii, Pristiophoromorphii und Ganopristomorphii sind vorgestellt.

Sieben neue Ordnungen: Acrodontiformes\*, Heptranchiformes, Hemiscylliiformes, Stegostomiformes, Triakiformes, Dasyatiformes und Pristiformes sind vorgestellt.

\*Acrodontiformes nov. vertret Polyacrodontiformes HERMAN & VAN WAES, 2012.

Fier neue Familien vorgestellt sind: Orthechinorhinidae, Pseudoechinorhinidae, Phorcynidae und Pastinachidae sind vorgestellt.

Zwei Familien: Anotodontidae und Parotodontidae sind abgestellt.

Schlüsselwörter: Zoologie, Paleontologie, Anatomie, Odontologie, Systematik, Entwicklung, Chondrichthyes, Euselachii, Neoselachii, Hybodontomorphii, Acrodontiformes, Chlamydoselachomorphii, Echinorhinomorphii, Orthechinorhinidae, Parechinorhinidae, Heptranchiformes, Orectolobomorphii, Orectolobiformes, Orectolobidae Squatiniformes, Squatinidae, Hemiscylliomorphii, Hemiscylliiformes, Phorcynidae, Hemiscylliidae, Ginglymos-tomatidae, Stegostomatidae, Pristiophoromorphii, Pristiophoriformes, Pristiophoridae, Propristiophorus, Pristio-phorus, Ganopristomorphii, Ganopristidae, Sclerorhynchidae, Triakiformes, Triakidae, Isuromorphii, Lamno-morphii, Odontaspididomorphii, Anacoracomorphii, Batoidei, Ptychodontiformes, Ptychotrygoniformes, Pristi-formes, Dasyiatiformes, Pastinachidae.

### Resumen

(Lutgard Kenis)

Un estudio detenido de la estructura radicular y de la morfología de la corona dental del conjunto de los taxones genéricos que existen para los cuatro Ordenes mencionados, y además un estudio de la mayoría de estos mismos datos de los taxones fósiles permiten volver a considerar el nivel sistemático de cada uno de ellos y de distribuir otra vez sus taxones genéricos en cuatro Super Ordenes: Chlamydoselachomorphii nov., Echinorhinomorphii *rev*. Orectolobomorphii *rev*. y Pristiophoromorphii *rev*.

Los Orectolobomorphii están subdivididos en tres Ordenes: Squatiniformes *rev.*, Orectolobiformes *sensu stricto\** y Hemiscylliiformes nov.

\*Orectolobiformes sensu stricto: Family Orectolobidae GILL, 1896.

Una reconstitución de la historia natural de cada uno de estos Super Ordenes de Chondrichthyes se propone.

Algunas características odontológicas y anatómicas permiten presumir qué taxón genérico pueda haber sido el ascendiente de los Pristiophoromorphii.

Una reconstitución de la historia natural de cada uno de estos Super Ordenes de los Chondrichthyes se propone.

Una Sintesis de las principal sugerencias\* concerniente la revisión de la Systematicá de los post-Triassic Selachii se propone e se comente.

\*Publicadas, entre 2010 y 2013, en la electronica Serias Géominpal Belgica.

Nuevo nuevos Super Ordenes: Hybodontomorphii, Hemiscylliomorphii, Anacoracomorphii, Isuromorphii, Odontaspididomorphii, Lamnomorphii, Scapanorhynchomorphii, Pristiophoromorphii e Ganopristomorphii sun propostos.

Siete nuevos Ordenes: Acrodontiformes\*, Heptranchiformes, Hemiscylliiformes, Stegostomiformes, Triakiformes, Dasyatiformes e Pristiformes sun propostos.

\*Acrodontiformes nov. reemplazo Polyacrodontiformes HERMAN & VAN WAES, 2012.

Cuatro nuevas Familias se proponen: Orthechinorhinidae, Pseudoechinorhinidae, Phorcynidae y Pastinachidae sun propostos.

Dos Familias: Anotodontidae e Parotodontidae sun suprimas.

Palabras-clave: Zoologia, Paleontologia, Anatomia, Odontologia, Systematicá, Evolución, Chondrichthyes, Eu-

selachii, Neoselachii, Hybodontomorphii, Acrodontiformes, Chlamydoselachomorphii, Echinorhinomorphii, Orthechinorhinidae, Parechinorhinidae, Heptranchiformes, Orectolobomorphii, Orectolobiformes, Orectolobidae Squatiniformes, Squatinidae, Hemiscylliomorphii, Hemiscylliiformes, Phorcynidae, Hemiscylliidae, Ginglymos-tomatidae, Stegostomatidae, Pristiophoromorphii, Pristiophoriformes, Pristiophoridae, Propristiophorus, Pristiophorus, Ganopristomorphii, Ganopristidae, Sclerorhynchidae, Triakiformes, Triakidae, Isuromorphii, Lamno-morphii, Odontaspididomorphii, Anacoracomorphii, Batoidei, Ptychodontiformes, Ptychotrygoniformes, Pristi-formes, Dasyiatiformes, Pastinachidae.

## Resumo

### (Carla Banjai)

Um estudo minucioso da estrutura radicular e morfologia da coroa dentária do conjunto de os généricos existentes para as quatro Ordens mencionadas, e também um estudo da maioria destes mesmos dados para táxons fósseis permitem reconsiderar o nível sistemático de cada um deles e de redistribuir suas taxas genéricas em três Super Ordens: os Chlamydoselachomorphii, os Orectolobomorphii *rev*. y os Pristiophophoromorphii rev. estão propostos.

Os Orectolobomorphii rev. estão subdivididos em tres Ordens: os Squatiniformes, os Orectolobiformes sensu stricto\* y os Hemiscylliiformes nov.

\*Orectolobiformes sensu stricto: Family Orectolobidae GILL, 1896.

Algumas características odontológicas e anatômicas permitem presumir que o taxon genérico possa ter sido o ascendente dos Pristiophoromorphii.

Uma síntese crucial das principais sugestões\* a respeito da revisão das Sistemáticas de post-Triassic Elasmobranchii é apresentada e comentada.

\*Publicado entre 2010 e 2013 nas séries eletrônicas Géominpal Belgica.

Nove novos Super Ordens: Hybodontomorphii, Hemiscylliomorphii, Anacoracomorphii, Isuromorphii, Odontaspididomorphii, Lamnomorphii, Scapanorhynchomorphii, Pristiophoromorphii e Ganopristomorphii estão propostos.

Sete novos Ordens: Acrodontiformes\*, Heptranchiformes, Hemiscylliiformes, Stegostomiformes, Triakiformes, Dasyatiformes e Pristiformes estão propostos.

\*Acrodontiformes nov. subsistuto Polyacrodontiformes HERMAN & VAN WAES, 2012.

Cuatro novas Famílias estsão propostas: Orthechinorhinidae, Pseudoechinorhinidae, Phorcynidae e Pastinachidae estão propostos.

Duas Familias: Anotodontidae e Parotodontidae estão suprimas.

**Palavras chave:** Zoologia, Paleontologia, Anatomia, Odontologia, Sistemática, Evolução, Chondrichthyes, Euselachii, Neoselachii, Hybodontomorphii, Acrodontiformes, Chlamydoselachomorphii, Echinorhinomorphii, Orthechinorhinidae, Parechinorhinidae, Heptranchiformes, Orectolobomorphii, Orectolobiformes, Orectolobidae Squatiniformes, Squatinidae, Hemiscylliomorphii, Hemiscylliiformes, Phorcynidae, Hemiscylliidae, Ginglymostomatidae, Stegostomatidae, Pristiophoromorphii, Pristiophoriformes, Pristiophoridae, Propristiophorus, Pristiophorus, Ganopristomorphii, Ganopristidae, Sclerorhynchidae, Triakiformes, Triakidae, Isuromorphii, Lamnomorphii, Odontaspididomorphii, Anacoracomorphii, Batoidei, Ptychodontiformes, Ptychotrygoniformes, Pristi-formes, Dasyiatiformes, Pastinachidae.

### Резюме

### (Jacques Herman & Evgeny Popov)

Тщательное исследование строения корня и морфологии коронок зубов всех современных родовых таксонов из состава четырех отрядов эласмобранхий, указанных в заголовке публикации, а также большинства из имеющихся морфологических данных по ископаемым таксонам этих отрядов, позволяют пересмотреть систематическое положение каждого из них и перераспределить их в трех надотрядов: Chlamydoselachomorphii, Squatinomorphii nov. и Pristiophoromorphii rev. Надотряд Squatinomorphii разделен на вещи Отряда: Squatiniformes, Orectolobiformes *sensu stricto*\*, Hemiscylliiformes и Stegostomatiformes.

\*Orectolobiformes sensu stricto: Orectolobidae GILL, 1896.

Восстановлена естественная история для всех трех новых надотрядов хрящевых рыб.

Некоторые зубные и анатомические признаки позволяют предположить родов ковровых акул предковый таксон для надотряда Pristiophoromorphii.

Представлено обобщение основных предложений\* по ревизиии систематики пост-триасовых эласмобранхий, с комментариями.

\*Опубликованы с 2010 по 2013 год, в электронной серии издания Géominpal Belgica.

В синтезе главный преподаватель\* относительно пересмотра систематики пяти после-Triassic сущест вующий Selachii - и комментируют.

Девять новых Super-Отряда представлены: Hybodontomorphii, Hemiscylliomorphii, Anacoracomorphii, Isuromorphii, Odontaspididomorphii, Lamnomorphii, Scapanorhynchomorphii, Pristiophoromorphii и Ganopristomorphii.

Семь новых Отряда Представлены: Acrodontiformes\*, Heptranchiformes, Hemiscylliiformes, Stegostomiformes, Triakiformes, Dasyatiformes и Pristiformes.

\*Acrodontiformes nov. Заменяет Polyacrodontiformes HERMAN & VAN WAES, 2012.

Четыре новых Семейств представлены: Acrodontidae, Orthechinorhinidae, Pseudoechinorhinidae, Phorcynidae, и Pastinachidae.

Два Семейств: Anotodontidae и Parotodontidae овощей удалены.

**Ключевые слова:** зоология, палеонтология, анатомия, одонтология, систематика, эволюция, хрящевые рыбы, Euselachii, Neoselachii, Hybodontomorphii, Acrodontiformes, Chlamydoselachomorphii, Echinorhinomorphii, Orthechinorhinidae, Parechinorhinidae, Heptranchiformes, Orectolobomorphii, Orectolobiformes, Orectolobidae, Squatiniformes, Squatinidae, Hemiscylliomorphii, Hemiscylliiformes, Phorcynidae, Hemiscylliidae, Ginglymostomatidae, Stegostomatidae, Pristiophoromorphii, Pristiophoriformes, Pristiophoridae, Isuromorphii, Lamnomorphii, Odontaspididomorphii, Anacoracomorphii, Batoidei, Ptychodontiformes, Ptychotrygoniformes, Pristiformes, Dasyiatiformes, Pastinachidae.

## 2. Introduction

The structure of the dental root of the diverse species, living or fossil, attributed to the Genus *Chlamydoselachus* is so particular that none of the definitions proposed by E. Casier in 1947, or by J. Herman and H. Van Waes in 2012 can be used for their qualification.

The general morphology and the histology of the dental crown of the teeth of these taxa present also some very singular characteristics.

These elements associated with the principal anatomical characteristics of their living representatives seemed sufficient to allow considering this Order as a Super Order: the Chlamydoselachomorphii HERMAN & VAN WAES, 2012.

For the Order Squatiniformes and the Order Orectolobiformes, similar arguments allow reconsidering the entirety of the phylogenetic relations existing between the diverse Genera and Families which were classically attributed to these two Orders.

The Super Order Squatinomorphii will include two new Orders: The Order Hemiscylliiformes and the Order Stegostomiformes.

The Natural History of each of these diverse evolution lineages may be reconstituted, from the Lower Jurassic till today.

Some odontological characteristics, associated with some anatomical data, seem to make it possible to point out which were the ancestors of the Super Order Pristiophoromorphii.

The odontological characteristics of numerous generic taxa generally considered as *Incertae Family* or *Incertae Order* are re-examined and allow proposing a more precise systematics position for the majority of them.

The recent\* and logical reassessment of the fossil Genus *Ganopristis* ARAMBOURG, 1935 induces *ipso facto* the reassessment of the Family Ganopristidae HERMAN, 1977 and this of the Order Ganopristiformes HERMAN & VAN WAES, 2012.

\*See Bibliography-Systematics: Cappetta 2012, p.: 375.

Diverse obvious anatomical data, such as the possession of two pectoral fins distinct\* from their two pelvic fins and the possession of two dorsal fins, are sufficient to realize that all the extinct taxa included in the Order Ganopristiformes were Neoselachii.

\*Not fused.

Taphonomy allows demonstrating that their five pairs of gill slits were laterally positioned and not ventrally, ultimate confirmation of their affiliation to the Neoselachii.

Fundamental anatomical\* and odontological\*\* characteristics allow including all the members of the Order Ptychodontiformes HERMAN & VAN WAES, 2012 in the Super Order Hybodontomorphii nov.

\*Orbitostylic articulation of their jaw, possession of two dorsal fins with fin-spine. \*\*Primary anaulacaurhyzid structure of their dental root.

The Systematics of the two Super Orders Hybododontomorphii and Batomorphii require further odontological investigations.

### An electronic publication does not need Indexes.

## **3. Introduction**

La structure de la racine dentaire des diverses espèces, tant vivantes que fossiles, attribuées au Genre *Chlamydoselachus* est si particulière qu'aucun des qualificatifs proposés par E. Casier en 1947, ou par J. Herman et H. Van Waes en 2012, ne convient à la définir.

La morphologie générale et l'histologie de la couronne dentaire des dents de ce taxon présentent également des caractéristiques très particulières.

Ces éléments réunis, joints aux principales caractéristiques anatomiques de leurs représentants actuels, semblèrent suffisants pour permettre de considérer cet Ordre comme un nouveau Super Ordre : Les Chlamydoselachomorphii HERMAN & VAN WAES, 2012.

Pour l'Ordre des Squatiniformes et l'Ordre des Orectolobiformes, des arguments similaires permettent de reconsidérer l'ensemble des liens phylogénétiques existant entre les divers Genres et Familles leurs étant classiquement attribués.

Le Super Ordre des Squatinomorphii comprendra deux nouveaux Ordres : les Hemiscylliiformes et les Stegostos -tomiformes.

L'Histoire Naturelle de chacune de ces diverses lignées évolutives peut être reconstituée, depuis le Jurassique inférieur jusqu'à nos jours.

Certaines caractéristiques odontologiques, associées à quelques données anatomiques, semblent permettre de désigner la souche ancestrale du Super Ordre des Pristiophoromorphii.

Les caractéristiques de nombreux taxa génériques généralement considérés comme *Incertae Family* ou *Incertae Order* sont réexaminés et permettent, pour la plupart d'entre eux, de suggérer une position systématique plus précise.

La récente\* et logique revalidation du Genre fossile *Ganopristis* ARAMBOURG, 1935 entraine *ipso facto* la revalidation de la Famille Ganopristidae HERMAN, 1977 et de l'Ordre des Ganopristiformes HERMAN & VAN WAES, 2012.

\*Voir: Bibliography-Systematics: Cappetta 2012, p.: 375.

Diverses données anatomiques fondamentales, comme la possession de deux nageoires pectorales et de deux nageoires pelviennes distinctes\*, fonctionnellement indépendantes, ainsi que la possession de deux nageoires dorsales, sont suffisantes pour comprendre que tous les taxa inclus dans l'Ordre des Ganopristiformes étaient des Neoselachii.

\*Non fusionnées.

La Taphonomie permet de mettre en évidence le fait que leurs cinq paires de fentes branchiales étaient positionnées sur leurs flancs et non sur leur face ventrale, ultime confirmation de leur appartenance aux Neoselachii.

Diverse caractéristiques anatomiques\* et odontologiques\*\* fondamentales permettent d'intégrer tous les membres de l'Ordre des Ptychodontiformes HERMAN & VAN WAES, 2012 au sein du Super Ordre Hybodontomorphii nov.

\*Articulation orbitostylique de leur mâchoire, possession de deux nageoires dorsales pourvues d'une épine. \*\*Anaulacaurhyzie primaire de leur racine dentaire.

La Systématique des deux Super Ordres Hybododontomorphii et Batomorphii nécessite des recherches odontologiques supplémentaires.

### Une publication électronique ne nécessite plus d'Index.

## 4. Introductie

De structuur van de tandwortel van de verschillende soorten, levende of fossiele, toegeschreven aan het Genus

*Chlamydoselachus* is zo uitzonderlijk dat geen enkele kwalificatie voorgesteld door E. Casier in 1947, of door J. Herman en H. Van Waes in 2012 geschikt is voor zijn benoeming.

De algemene morfologie en histologie van de tandkroon van de tanden van dit taxon vertonen ook uitzonderlijke karakteristieken.

Deze elementen, geassocieerd met de belangrijkste anatomische karakteristieken van hun levende taxa, scheen voldoende te zijn om deze Orde te beschouwen als één nieuwe Super Orde: de Chlamydoselachomorphii HERMAN & VAN WAES, 2012.

Voor de Orde Squatiniformes en de Orde Orectolobiformes, leiden gelijksoortige argumenten tot een herbeschouwing van het geheel van de bestaande phylogenitische relaties tussen de Genera en Families die hen gewoonlijk toegeschreven worden.

De Super Orde Squatinomorphii zal twee nieuwe Orden bevatten: de Orde Hemiscylliiformes en de Orde Stegostomiformes.

De Natuurlijke Historie van elk van deze diverse evolutieve lijnen mag gereconstrueerd worden, vanaf het Onder Jurassic tot vandaag.

Enkele odontologische gegevens, geassocieerd met enkele anatomische gegevens, schijnen het mogelijk te maken de voorouders van de Super Orde Pristiophoromorphii te bepalen.

De odontologische kenmerken van talrijke generische taxa die algemeen beschouwd worden als *Incertae Familie* of *Incertae Orde*, zijn opnieuw onderzocht. Het is nu mogelijk aan het merendeel van deze een preciezere systematieke positie toe te kennen.

De recente\* en logische herwaardering van het fossiele Genus *Ganopristis* ARAMBOURG, 1935 impliceert de herwaardering van de Familie Ganopristidae HERMAN, 1977 en van de Orde Ganopristiformes HERMAN & VAN WAES, 2012.

\*Zie: Bibliography-Systematics: Cappetta 2012, blz.: 375.

Verschillende fundamentele anatomische gegevens, zoals het bezit van twee pectorale vinnen, twee afzonder-

lijke\* pelvische vinnen, die onafhankelijk van elkaar kunnen bewegen en het bezit van twee rugvinnen, zijn voldoende om te begrijpen dat al de taxa van de Orde Ganopristiformes, Neoselachii waren.

\*Niet gefusioneerd.

Taphonomie demonstreert het feit dat hun vijf paren van kieuwen zich op hun zijkanten bevonden en niet op hun buik, ultieme bevestiging van hun toebehoren aan de Neoselachii.

Verschillende fundamentele anatomische\* en odontologische\*\* karakteristieken laten toe al de leden van de Orde Ptychodontiformes HERMAN & VAN WAES, 2012 te integreren in de Super Orde Hybodontomorphii nov.

\*Orbitostylieke articulatie van hun kaak, het bezit van twee rugvinnen met stekel. \*\* Primaire anaulacaurhyzie van hun tandwortel.

De Systematiek van de twee Super Orden Hybododontomorphii en Batomorphii vereist bijkomend odontologisch onderzoek.

### Een elektronische publicatie heeft geen Index nodig.

## 5. Euselachii and Neoselachii

### 5.1. Euselachii

This denomination was introduced, in 1902, by Hay, but insufficiently detailed.

After the compilation of the data furnished by the classics of the Chondrichthyan Systematics\*, it is possible to signalize the following characteristics, admitted by all their authors: an Euselachii is a Chondrichthyes characterized by teeth disposed in parallel rows and presenting a primary anaulacorhyzid root.

An Euselachii possesses two dorsal fin spines and all vertebrae of their vertebral column present a circularshaped section.

\*Hay 1902, Casier 1947, Berg 1958, Gluckman 1964, Maisey 1976, Zangerl 1981 and Grogan & Lund 2008.

The Euselachii are presumed to be oviparous but, in fact, none of their skeletons discovered have demonstrated this hypothesis. Their mode of reproduction remains unknown.

Fossil remains of their oldest representatives were discovered in strata of the Devonian Period. Their latest representatives survive to the Lower Cretaceous Period.

### 5.2. Neoselachii

The Neoselachii are Chondrichthyes characterized by teeth disposed in parallel or imbricated rows and organized into a hierarchical vascularization dental root type: chlamydoselachorhyzid, anaulacorhyzid, hemiaulacorhyzid, holaulacorhyzid, secondary anaulacorhyzid or polyaulacorhyzid.

The enamel of their dental crown is constituted by the superposition of three\* distinct levels.

\*The dental crown of the Euselachii is constituted by the superposition of only two distinct levels of different crystalline compounds.

Some Neoselachii are still in possession of two dorsal fin spines, the majority of them presents no dorsal fin spines.

According to its degree of evolution in a same Family, a Neoselachii may be oviparous, ovoviviparous or aplacental viviparous.

The Neoselachii are also characterized by some singularities concerning the composition of their vertebral column. Their anterior vertebrae generally present an ancestral circular-shaped section, but some of them present an oval-shaped section.

The remains, isolated fossil teeth, of the oldest taxa attributed to the Neoselachii were discovered in Triassic strata.

### 5.3. Suggestion

An anatomical distinction may be proposed to distinguish Euselachii and Neoselachii: The type of articulation of their jaws with their neurocranium.

An Euselachii is a Selachii having an orbitostylic type of articulation turning them into passive, or better said sluggish, predators. A Neoselachii is a Selachii having an autostylic type of articulation turning them into active predators.

An Euselachii is a Selachii having five pairs of gill-slits, two dorsal fins with fin-spines and teeth with a chlamydoselachorhyzid, hexanchorhyzid or polyhemiaulacorhyzid root-structure.

## 6. Additional recent and fossil materials

## **6.1.** Additional recent material

In addition to the material examined between 1977 and 1992, the senior-author had the possibility to examine the dentition of 126 jaws of the 22 following taxa: six jaws of Chlamydoselachus anguineus GARMAN, 1884 from the North Atlantic and two from Japan, twenty-four jaws of Squatina squatina (LINNAEUS, 1758) from the Mediterranean Sea, four jaws of Brachaelurus waddi (BLOCH & SCHNEIDER, 1801) from South-West Australian coasts, ten jaws of Ginglymostoma brevicautatum GÜNTHER, 1867 from the western African coasts and three others from the Azores Islands, five jaws of Nebrius ferrugineus (LESSON, 1831) from northern Australia, six jaws of Orectolobus maculatus\* (BONNATERRE, 1788) from southern Australia, four jaws of Stegostoma fasciatum HERMANN, 1783 from northern Australia, two jaws of Hemiscyllium ocellatum\* (BONNATERRE, 1788) from northern Australia, five jaws of Hemiscyllium freycineti\* QUOY & GAIMARD, 1824 from southern Borneo, three jaws of Hemiscyllium trispeculare\* RICHARDSON, 1843 from northern Australia, one jaw of Hemiscyllium hallstromi\* WHITLEY, 1967 from southern Papua, ten jaws of Chiloscyllium griseum\* MÜLLER & HENLE, 1838 from Indonesia, six jaws of Chiloscyllium punctatum\* MÜLLER & HENLE, 1838 from northern Australia, one jaw of Chiloscyllium caeruleopunctatum\* PELLEGRIN, 1914 from Indonesia, seven jaws of Chiloscyllium indicum\* (GMELIN, 1789) from Indonesia, three jaws\* of Orectolobus japonicus REGAN, 1906 from Japan, five jaws\* of Orectolobus maculatus (BONNATERRE, 1788) from Japan, two jaws\* of Orectolobus wardi WHITE, 1936 from northern Australia, one jaw\*of Eucrossorhinus dasypogon (BLEEKER, 1867) from northern Borneo, two jaws\* of Sutorectus tentaculatus (PETERS, 1864) from south-eastern Australia, four jaws\* of Pistiophorus japonicus GÜNTHER, 1870 from southern Japan, three jaws of Pistiophorus schoederi\* SPRINGER & BULLIS, 1960 from Florida, U.S.A., three jaws\* of Pliotrema warreni REGAN, 1906 from off Madagascar, and three Rhincodon typus from California, U.S.A..

\*From stuffed specimens, making a taxonomical control possible.

Mr Chris Avila (Aquaculturist, Toronto, Canada) and Mrs Helen Racz-Loren (Aquaculturist, Montevideo, Uruguay) furnished plenty of eggs of diverse taxa of the Orectolobiformes (*sensu* Applegate 1972) as well as photographs of embryos and juvenile specimens of the same Order.

This precious information allowed a better comprehension of the ontogeny of the representatives of this Order.

## **6.2.** Additional fossil material

Numerous prospections, realized between 1974 and 2008, by the senior-author and his field friends of diverse nationalities in all the Triassic, Upper Cretaceous and Cenozoic levels of Belgium allowed the examination of a little more than eight thousand teeth of Squatiniformes, Orectolobiformes and Pristiophoriformes.

## 7. Super Order Chlamydoselachomorphii nov.

It is the isolated root type structure and the singular constitution of their dental crown which allow suggesting the proposal for a Super Order to distinguish their extant and rare Eocene representatives from all the other Chondrichthyes.

This Super Order is based on the single Order Chlamydoselachiformes HERMAN & VAN WAES, 2012.

## **Order Chlamydoselachiformes HERMAN & VAN WAES, 2012**

Considering the numerous odontological characteristics that the extant and extinct representatives of the Family Chlamydoselachidae, as well as the numerous odontological characteristics that the extinct representatives of the Family Phoebodontidae have in common, these two Families were considered as members of this Order.

### Family Chlamydoselachidae GARMAN, 1884

This Family is represented by its single extant Genus *Chlamydoselachus* GARMAN, 1884 and the extinct Genus *Proteothrinax* PFEIL, 2012 of Middle Eocene age.

### Genus Chlamydoselachus GARMAN, 1884

Since 2009, this Genus includes two extant species *Chlamydoselachus anguineus* GARMAN, 1884 and *Chlamydoselachus africana* EBERT & COMPAGNO, 2009 and the extinct species: *Chlamydoselachus landinii* CARRILLO-BRICENO, AGUILERA & RODRIGUEZ, 2014, based on isolated teeth discovered in one level of the Neogene Period in the Bordon and Manabí Basins (central eastern Pacific).

See Distribution map on: www.ko.m.wikipedia.org

### Family Phoebodontidae WILLIAMS, 1985

This Family regroups, at least, two Paleozoic Genera: Genus *Phoebodus* EASTMAN, 1899 and Genus *Omalodus* GINTER & IVANOV, 1996.

The general morphology of these two extinct Genera allows considering them as possible ancestors of the Genus *Proteothrinax* PFEIL, 2012.

The lack of discoveries of fossil chlamydoselachoid teeth in the Permian, Triassic and Jurassic strata makes their inclusion in the Order Chlamydoselachiformes purely hypothetical.

The dental root of the teeth of the Genera *Phoebodus* and *Omalodus* possesses the same root-type as the dental root of the Genera *Proteothrinax* PFEIL, 2012 and *Chlamydoselachus* GARMAN, 1884.

The dental crown of the representatives of the Genera *Phoebodus* and *Omalodus* presents also large diastema separating the cuspid and cusplets from their dental crown.

### 7.1. Living representatives of the Order Chlamydoselachiformes

### Generalities

The two extant species of the Genus *Chlamydoselachus* GARMAN, 1884 are ovoviviparous and have six pairs of gill slits. The lower extremities of the first one are connected through their throat. They have no dorsal fin spines.

Their reproduction type, ovoviviparity, is the most evolved one for the Chondrichthyes, which contrasts with the geological age of their ancestors.

### Distribution of the two extant species

### Chlamydoselachus anguineus GARMAN, 1884 (Plate 9 to 13 and their comments)

### Generalities

The diverse populations of *Chlamydoselachus anguineus* are worldwide scattered and seem to have very few relations between them. See its distribution map on: <u>www.nl.wikipedia.org</u>.

In its discovery area, in the Japanese Suruga Bay this species may be encountered between 50 to 200 metres depth, but in the north-eastern Atlantic it is an inhabitant of the lower parts of the continental zones and the abyssal zone: between 120 to 1.450 metres depth.

The recently discovered populations of *Chlamydoselachus africana* seem to be confined to three distinct zones

along the African coasts.

The first one is located off the western and eastern coasts of the Cape of Good Hope, the second is located off the north-east of Durban, and the third is a long zone oriented South-North off southern Namibia to the extreme northern part of Angola. See its distribution map on: www.de.academic.ru

### **Restricted distribution of the North East Atlantic specimens**

Except for Pierre Gueguen, no other English, Breton, French, German or Spanish captains fishing in the same Atlantic Sectors seem to have ever caught a *Chlamydoselachus anguineus*.

This fact seems quite a certainty because the senior-author had many times the possibility to communicate by TSF with these captains in their language.

Pierre Gueguen, his Breton friends and these other captains, had a much greater knowledge of the Central, the North and the East Atlantic fauna inhabiting these areas between 200 and 1.600 metres depth than many European biologists.

Except for Pierre's friend, who caught a dozen of couples of *Chlamydoselachus anguineus*, always in the same Trench, none of the other captains had ever caught one specimen of this species.

Pierre Gueguen obtained the precise localisation of the catch places of these specimens from his friends, but he had to promise that he would never go trawling in these places and that the senior-author accompanying him would never mention these places.

This destructive kind of fishing is definitely forbidden now. Consequently the population of *Chlamydoselachus anguineus* can try to survive in this environment.

*Chlamydoselachus anguineus*, considered as a living fossil, is only represented by some extremely rare communities, or populations, having a minimal distribution area. It may correspond to the distribution area of a medium-sized galatheiform decapod\*, frequently encountered in their stomachs, between fresh remains of squids\*\* and corrupted teleostean\*\*\* flesh.

\*Identifiable as: two, or three, species of the Genus Munidopsis WHITEAVES, 1874.

\*\*Apparently: one species of the Genus Taningia JOUBIN, 1931.

\*\*\*Principally difficult identifiable species of the Genera *Nezumia* JORDAN *in* JORDAN & STAR, 1904 and *Coryphaenoides* GUNNERUS, 1765 of the Family Macrouridae GILBERT & HUBBS, 1916.

In fact, it is one of the best examples to illustrate the senior-author's conception of the term 'species'. Once the distance separating different populations of one species began to be too large to make genetic mixings of its diverse populations possible, some may initiate separate evolutions which finish by specific distinctions.

For references, see: Compagno 1984, Ebert & Compagno 2009 and Herman, Hovestadt-Euler & Hovestadt 1993.

### **Additional reflections**

The holotype of *Chlamydoselachus anguineus* was discovered in Japanese waters in 1884 and later in diverse parts of the world: eastern, central and western parts of the North Atlantic Ocean, in some places of the central part of the South Atlantic Ocean, in some places off the eastern coasts of Australia, off all the coasts of New Zealand, in some places of the central part of the Pacific, off the coasts of south California and off the coasts of northern Argentina.

After the description of the second species. *C. africana*, attributed to this Genus, the genetic code of all the diverse precited populations has never been controlled and it is not sure that all these populations are representatives of *C. anguineus* GARMAN, 1888.

They have the same environment in common: deep oceanic waters, which means between 120 and 1480\* metres depth.

\*Record signalized to the senior-author by Breton fishermen.

### See Distribution map on: <u>www.nl.wikipedia.org</u>

### Chlamydoselachus africana EBERT & COMPAGNO, 2009

This recently described species regroups populations dispersed off southern coasts of Africa, from northern Angola to southern Namibia and off the eastern coasts of South Africa to the coasts of Natal.

They live between 1.100 and 1.500 metres depth off the western coasts of Africa, but on the eastern coasts of Africa, they may be encountered in waters of 250 to 350 metres depth.

The influence of the Benguela Stream is not sufficient to explain this depth-range difference.

### 7.2. Odontological characteristics of the Order Chlamydoselachiformes

The odontological characteristics of the teeth of all the extant or extinct species attributed to this Genus *Chlamydoselachus* may be summarized as follows.

### **Root characteristics**

Depending on their age, their dental root presents a more or less complete superficial median grove flanked by two extern depressions.

The structure of their dental root corresponds with none of the five types defined by E. Casier in 1947: anaulacorhizy, hemiaulacorhizy, holaulacorhizy, polyaulacorhizy and secondary anaulacorhizy nor with the additional extern polyhemiaulacorhizy type defined by J. Herman and H. Van Waes in 2012.

Therefore a seventh vascularization type needed to be proposed for their unique dental root vascularization: the chlamydoselachorhizy.

This one may be described as follows: A flat polygonal root presenting a light medio-intern protuberance presenting a central grove.

### **Crown characteristics**

The dental crown is constituted by three isolated smooth cuspids separated by a distema which may be filled in adult specimens. (See GARMAN, 1888). These diastema are also visible on the drawings reproduced on www.commons.wikimedia.org and on Plate 11 and Plate 12 of this Publication.

The dental crown of the mature specimens of the two extant species possesses, between the three main cuspids, two intermediary smaller cusplets.

### Singularity

Chlamydoselachus anguineus has the longest duration of gestation of all the vertebrates: 3 years and 6 months.

Their embryos survive in the uterus of their mother by the progressive absorption of the content of their yolk.

### **Recent data**

A new fossil species attributed to the Genus *Chlamydoselachus*: *Chlamydoselachus landinii* CARRILLO-BRICENO, AGUILERA & RODRIGUEZ, 2014 has been discovered in the central eastern Pacific. (Personal information: Jürgen Pöllerspock)

> For references: See: Cabrillo-Briceno and Aguilera & Rodriguez 2014.

### 7.3. Principal Biological characteristics of the Order Chlamydoselachiformes

The possession of six gill slits, the absence of dorsal fin spines and their ovoviviparity are their principal biological characteristics.

### 7.4. Biological data detectable on fossil skeletons of the Order Chlamydoselachiformes

The possession of six gill slits and the absence of dorsal fin spines seem to be certain\* for the Upper Cretaceous to the Oligocene taxa.

\*Sources of information: Three incomplete skeletons of two private Collections.

But for the pre-Cretaceous taxa, nothing is sure. The geological period of their acquisition of their sixth gill slit remains also unknown, as well as the strange configuration of the first one.

## 7.5. Fossil representatives of the Order Chlamydoselachiformes

The eight following fossil taxa were also attributed to this Genus: *Chlamydoselachus bracheri* PFEIL, 1983, *Chlamydoselachus fiedleri* PFEIL, 1983, *Chlamydoselachus garmani* WELTON *in* PFEIL, 1983, *Chlamydoselachus, Chlamydoselachus goliath* ANTUNES & CAPPETTA, 2002, *Chlamydoselachus gracilis* ANTUNES & CAPPETTA, 2002, *Chlamydoselachus lawleyi* DAVIS, 1887, *Chlamydoselachus thomsoni* RICHTER & WARD, 1990 and *Chlamydoselachus tobleri* LERICHE, 1929.

In 2012, Seposki added one fossil taxon to this list: *Chlamydoselachus keyesi* MANNERING & HILLER, 2008 but *Chlamydoselachus tatere* CONSOLI, 2008 seems to have been ignored.

### Locality and strata of their discovery

*Chlamydoselachus bracheri* PFEIL, 1983 was discovered in a Miocene level from Austria, *Chlamydoselachus giedleri*\* PFEIL, 1983 was discovered in an Eocene level from Austria, *Chlamydoselachus garmani* WELTON *in* PFEIL, 1983 was discovered in a Lower Miocene level in California, U.S.A., *Chlamydoselachus goliath* ANTUNES & CAPPETTA, 2002 was discovered in an Upper Campanian level in Angola, *Chlamydoselachus gracilis* ANTUNES & CAPPETTA, 2002 was discovered in a level of Upper Campanian or Lower Maastrichtian age in Angola, *Chlamydoselachus keyesi* MANNERING & HILLER, 2008 was discovered in a level of Thanetian age in New Zealand, *Chlamydoselachus tatere* CONSOLI, 2008, *Chlamydoselachus lawleyi* DAVIS, 1887 was discovered in a Lower Pliocene level in Italy, and may be considered as a synonym of *Chlamydoselachus anguineus* GARMAN, 1884, *Chlamydoselachus tobleri* LERICHE, 1929 was discovered in an Oligocene or Miocene level in La Trinidad.

\*This species could be the ancestor of Chlamydoselachus bracheri PFEIL, 1983.

### Habitat of these fossil taxa

The three Cenozoic taxa: *Chlamydoselachus bracheri* PFEIL, 1983, *Chlamydoselachus fiedleri* PFEIL, 1983 and *Chlamydoselachus lawleyi* DAVIS, 1887 were discovered in deep-water sediments. All the other extinct taxa seem to have been inhabitants of shallow waters.

The two Mesozoic taxa: *Chlamydoselachus goliath* ANTUNES & CAPPETTA, 2002, *Chlamydoselachus gracilis* ANTUNES & CAPPETTA, 2002 were discovered in cretaceous shallow water sediments. All the associated fossils species seem to confirm this paleoecological interpretation.

*Chlamydoselachus garmani* WELTON *in* PFEIL, 1983, represented by more than forty huge Miocene teeth were discovered in two different volcano-mud submarine deposits, which makes it difficult to precise their original paleoecological environment.

The few teeth known of *Chlamydoselachus tobleri* LERICHE, 1929 were discovered in a volcano-mud submarine deposits, which makes it difficult to precise their original paleoecological environment.

Ideal illustrations of the teeth of diverse extinct taxa of cf. *Chlamydoselachus* are visible on the following sites: www.sharks-references.com, www.homepage2.nifty.org and www.it.wikipedia.org

All together, these data allow supposing that the diverse fossil populations of the Genus *Chlamydoselachus* were, since the Transition Eocene-Oligocene, inhabitants of deep waters.

## 7.6. Natural History of the Order Chlamydoselachiformes and Conclusion

### Natural History of this Order: Evolution of its geographical and depth distribution

### Spatio-temporal distribution

The different and relatively isolated extinct populations of this Genus were shallow water inhabitants during the Upper Cretaceous Period and seem to have become inhabitants of deep waters, since the Middle Eocene.

Their extant representatives were never observed (filmed) crossing the submarine mountain ridges dividing the Atlantic bottoms into numerous parallel elongated distribution areas.

If they did not, or do not cross these ridges, the genetic difference between their populations will progressively increase, particularly if the gestation period lasted as long as today.

### Mio-Pliocene taxa

During this period, the Family Chlamydoselachidae is represented by only one Genus: the Genus *Chlamydoselachus*, represented by only two species: *Chlamydoselachus bracheri* PFEIL, 1983, which was discovered in a Miocene level from Austria and *Chlamydoselachus garmani* WELTON *in* PFEIL, 1983, which was discovered in a Lower Miocene level in California, U.S.A..

The teeth of the Genus *Chlamydoselachus* discovered in the Lower Pliocene of the Parma Province (northern Italia) by Franco Cigala-Fulgosi in 1996 are attributable to *Chlamydoselachus anguineus* GARMAN, 1884.

The specific taxon *Chlamydoselachus lawleyi* DAVIS, 1887 was discovered in a Lower Pliocene level in Italy, but may be considered as a synonym of *Chlamydoselachus anguineus* GARMAN, 1884.

It seems that, during this period, the representatives of the Genus *Chlamydoselachus* were all inhabitants of very deep waters, which could be the reason for the extreme scarcity of discoveries of their teeth.

Coastal, coastal shelves and continental slopes deposits of this period were, and remain, the more intensively prospected levels of the world. The simplest explanation for this scarcity is that they had definitively abandoned shallow waters and the upper part of the continental slopes.

### Oligo-Miocene taxa

During this period, the Family Chlamydoselachidae is also represented by only one Genus: the Genus *Chlamydoselachus* and only one species: *Chlamydoselachus tobleri* LERICHE, 1929, which was discovered in Oligocene or Miocene mud volcano deposits in the Gulf of Mexico (La Trinidad).

Geologically, it is important to point out that these levels are considered as submarine volcano deposits, which allows supposing that these fossils were remains of deep-water inhabitants.

Since this period, teeth of the Genus *Chlamydoselachus* were only, sporadically and rarely discovered in very deep-water sediments, insufficiently prospected but quite non-existent on the European or American platforms.

### Eocene taxa

During this period, the Family Chlamydoselachidae is represented by two taxa: *Chlamydoselachus fiedleri* PFEIL, 1983, which was discovered in an Eocene level from Austria and *Proteothrinax baumgarteneri*, which was also discovered in an Eocene level from Austria.

The odontological characteristics of *Chlamydoselachus fiedleri* PFEIL, 1983, confirm its attribution to this Genus, and the associated fossils confirm that these two taxa were inhabitants of deep waters.

Both taxa are inhabitants of deep waters and are, presently, exclusively known from Southern Germany.

Their generic and familial attributions are difficult to deny.

### Paleogene taxa

During this period, the Family Chlamydoselachidae is only represented by two taxa: *Chlamydoselachus tatere* CONSOLI, 2008 which was discovered in a level of Danian age in New Zealand and *Chlamydoselachus keyesi* MANNERING & HILLER, 2008, which was discovered in a level of Thanetian age in New-Zealand.

The odontological characteristics of these two taxa seem sufficient to consider these two taxa as ancestors of the Genus *Proteothrinax* PFEIL, 2012.

But the isolated teeth of *C. keyesi* MANNERING & HILLER, 2008 are the first ones which seem attributable to a member of the Family Chlamydoselachidae. Their attribution to the Genus *Chlamydoselachus* itself requests further examinations.

### Cretaceous taxa

During this period, the Family Chlamydoselachidae is represented by three taxa: *Chlamydoselachus goliath* ANTUNES & CAPPETTA, 2002, which was discovered in an Upper Campanian level in Angola, *Chlamydoselachus gracilis* ANTUNES & CAPPETTA, 2002, which was discovered in a level of Upper Campanian of Lower Maastrichtian age in Angola, *Chlamydoselachus thomsoni* RICHTER & WARD, 1990, which was discovered in a Campanian level in Ross Island, Antarctica.

The fossil teeth of *Chlamydoselachus thomsoni* were discovered in sediments which may be considered as shallow and warm water sediments\*.

\*Deduction based on the determination of the diverse invertebrate taxa discovered in the same strata.

But the senior-author considers that, considering their geological age, the generic assessment of the four following extinct taxa: *Chlamydoselachus thomsoni* RICHTER & WARD, 1990, *Chlamydoselachus goliath* ANTUNES & CAPPETTA, 2002 *Chlamydoselachus gracilis* ANTUNES & CAPPETTA, 2002 and *Chlamydoselachus tatere* MANNERING & HILLER, 2008 to the Genus *Chlamydoselachus* GARMAN, 1884 requests further revisions.

For references, see Bibliography: Compagno 1984, Antunes & Cappetta 2002, Consoli 2008, Davis 1887, Leriche 1929, Mannering & Hiller 2008, Pfeil 1983 and Richter & Ward 1990.

The oldest taxa of chlamydoselachoid-like Chondrichthyes were discovered in some Upper Cretaceous strata in an area covering a small part of the African Continent and a small part of the southernmost part of the Antarctic Continent.

At the end of the Jurassic, South America, Africa, the Arabian Peninsula, the Middle East, Antarctica, Australia, India, and Madagascar still formed a single continental mass.

But during the lowermost Cretaceous, this huge continental mass broke up into different Plates.

During the Campanian Period, the distance\* separating the marine Upper Cretaceous strata of Angola and these of the southern part the Antarctic Continent may be estimated to have been approximately 6.000 kilometres, but their climatic conditions were still very relatively identic, because they were positioned in the same latitudes.

\*According to Bless & Fernandez-Narvaiza 2000, see Bibliography.

The fact that the initial distribution area of the ancestors of the Order Chlamydoselachiformes was very large, may explain the possibility of the progressive dispersal of their representatives in diverse directions, but only where sea water temperatures were similar.

If their geographical dispersion is easy to explain, their progressive conquest of deeper and deeper zones seems to be a physiological response to extern ecological aggressions diminishing their competitiveness with more evolved shallow water predators.

Their dentition was surely as efficient as presently, but their very long gestation duration, of more than three years, certainly diminished their possibility to compete with members of any other Chondrichthyes Order.

### **Old illustrations**

The oldest illustrations of fossil teeth, surely attributable to the Genus *Chlamydoselachus* were published by Davis in 1887, Leriche 1929, Pfeil 1983 and Welton *in* Pfeil 1983.

### **Recent illustrations**

The senior-author is particularly thankful to Jürgen Pollerspöck for the understanding of the dentition of various fossil teeth attributed to the Genus *Chlamydoselachus* between 2008 and 2012.

### Conclusion

All these biological and odontological characteristics seem sufficient to consider the former Order Chlamydoselachiformes as a new Super Order, the Super Order Chlamydoselachomorphii.

### 7.7. Ontogeny of the teeth of the Super Order Chlamydoselachomorphii

The structure of their dental root passes from holaulacorhizy, when juvenile, to secondary anaulacorhizy when

adult. This stadium is considered as a new root morphotype, called the chlamydoselachorid step. Their dental crown, constituted by three principal cuspids, lies on the top of their dental root. These principal cuspids are separated by more or less large diastema, in which may appear two additional smaller cuspids.

According to the different Genera included in this Super Order, more or less pronounced vertical striations constitute the crown ornamentation.

### Genus Proteothrinax PFEIL, 2012

The mono-specific Genus *Proteothrinax* PFEIL, 1983 is based on *Proteohrinax baumgartneri* (PFEIL, 1983), first described as *Thrinax baumgartneri* PFEIL, 1983 represented by two relatively complete teeth and two isolated crowns discovered in a Lutetian level near Salzburg (Austria).

Personal communication from Dr. Fritz Pfeil: Thrinax PFEIL, 1983 which is Proteothrinax, since I re-named it in 2012 on April 1st, was only found in what I would call deep-water's sediments, better in sediments of the continental slope.

### **Suspending questions**

The moment of their transition from oviparity to ovoviviparity and the moment of the acquisition of their sixth gill slit remain unknown.

They were maybe concomitant, because of the necessity of a sensible increase of oxygen when passing from oviparity to ovoviviparity, but that remains a pure hypothetical suggestion.

## 8. Order Squatiniformes de BUEN, 1926

## 8.1. Living representatives

According to Compagno 1984 and Cappetta (2006: p.: 397, 2012: p.: 146, fig.: 134), this Order is based on the Family Squatinidae, based on the single Genus *Squatina* DUMERIL, 1806.

### Family Squatinidae BONAPARTE, 1838

### **Systematics**

### Genus Squatina DUMERIL, 1806 (See Plates 19 to 21 and comments)

The Genus Squatina regroups the 23 following extant species: S. squatina (LINNAEUS, 1758), S. dumeril LESUEUR, 1818, S. aculeata CUVIER, 1818, S. oculata BONAPARTE, 1840, S. japonica BLEEKER, 1858, S. californica AYRES, 1859, S. armata (PHILIPPI in KRUMWEIDE, 1887), S. nebulosa REGAN, 1906, S. australis REGAN, 1906, S. africana REGAN, 1908, , S. tergocellata McCULLOCH, 1914, S. argentina (MARINI, 1930), S. guggenheim MARINI, 1936, S. punctata MARINI, 1936, S. tergocellatoides CHEN, 1963, S. formosa SHEN & TING, 1972, S. occulta VOOREN & da SILVA, 1992, S. mexicana CASTRO-AGUIRRE, ESPINOZA-PEREZ & HUIDOBRO-CAMPOS, 2007, S. heteroptera CASTRO-AGUIRRE, ESPINOZA-PEREZ & HUIDOBRO-CAMPOS, 2007, S. albipunctata LAST & WHITE, 2008, S. pseudocellata LAST & WHITE, 2008 and S. caillieti WALSH, EBERT & COMPAGNO, 2011.

According to Cappetta (2006: p.: 381-382), thirty-three fossil species may be included in this Genus, of which the validity is difficult to appreciate without specimens collected in their type locality and type level.

The senior-author had the possibility to examine more than two thousand of fossil teeth of this Genus, but only of the six following taxa: *S. decipiens* DALINKEVICIUS, 1935, *S. havreensis* HERMAN, 1977, *S. hassei* LERICHE, 1929, *S. prima* WINKLER, 1876, *S. crassa* DAIMERIES, 1889 and *S. angeloides* VAN BENEDEN, 1873, all being common Belgian fossil taxa.

The geographical distribution and the principal ecological data of the twenty-three extant species of the Genus *Squatina* are shortly examined. These taxa are examined according to their order of discovery.

### Generalities

These flat benthic and generally partially embedded taxa, metric-sized, are very efficient predators of small Selachii and Teleostei unable to detect them because of the very low vibrations produced by their own respiration. All the extant species of the Genus *Squatina* possess two monofid or multifid barbels located just below the anterior part of their mouth.

Only one extant species, *Squatina aculeata* DUMERIL, 1829, possesses a mid-dorsal continuous line of very thick dermal denticles.

### Habitat

All the extant taxa of the Genus *Squatina* are inhabitants of intertidal and coastal sandy or muddy bottoms. Some species are able to live in brackish water.

Some populations seem to be permanent inhabitants of deeper waters: from 50 to 80 metres and other ones from 80 to 160 metres depth\*.

\*Information received from Japanese and African fishermen.

Such data allow supposing that populations of different species may occupy the same area, but at different depths.

The majority of them embed their body in the sediments, from which their head, or sometimes only their eyes, protrude.

The principal honest observation is that these diverse extant taxa of this Genus are only identifiable by their colour patterns, but that the teeth of the majority of its taxa are morphologically nearly, if not completely, identic.

This conviction results from a simple experience. The senior-author has compared four jaws or four specimens of the same sex and the same length of four different species\* and observed, with satisfaction, that light differences of the morphology of their apron and small differences between the ratio height-width exists for the anterior teeth of these four specimens.

\*S. squatina, S. aculeata, S. dumeril and S. oculata.

But once he had extracted all the teeth from these four jaws and mixed them, he was unable to reconstruct these four dentitions.

But it is an undeniable fact that their different colour patterns make it easy to identify these different taxa, which suggests that their genetic code is really distinct.

The opening and the continuous enlargement of the Atlantic Ocean for more than hundred sixty millions of years completely interrupted the relations, which logically existed between the diverse ancestral populations of these four extant Atlantic species.

### Anatomical singularities of the extant representatives of the Genus Squatina

Far more than the representatives or the Genera *Orectolobus*, *Sutorectus* and *Eucrossorhinus*, the individuals of all the populations of the diverse species of the Genus *Squatina* remain moving animals and, presently active swimmers.

For swimming behaviour, See:

www.peteularson.net , www.telegraph.co.uk , www.sharks.ch or www.sonnerneinseln-fuerteventuras.de

### Mass of the head

Their rounded head represents a little more than the fifth of the weight of their body.

### Neurocranium

The neurocranium of all the extant representatives of the Genus *Squatina* is singularly flat and covered by massive hexagonal flat denticles, highly calcified and interconnected.

### Vertebral column

According to the species, their vertebral column presents a variable number of anterior vertebrae slightly flattened, having a very slightly oval-shaped\* transversal section.

\*Personal information from Helen Racz-Loren (Uruguay) concerning the two following species: *Squatina squatina* (LINNAEUS, 1758) and *Squatina argentina* (MARINI, 1930).

The diverse extant representatives of the Genus *Squatina* are animals resting on the sea bottom, but having conserved an important swimming activity\*.

\*For examples, see photographs on diverse Internet sites: <u>www.peteularson.net</u> , <u>www.telegraph.co.uk</u> , <u>www.sharks.ch</u> or <u>www.sonnerneinseln-fuerteventuras.de</u>

Other populations of some species, such as these of *Squatina squatina* are\* seasonal migrators, migrating during the summers in northern directions, and during the winters in southern directions.

\*Observations realized before their over-catching of the last sixty years.

When eating<sup>\*</sup>, the body of all the extant representatives of the species of the Genus *Squatina* is straightened up on their pectoral fins. Their mouth is open at its maximum and their neck forms an angle of  $45^{\circ}$  or more with the sea bottom.

The physical problem\* of such a position is possible thanks the very high calcification and the oval-shaped form of the five anterior vertebrae of their vertebral column.

\*For example, see: <u>www.putenauplongee.com</u>

For turning them into sudden and instantaneous predators in quasi permanent resting position on the sea bottom an additional enforcement of the anterior part\* of their vertebral column was necessary.

\*This one is constituted by seven to nine highly calcified oval-shaped *cervical* vertebrae.

The progressive abnormal enforcement of the calcification of these vertebrae is observable on their embryos.

### Anatomical singularities of the extant representatives of the three Genera: *Orectolobus, Sutorectus* and *Eucrossorhinus* (Family Orectolobidae *sensu* GILL, 1896)

In contrast with the populations of the Genus *Squatina*, the diverse representatives of the three Genera *Orectolobus* BONAPARTE, 1834, *Sutorectus* WHITLEY, 1939 and *Eucrossorhinus* REGAN, 1908 are permanently, perfectly camouflaged. They are bottom inhabitants that attack and swallow their preys by sudden jumps.

Their quasi constant immobility and their head being more massive than the head of the species of the Genus *Squatina*, they need a stronger calcification of the anterior part of vertebral column.

In fact, the five to seven anterior vertebrae of the vertebral column of all the representatives of the Family Orectolobidae (*sensu* GILL, 1896) are more calcified and present an oval-shaped transversal section.

The ontogeny of their embryos could demonstrate that this phenomenon appears in the first months of their growth and is completely achieved just before they are released into the water.

These observations induce the reconsideration of the generic attribution of all the Upper Cretaceous to Upper Oligocene taxa, classically attributed to the Genus *Squatina* DUMERIL, 1806.

Considering their strong morphological and structural odontological similarities, they could represent the diverse species constituting the phylogenetic link between the Jurassic representatives of the Genus *Pseudorhina* JAEKEL, 1898 and the post Miocene squatinid taxa.

A histological study of the teeth of all the Upper Cretaceous to Oligocene taxa attributed classically to the Genus *Squatina* could surely resolve this problem.

In fact, the first fossil representatives of the Genus *Squatina* DUMERIL, 1806, or Genus *Squatina* (*sensu stricto*) in Europe seem to be of Lower Miocene Age.

# Logical reflections applied to the research of possible ancestors of extant taxa

The senior-author has always in mind the successful expeditions of 1911-1915 to the Spitzberg Islands.

Dr. Jean-Pierre Lehman, then Director of the M.N.H.N. (Paris, France) explained to him the logical approach which had allowed the discovery and the description of the evolution of the Placodermes fishes.

Numerous fossils of their ancestors were known from Europe, and diverse fossils of their descendants were known from Greenland. Dr. Erik Jarvik\* and Dr. Erik Stensiö\* were the first palaeontologists to suggest that the missing links had to be researched between these two places, and, most precisely, in Devonian strata of the Spitzberg Islands. These fossils were indeed waiting for their discovery, in these Islands and in the suggested strata.

\*S.M.N.H. (Stockholm, Sweden).

What was so brilliantly demonstrated for Paleozoic fishes should even be easier to demonstrate for Mesozoic and Cenozoic fishes, represented by numerous fossil skeletons and numerous extant taxa.

### Squatina squatina (LINNAEUS, 1758) (See Plates 20 and 21 and comments)

### Distribution

This species was represented by numerous populations present along all the western European coasts, the Mediterranean coasts, the Black Sea coasts and the Moroccan coasts.

See Distribution map on: www.britannica.com or www.commonwikimedia.org

The multiple populations forming this species had a continuous distribution, allowing a constant mingling of their individuals.

*Squatina squatina* figures on many illustrations of fish markets of the 18<sup>th</sup> century and was then a very common inhabitant of the Channel and the North Sea sandy banks.

But, presently this species has virtually disappeared from much of its former distribution areas along the Northeast Atlantic and Mediterranean coasts.

In 1986, fishermen said to the senior-author, who then started a comparative collection of chondrichthyan jaws, that it was a very rare species and they informed him when some specimens were caught.

It was still an inhabitant of the continental shelves, living in the infra-tidal zone to a depth of circa 160 metres.

For references, see Bibliography: Compagno 1984, Herman, Hovestadt-Euler & Hovestadt 1992, Marsili 2008 and Poll 1947.

### Singularities

Small dermal denticles are present on the anterior part of their pectoral fins.

The occipital opening of their neurocranium, as well as their first vertebrae are oval-shaped.

### Remark

The fossils considered and illustrated as possible osteoderms of small lacertilian reptiles in *Géominpal Belgica* **5** (Part 3: Plate 2: figs.: 1a-1c) are more likely dermal denticles of *Squatina angeloides* (VAN BENEDEN, 1873).

### **Reproduction mode**

Aplacental viviparity

### Squatina dumeril LESUEUR, 1818

### Distribution

This species is represented by four populations of various importance of geographical extension. The more important one may be encountered along the western coasts of the U.S.A., from the Mexican boundary to the Canadian boundary.

### See Distribution map on: www.fr.wikipedia.org

The territory of the second population includes all the coasts of Cuba and Jamaica. The third population has a distribution limited to the eastern coasts of Venezuela, and the last one inhabits the northern coasts of Columbia, Venezuela and Dutch Guyana.

*Squatina dumeril* is an inhabitant of deep waters\*, but it may, occasionally, be encountered in shallower waters. \*Depth records attaining 1.320 metres.

Its discontinuous distribution seems to result from successive Eocene to Holocene tectonic events.

### Singularities

This species possesses thick dermal denticles on the anterior part of its pectoral fins and two short bifid barbels on each lower side of its mouth.

### Squatina aculeata CUVIER, 1818

### Distribution

This species is represented by populations inhabiting a very large and continuous area which extends from the southernmost coasts of Angola to southern Portugal and Spain and all the western coasts of the Mediterranean Sea.

### See Distribution map on: www.fr.wikipedia.org

Its primary absence in the eastern Mediterranean seems to result from post-Miocene tectonic events.

*Squatina aculeata* lived and still survives on some muddy bottoms of 30 metres to 500 metres depth, but it seems that this species has nearly disappeared from the northern Mediterranean coasts.

### **Reproduction mode**

Aplacental viviparity

For references, see: Compagno 1984, Massili 2008 and Morey, Serena, Mancusi, Coelho, Seasay, Litvinov & Dulvy 2013.

### Squatina oculata BONAPARTE, 1840

### Distribution

This species is represented by populations inhabiting\* the same area as those of *Squatina aculeata* but also all the eastern part of the Mediterranean Sea.

\*See Distribution map on: www.nl.wikipedia.org

These two species were, and remain, frequently misidentified because the typical large colour patterns of their bodies vary considerably in size, distribution and intensity.

The diverse populations of *Squatina oculata* are inhabitants of the continental shelf from *circa* 20 to 100 metres depth, but to 500 metres depth in tropical waters, searching apparently to remain in waters having similar temperatures.

### **Reproduction mode**

### Ovoviviparous

For references, see: Bonaparte 1840, Compagno 1984, Massili 2008 and Morey, Serena, Mancusi, Coelho, Seasay, Litvinov & Dulvy 2013.

### Squatina japonica BLEEKER, 1858

### Distribution

The diverse populations constituting this species are densely concentrated on the northern coasts of Taiwan, the eastern coasts of China, all the Korean coasts, all the southern coast of the Japan Sea and the eastern coasts of Japan.

See Distribution map on: <u>www.search.seaa.jp</u>

Some isolated populations inhabit the northern part of the Philippines Islands. The populations of *Squatina japonica* are inhabitants of the upper part of the continental slope, living principally between 150 and 200 metres depth. But, some isolated individuals were, sporadically, caught between 200 and 250 metres depth\* off the southern Japanese coasts.

\*2002: Japanese fishermen's communications.

### **Reproduction mode**

### Ovoviviparous

For references, see: Bleeker 1858 and Compagno 1984.

### Squatina californica AYRES, 1859

### Distribution

This species is represented by two dense populations, the first inhabiting the north-west American coasts from southern Alaska to the point of Baja California and the Sea of Cortez and the second one inhabiting nearly all the south-west American coasts from northern Ecuador to the Magellan Strait.

Squatina californica was never signalized between northern Ecuador and Guadalahera harbour in Mexico.

### See Distribution map on: <u>www.nl.wikipedia.org</u>

The complex geological history of the formation of La Cordilleras de los Andes allows supposing that the separation of the two groups of populations of *Squatina californica* occurred after the Eocene-Oligocene Transition.

This Transition is marked in this part of the Pacific Ocean by the dislocation and the submersion of some ancient archipelagos and maybe of a micro-continent and some archipelagos.

Only objective DNA analyses of specimens of these two groups could ensure their consanguinity.

### A review of the successive taxonomic propositions

In 1859, Ayres proposed a new American species of the Genus *Squatina*, which he called *Squatina californica*. In 1859, Philippi proposed another new American species of the Genus *Squatina*, which he called *Squatina armata*. In 1984, Compagno synonymised *Squatina californica* and *Squatina armata*. In 1967, Kato, Springer and Wagner considered *Squatina californica* as a valid species, but that *Squatina armata* was a junior synonym of the first one. In 2002, Compagno, using only morphological arguments, revalidated *Squatina armata*. In 2010, Stelbrink, von Rintelen, Cliff & Kriwet, using mitochondrial DNA genetic data demonstrated that *Squatina californica* is closely related to the European species *Squatina dumeril*, but they did not give an opinion concerning the two American taxa.

According to the same authors, Stelbrink, von Rintelen, Cliff and Kriwet, these two species are estimated to have diverged approximately 6 million years ago, when geologists consider that the Isthmus of Panama had completely emerged.

That is an interesting suggestion, but none of these authors explained how did these squatinid populations\* succeed in crossing a North Atlantic Ocean of 8.000 kilometres width, numerous oceanic ridges and numerous abyssal depths existing between these ridges?

\*Populations unable to colonize water of more than 350 metres depth.

The same authors also demonstrated that *Squatina californica* from the Gulf of California differed genetically from the two other ones but admit that they cannot guarantee their species-level distinction.

Personal conclusion: the validity of the majority of the extant *Squati*na taxa is more than dubious and is waiting

for a complete genetic revision.

### **Depth record**

*Squatina californica* prefers soft and flat bottoms as near to the shore as possible, river-mouths and bays and it is also an inhabitant of *Sargassum*\* zones.

\*Sargassum is a Genus regrouping diverse species of Algae of very large size of the Family Phaeophyccaea (brown Algae).

Individuals of *Squatina californica* live generally isolated and more or less embedded in the bottom, but to change feeding places they are able to swim quickly above the sea bottom.

Off California, *Squatina californica* individuals are commonly caught at a depth comprised between 3 to 50 metres, but they have also been caught at depths of more than 240 metres\*.

\*Californian fishermen's information.

### **Reproduction mode**

Aplacental viviparity

For references, see: Ayres 1859, Compagno 1859, Escobar-Sanchez, Abitia-Cardenas & Galvan-Magnan 2007, Fouts & Nelson 1999, Gaida 1997, Natanson & Cailliet 1986 and Stelbrink, von Rintelen & Kriwet 2010.

### Squatina armata (PHILIPPI in KRUMWEIDE, 1887)

### Distribution

The distribution area of this species is nearly identic to the distribution of the southern groups of populations of *Squatina californica* AYRES, 1859.

The major difference is that populations of *Squatina armata* were and are still mentioned in records that contain the fishing catches from the Columbian coasts.

See Distribution map on: www.en.m.wikipedia.org

Juvenile individuals of Squatina armata are generally encountered in shallower waters\* than adult specimens.

\*Which means between 50 and 90 metres depth.

Adult individuals are common inhabitants of sea bottoms of 100 to 200 metres depth. Most of them are solitary animals.

### Singularity

The growth rings observable on the oval vertebrae seem to result more from the size of the individual than from its age.

### **Reproduction mode**

### Ovoviviparity

For references, see Bibliography: Breder & Rosen 1966, Cailliet, Mollet, Pittenger, Bedford & Natanson1992, Compagno 1984, Compagno 2002, Compagno & Dando 2005, Ebert 2003, Escobar-Sanchez, Abitia-Cardenas & Galvan-Magnan 2007, Fouts & Nelson 1999, Gaida 1997, Natanson & Cailliet 1986, Stelbrink, von Rintelen, Cliff, & Kriwet 2010.

### Squatina nebulosa REGAN, 1906

### Distribution

All the populations of this species are densely concentrated in one part of the North-West Pacific including all the coasts from northern Taiwan to northern Korea and all the coasts of Japan.

### See Distribution map on: www. nl.m.wikipedia.org

*Squatina nebulosa* individuals may be encountered from the coastal zone and the continental slope to a depth of 200 metres.

### **Reproduction mode**

Ovoviviparity For references, see: Compagno 1984 and Regan 1906.

### Squatina australis REGAN, 1906

### Distribution

This species regroups numerous homogenous populations living exclusively in a limited area\* including all the coasts of Tasmania and the southern coasts of Australia.

\*See Distribution map on: www.fr.academic.ru

Squatina australis may be encountered from a coastal sandy area to a depth of nearly 280 metres\* depth.

\*Information from Australian fishermen (2008).

### **Reproduction mode**

### Ovoviviparity

For main references, see Bibliography: Compagno 1984 and Regan 1906.

### Squatina africana REGAN, 1908

### Distribution

The populations of *Squatina africana* have a large distribution area along the South-East coasts of Africa, from the Cape of Good Hope to the northern coasts of Mozambique.

### See Distribution map on: www.nl.m.wikipedia.org

### **Depth record**

Individuals of Squatina africana may be encountered from the coastal zones to more than 450 metres depth.

A small isolated population occupies the southern coasts of Madagascar. Its isolation started when Madagascar was separated from the African continent by the successive Plate Tectonic events having later produced the Great African Rift.

The present position of Madagascar dates from the Early Cretaceous, which allows supposing that the common ancestral populations of the two extant ones could be searched in Lower or Middle Cretaceous levels of both the distribution areas of their living representatives.

### **Reproduction mode**

### Ovoviviparity

For main references, see: Compagno 1984 and Regan 1908.

### Squatina tergocellata McCULLOCH, 1914

### Distribution

The relatively dense populations of *Squatina tergocellata* occupy a long and quasi continuous sandy zone extending from the south oriental coasts of Australia to the Great Australian Bay.

### See Distribution map on: www.nl.m.wikipedia.org

### **Depth record**

*Squatina tergocellata* is a common inhabitant of the continental shelf and upper slopes of this part of Australia. Deepest records found in scientific publications seem to be of 300 metres depth.

### **Reproduction mode**

Ovoviviparity

For main references, see: Compagno 1984 and McCulloch 1914.

### Squatina argentina (MARINI, 1930)

### Distribution

The diverse populations of *Squatina argentina* are concentrated in a long and virtually continuous zone extending from the Atlantic coasts between Bahia Blanca, in southern Argentina, to Rio de Janeiro, in southern Brazil.

### See Distribution map on: www.nl.m.wikipedia.org

#### **Depth record**

*Squatina argentina* is a common inhabitant of the continental shelf and upper slopes of this part of the South Atlantic, which is, according to the catches' reports, generally encountered between 100 and 400 metres depth.

### **Reproduction mode**

Ovoviviparity

For references, see: Compagno 1984 and Marinari 1930.

### Squatina gugenheim MARINI, 1936

### Distribution

The diverse populations of *Squatina gugenheim* occupy nearly the same territory as these of *Squatina argentina*, but have never been signalized more northern than the Cape of San Sebastian, southern Brazil.

See Distribution map on: www.nl.m.wikipedia.org

### **Depth record**

According to FisfBase data, *Squatina gugenheim* is principally a marine species inhabiting sandy or muddy bottoms at depths comprised between a few metres and 360 metres, but it may also be encountered in brackish waters.

### **Reproduction mode**

Ovoviviparity

For references, see: Colonello, Luciflora & Massa 2007, Compagno 1984, Marinari 1936 and Vögler, Milessi & Quinones 2003.

### Squatina punctata MARINI, 1936

### Distribution

The diverse populations of *Squatina punctata* occupy a long and continuous area extending from Punta Rasa, in Argentina to the vicinity of Aracaju Harbour in Brazil, cohabiting locally with small populations of *Squatina gugenheim*.

### See Distribution map on: www.nl.m.wikipedia.org

### **Depth record**

According to FisfBase data, *Squatina punctata* is a marine species inhabiting sandy bottoms at depths comprised between 10 metres and 80 metres. Contrarily to *Squatina gugenheim*, this species seems to have never been encountered in brackish waters.

### **Reproduction mode**

### Ovoviviparity

### For main references, see: Compagno 1984, Marinari 1936 and Menezes, Menezes, Figueiredo & Moura 2003.

### Squatina tergocellatoides CHEN, 1963

### Distribution

Squatina tergocellatoides seems to have a distribution area restricted to the western coasts of Taiwan and the opposite coasts of southern China.

### See Distribution map on: www.fr.m.wikipedia.org

Individuals of *Squatina tergocellatoides* are inhabitants of sandy bottoms at depths comprised between 100 and 300 metres.

### **Reproduction mode**

Aplacental viviparity

This obliges us to consider this species as a more evolved taxon than the other representatives of this Genus.

For main references, see: Chen 1963 and Compagno 1984.

### Squatina formosa SHEN & TING, 1972

### Distribution

The species *Squatina formosa* is represented by diverse populations scattered on the coasts of Taiwan (Formosa) and may be encountered at depths comprised between 50 and 300 metres.

See Distribution map on: <u>www.fr.m.wikipedia.org</u>

### **Reproduction mode**

Ovoviviparity

For references, see: Compagno 1984, Compagno 2005, SHEN & TING, 1972 and Walsh & Ebert 2007.

### Squatina occulta VOOREN & da SILVA, 1992

### Distribution

The species *Squatina occulta* is, presently, only known by some individuals trawled on the continental shelf of the southernmost part of Brazil, Uruguay and northern Patagonia (Argentina) at depths\* comprised between 5 and 180 metres.

\*Brazilian fishermen's information.

See Distribution map on: www.discoverlife.org

### **Reproduction mode**

### Ovoviviparity

For main references, see: Compagno 1984 and Vooren & da Silva, 1992.
#### Squatina mexicana CASTRO-AGUIRRE, ESPINOZA-PEREZ & HUIDOBRO-CAMPOS, 2007

## Distribution

This species was, originally, based on only two male specimens caught between 70 and 180 metres depth, in the Gulf of Mexico.

#### See Distribution map on: www.artesdepesca.blogspot.com

## Mode of reproduction

Unknown

For reference, see: Castro-Aguire, Espinoza-Perez & Huidobro-Campos, 2007.

## Squatina heteroptera CASTRO-AGUIRRE, ESPINOZA-PEREZ & HUIDOBRO-CAMPOS, 2007

## Distribution

The original description of this species precises only that its two first representatives were caught in the Gulf of Mexico, between 157 and 164 metres depth.

#### Mode of reproduction

Unknown

For reference, see: Castro-Aguirre, Espinoza-Perez & Huidobro-Campos, 2007.

#### Squatina legnota LAST & WHITE, 2008

The few specimens of *Squatina legnota* known (2012) were caught in some scattered places of coastal zones of southern Indonesia. This species is supposed, by its inventors, to be far more common in deeper waters.

See Distribution map on: www.commons.wikimedia.org

#### Mode of reproduction

Supposed aplacental viviparity

For reference, see: Last & White, 2008.

#### **Relation with other Pacific species of the Genus** *Squatina*

Recent phylogenetic analyses realized in 2010 by Stelbrink, von Rintelen, Cliff & Kriwet based on mitochondrial DNA, allow considering that *Squatina legnota* and *Squatina formosa* are genetically very close, if not directly related.

These two species have for nearest relatives the two species *Squatina formosa* and *Squatina tergocellatoides*, two other Asian species.

Such results are very important to understand the progressive dispersal of the squatinid populations in this Pacific zone.

For reference, see: Stelbrink, von Rintelen, Cliff & Kriwet 2010.

#### Squatina albipunctata LAST & WHITE, 2008

#### Distribution

The small populations of *Squatina albipunctata* are generally encountered along the eastern coast of Australia, resting on shallow sandy bottoms without corals, from depths of 20-30 metres to more than 400 metres.

## See Distribution map on: www.australianmuseum.net.org

#### Mode of reproduction

Ovoviviparity

For references, see Bibliography: Hoese, Bray, Paxton & Allen 2006 and Last & White, 2008.

## Squatina pseudocellata LAST & WHITE, 2008

#### Distribution

The local small populations of *Squatina albipunctata* are scattered in a large distribution zone which covers the main part of the continental shelf of the north-west coast of Australia.

See Distribution map on: www.bie.ala.org.au

Individuals of this species were caught between 120 and 320 metres depth.

#### Mode of reproduction

#### Ovoviviparity

For reference, see: Last & White, 2008.

## Squatina caillieti WALSH, EBERT & COMPAGNO, 2011

#### Distribution

The taxon *Squatina caillieti* was, and remains (End of 2013) represented by only one specimen, initially considered as a juvenile of *Squatina Formosa*, but presenting some obvious morphological differences with the juvenile specimens of this last one.

This unique female specimen was discovered in the Philippines Islands and was caught between 363 and 385 metres depth.

## Mode of reproduction

Unknown, presumed Ovoviviparity

For reference, see: Pollenstöck 2013 and Walsh, Ebert & Compagno, 2011.

# 8.2. Odontological characteristics of the Genus Squatina

Pitifully, the teeth of these diverse fossil skeletons were never sufficiently described or illustrated to allow a modern reinterpretation. In the following paragraph, all the available data are examined taxon per taxon.

# 8.3. Principal Biological data of the Genus Squatina

## Anatomical data

All the extant taxa reported to this Genus are very flattened Chondrichthyes in possession of five pairs of gill slits and without dorsal fin spines.

The occipital opening of their neurocranium, as well as their first vertebrae are oval-shaped.

## **Distribution data**

The 23 extant species of this Genus are distributed in 8 distinct zones occupied by one to four species.

2 species: *S. dumeril* and *S. mexicana*, inhabit the North-West part of the Atlantic Ocean.

4 species: S. squatina, S.aculeata, S. oculata and S. heteroptera, inhabit the eastern part of the Atlantic Ocean.
3 species: S. tergocellata, S. argentina and S. occulta.

## inhabit the western part of the Atlantic Ocean. 4 species: *S. californica, S. armata S. punctata* and *S. guggenheim*, inhabit the North East Pacific Ocean.

2 species: *S. legnota* and *S. caillieti* inhabit the Central East Pacific Ocean, respectively some eastern islands of Indonesia and some northern islands of the Philippines

3 species: *S. australis, S. albipunctata* and *S. pseudocellata* are endemic to Australia.

1 species: *S. africana* inhabits the West of the Indian Ocean.

4 species: *S. japonica, S. nebulosa, S. tergocellatoides* and *S. formosa,* inhabiting the north-western part of the Pacific Ocean.

The Genus Squatina was never reported in the northern part of the Indian Ocean.

## Depth record, species per species

## **First group**

The diverse populations of *S. dumeril* inhabit bottoms from 3\* to 1.375 metres and these of *S. Mexicana*, according to the source\*\* consulted, from 3\* to 45, or from 3\* to 150 metres.

## Second group

The diverse populations of *S. squatina* may be encountered from 3\* to 150 metres and, exceptionally, deeper. The individuals of *S. aculeata*, according to the sources\*\* consulted are inhabitants of bottoms comprised between 120 to 200 metres, or between 30 to 500 metres. These of *S. occulata*, according to the sources\*\* consulted, inhabit bottoms comprised between 3\* to 500 metres, or from 60 to 80 metres and the catches of the *S. heteroptera* are constantly reported from 157 to 164 metres depth.

## Third group

The diverse sources\*\* consulted furnish constant catches' data for *S. tergocellata*: from 128 to 400 metres, for *S. argentina*: from 100 to 400 metres and for *S. occulta*, considered as a species very difficult to identify, and supposed to be living between 20 and 500 metres depth.

#### Fourth group

According to the source\*\* consulted *S. californica* inhabits bottoms comprised between 3\* to 100 metres, or 3\* to 205 metres, or even 375 metres, *S. armata* may be encountered between 3\* to 45 metres, or 3\* to 230 metres, or to a maximum of 100 metres, *S. punctata* is common between 10 to 80 metres, or from 10 to 150 metres, or from 130 to 315 metres, or from 35 to 415 metres. *S. Guggenheim* individuals are caught between 3\* to 205 metres, or between 3\* to 360 metres, or between 10 to 150 metres depth.

## **Fifth group**

The depth of the catches of the single specimen known of *S. legnota* is unknown and *S. caillieti* inhabits bottoms comprised between 363 to 385 metres depth.

#### Sixth group

According to the sources\*\* consulted *S. australis* may be encountered between 15 to 256 metres, or from 3\* to 400 metres depth. *S. albipunctata* may be encountered between 130 to 315 metres, or between 315 to 415 metres depth and *S. pseudocellata* is constantly mentioned as living between 150 to 312 metres depth.

#### Seventh group

This group is represented by the sole species *S. Africana*, constantly reported as inhabiting depths comprised between 3\* and 500 metres.

## **Eighth group**

The depth records mentioned in the diverse sources\*\* consulted are identic and mention that *S. japonica* inhabits bottoms comprised between 3\* to 300 metres depth, *S. nebulosa* between 3\* to 200 metres, *S. tergocellatoides* between 100 to 300 metres and *S. Formosa* between 100 to 300 metres.

\*3 metres depth were chosen to include the interdal zone. \*\*Read: Catches' locality data.

## **Principal observation**

Except for *Squatina dumeril*, which is able to live to nearly 1.400 metres depth, rare are the extant taxa of the Genus *Squatina* able to live deeper than 400 metres.

## **Interesting observation**

The Genus Squatina has no extant representatives along all the northern coasts of the Indian Ocean.

## Explanation for the success of *Squatina dumeril*

After having consulted the scientific publications concerning the physiology, the anatomy and the fossil records attributed or attributable to this species, the senior-author supposes that the populations of *Squatina dumeril* are the oldest Atlantic extant representatives of this Genus.

## S. heteroptera CASTRO-AGUIRRE, ESPINOZA-PEREZ & HUIDOBRO-CAMPOS, 2007

The holotype was caught between 157 and 164 metres depth off the Central Mexican Atlantic Coast. Additional specimens were signalized, between 2008 and 2012, caught in waters of 80 to 180 metres depth, all from off the Atlantic Mexican coasts.

## S. caillieti WALSH, EBERT & COMPAGNO, 2011

The holotype was caught between 363 and 385 metres depth in the Western Pacific off the Philippines waters. The senior-author has read nothing about more recent catches.

# **Reflections concerning the distribution of the Genus** *Squatina*

The geographical and bathygraphical distribution of the diverse extant taxa of the Genus *Squatina*, joined to the geological data provided by the Plate Tectonic events allow supposing that these taxa have ancestors which were separated from each other before the complete uplift of the Cordilleras de los Andes, but also that the North-West Atlantic taxa are not the descendants of any Pacific taxa.

# Searching an explanation for its absence in the northern Indian Ocean

Problematic or not, all the biologists are obliged to admit the complete lack of any catches mentioned of the Genus *Squatina* in this part of the world.

The principal argument allowing an explanation for this fact is that most of the basins of this part of the Indian Ocean have practically no continental shelf, but only coastal zones with depths of more than 5.000 metres.

The very high tectonic instability of this country is marked by intense seismic events disturbing frequently its intern and coastal areas.

The sea bottom in this zone of *circa* eleven thousands kilometres width is principally constituted by rocky areas too deep\* to allow the development of any population of a Genus inhabiting preferentially stable shallow sandy or muddy sea bottoms.

\*A very narrow and unstable continental shelf immediately followed by abyssal depths.

The only species of the Order Orectolobiformes (*sensu lato*) is *Rhincodon typus* SMITH, 1827 of the Family Rhinconidae SMITH, 1827, sporadically\* observed far off the Pakistanese coasts.

\*Last mentioned: February 2008, see www.theguardian.com

# 8.4. Biological data detectable on fossil skeletons attributed to the Genus Squatina

All the extinct taxa attributed to this Genus are also flattened Chondrichthyes in possession of five pairs of gill slits and without dorsal fin spines.

The opening of their neurocranium, as well as their first vertebrae are oval-shaped.

# 8.5. Fossil representatives of the Order Squatiniformes

## Remark

The best and the most complete source of illustrations of the teeth of all the extinct taxa of the Order Squatiniformes is the revised Handbook of Palaeoichthylogy – Vol. 3E. 2012. 512 p., 438 figs. Author: Henri Cappetta. Editor: Dr. Fritz Pfeil Verlag. München.

For illustrations concerning squatinid taxa, see: figs.: 132 to 134.

To avoid repetition of the same data: the dental crown of all the extant and extinct taxa of this Order overlaps the top of its dental root. Upper and lower teeth have the same morphology, but the upper teeth are a little bit smaller than the lower ones.

# Family Squatinidae BONAPARTE, 1836

This extant Family regroups the two following Genera: The extinct Genus *Pseudorhina* JAEKEL, 1898 and the extant Genus *Squatina* DUMERIL, 1806.

## Genus Pseudorhina JAEKEL, 1898

The fossil Genus *Pseudorhina* JAEKEL, 1898 is supposed to be represented by three taxa: *P. alifera* (MÜNSTER, 1842), *P. acanthoderma* (FRAAS, 1854) and *P. speciosa*\* MÜNSTER, 1856.

\*Pseudorhina speciosa is generally considered as a juvenile individual of Pseudorhina alifera.

## Odontological characteristics of the Genus Pseudorhina

## **Dental root**

All the teeth of the species attributed to this Genus have a hemiaulacorhyzid root with a well-developed mediointern protuberance and two relatively short\* and lateral lobes giving an arched form\*\* to their root.

\*Shorter than those of the taxa of the extant Genus *Squatina*.

\*\*Morphologically very similar to the root of the diverse extant Genera of the Family Orectolobidae.

## **Dental crown**

All the teeth of its generotype *Pseudorhina alifera* (MÜNSTER, 1842) have a principal cuspid with extern and intern convex sides and smooth and cutting edges presenting a dubious pair of minute lateral cusplets.

The width of their apron represents a third of the width of the crown. Their rounded apron presents an ovalshaped horizontal section.

#### Remark

All the teeth of *Pseudorhina acanthoderma* (FRAAS, 1854) have also a hemiaulacorhyzid root with a well developed medio-intern protuberance and two relatively short and lateral lobes giving an arched form to their root, but their crown possesses an obvious pair of lateral cusplets and a median keel.

## Biological characteristics of the Genus Pseudorhina

Only two barbels are discernable under the mouth of the skeleton of the holotype\* of *Pseudorhina alifera* (MÜNSTER, 1842), which is a valuable argument justifying its attribution to the Family Squatinidae BONAPARTE, 1836.

\*Specimen AMNH-N°: P.7486, preserved in the Collections of the American Museum of Natural History (New York), examined by the senior-author in July 1977.

# Conclusion

The strong similarity of the dental morphology of *Pseudorhina alifera* (MÜNSTER, 1842) with the dental morphology of the most primitive Orectolobidae allows suggesting that Genus *Pseudorhina* must be reduced to its holotype and that the systematic status of *Pseudorhina alifera* (MÜNSTER, 1842) requests revision and reconsideration.

The most remarkable detail to point out is that, far before the studies\* of Casier in 1947, Fraas and Münster, excellent anatomists, had understood its narrow phylogenetic relation with the extant Genus *Squatina* DUMERIL, 1806.

\*Concerning the vascularization and the innervation of the teeth of the Chondrichthyes.

The first idea of the inventor of a new species, having a deep knowledge of the living taxa, is often the best indication of the relative phyletic position of his new taxon.

This fact is confirmed when one of his colleagues chose his new species as generotype for the proposal of a new Genus. If so, this new Genus will progressively include more and more other species.

The validity of mono-specific Genera based only on some isolated teeth and remaining mono-specific is more dubious, except if they represent the missing link between other Genera.

## Pseudorhina alifera (MÜNSTER, 1842) or Thaumas alifera MÜNSTER, 1842

This species is based on a complete skeleton discovered in the Lower Tithonic of Bayern (southern Germany).

For original reference, see: Münster 1842: p.: 62, pl. 7, fig.: 1.

## Pseudorhina acanthoderma (FRAAS, 1854) or Squatina acanthoderma FRAAS, 1854

This species is based on a complete skeleton discovered in the Upper Kimmeridgian (top of the Middle Malm) of Baden-Würtemberg (southern Germany).

For original reference, see: Fraas: p.: 782 and pls.: 27 to 29.

## Pseudorhina speciosa (MÜNSTER, 1856) or Squatina speciosa MÜNSTER, 1856

This species is based on a complete skeleton discovered in the Lower Kimmeridgian (base of the Middle Malm) of Bayern (southern Germany).

For original reference, see: Münster 1856: p.: 148.

# Odontological characteristics of the fossil taxa attributed to the Order Squatiniformes

These may be summarized as follows: All the teeth of the extant and extinct representative taxa of the Squatiniformes possess teeth with a hemiaulacorhyzid root, a massive medio-intern protuberance, two lateral root lobes and a crown overlapping the top of their root on the extern side.

Their teeth are arranged in parallel files and never imbricated. Both sides of their dental crown are smooth. They are monocuspid and have a cylindrical rounded apron presenting a circular horizontal section. On fossil skeletons attributed to this Order, the presence of a lower symphyseal tooth file has never been mentioned.

## Genus Squatina DUMERIL, 1806

Cappetta, in his 2006 Catologue (pp.: 381-382) enumerated 32 fossil nominal taxa. In this list they are cited according to the year of their description: *S. alifera* (MÜNSTER, 1842), *S. draco* MÜNSTER, 1842, *S. fimbriatus* MÜNSTER, 1843, *S. muelleri* REUSS, 1846, *S. subserrata* (MÜNSTER, 1846), *S. carinata* GIEBEL, 1848, *S. acanthoderma* FRAAS, 1854, *S. speciosa* (MEYER, 1856), *S. helophora* (ROGOVICH, 1860), *S. marginata* (ROGOVITCH, 1860), *S. biforis* (LE HON, 1871), *S. angeloides* VAN BENEDEN, 1873, *S. danconai* LAWLEY, 1876, *S. prima* WINKLER, 1876, *S. alata* PROBST, 1879, *S. caudata* PROBST, 1879, *S. fraasi* PROBST, 1879, *S. cranei* 

WOODWARD, 1881, S. beyrichi NOETLING, 1885, S. baumbergensis von der MARCK, 1885, S. winkleri (DAIMERIES, 1888), S. crassa DAIMERIES, 1889, S. rupeliensis DAIMERIES, 1889, S. gaudryi PRIEM, 1901, S. occidentalis EASTMAN, 1904, S. gigantea AMEGHINO, 1906, S. minor EASTMAN, 1911, S. lerichei JORDAN & BEAL, 1913, S. crecelli WEILER, 1922, S. hassei LERICHE, 1929, S. decipiens DALINKEVICIUS, 1935 and S. frequens UNDERWOOD, 2002.

## Successive reconsiderations of this list

#### **Odontological arguments**

After odontological reconsiderations the senior-author considered that only the seven following taxa are attributable to the extant Genus *Squatina*: *S. prima* (WINKLER, 1876), *S. gaudryi* PRIEM, 1901, *S. occidentalis* EASTMAN, 1904, *S. lerichei* JORDAN & BEAL, 1913, *S. subserrata* (MÜNSTER, 1846), *S. angeloides* VAN BENEDEN 1873 and *S. hassei* LERICHE, 1929.

## S. subserrata (MÜNSTER, 1846) or Sphyrna subserrata MÜNSTER, 1846

This taxon is based on one isolated tooth discovered in a Miocene level of the Wien Basin. Its odontological characteristics confirm its attribution to the Genus *Squatina*.

\*Münster proposed the generic attribution *Sphyrna* for these teeth because the cutting edges of the teeth he had discovered were relatively similar to these of a *Squatina*: smooth and without lateral cusplets.

# For original reference, see: Münster 1846: p.: 21 and pl.: 2, fig.: 17.

## S. angeloides VAN BENEDEN, 1873

This taxon is based on a group of vertebrae\* of a squatinid Chondrichthyes, discovered by a workman in a nonprecised level of the Terhaegen Formation at Boom (Antwerp Province, Belgium).

\*Repository uncertain. The senior-author has never seen these vertebrae.

The authority of Professor P. J. Van Beneden obliged all his contemporary Belgian paleontologists to consider all the teeth of the Genus *Squatina* discovered in this Formation as teeth of *S. angeloides* VAN BENEDEN, 1873.

This option may be sustained by the fact that different extant taxa of the Genus *Squatina* rarely cohabit on muddy sea bottoms. But this fact does not confirm that all the Belgian Oligocene squatinid teeth were teeth of this species.

For original reference, see: Van Beneden 1873: p.: 384, no figuration.

## Remark concerning the personality of this eminent Belgian paleontologist.

According to his personal philosophical convictions, Professor P. J. Van Beneden (1809-1894), U.C.L. University (Leuven, Belgium), was, and remained, an obstinate anti-evolutionist. Everybody had to admit all his affirmations without any argument or figuration.

## S. prima (WINKLER, 1876) or Trigonodus primus WINKLER, 1876

This taxon is based on isolated reworked teeth discovered in the basal gravel of the Tuffeau de Licent Formation at Maret (Orp-le-Grand, Walloon Brabant Province, Belgium).

Hundreds of much better preserved specimens were later\* discovered in their original strata: shelly lenses in the Sands of Orp-le-Grand Formation (Late Selandian) in the same locality.

\*Prospections realized by the Senior-author and his first field friends between 1969 and 1974.

For original reference, see: Winkler 1876: p.: 14 and pl.:1, figs.: 18-20.

## S. gaudryi PRIEM, 1901

This taxon is based on isolated teeth discovered in the Lower Eocene of the Marne Department (France). The

odontological characteristics of these teeth confirm the attribution of this taxon to the Genus *Squatina*, but it could also be a junior synonym of *S. prima* WINKLER, 1873.

For original reference, see:

Priem 1901: p.: 265 and pl.:11, figs.: 23-24.

## S. occidentalis EASTMAN, 1904

This taxon is based on isolated teeth discovered in the Calvert Formation (Upper part of the Lower Miocene) in Maryland (Atlantic side of the U.S.A.).

The odontological characteristics of these teeth confirm the attribution of this taxon to the Genus Squatina.

For original reference, see: Eastman1904: p.: 71 and pl.:28, fig.: 1.

## S. lerichei JORDAN & BEAL, 1913

This taxon is based on isolated teeth discovered in the Monterey Formation (Miocene of California, U.S.A.).

Thanks to his friend Bruce Welton, the senior-author had the possibility to collect himself 52 specimens of this taxon in two Miocene Californian localities (July 1977).

The odontological characteristics of these teeth confirm the attribution of this taxon to the Genus Squatina.

For original reference, see: Jordan & Beal 1913: pp.: 253 and 255: fig.: b.

## S. hassei LERICHE, 1929

This taxon is based on three reworked teeth from the Tuffeau of Maastricht Formation (Maastrichtian, Upper Cretaceous) discovered in the E.N.C.I. quarry (Maastricht, The Netherlands).

The type series was retrieved in 1978 by the Senior-author in the Collections of the Department of Paleontology of the I.R.S.N.B., Brussels, Belgium.

Between 1970 and 1978, the senior-author and his first field fiends discovered more than 250 perfectly preserved teeth of this species in three different Horizons of the Tuffeau of Maastricht Formation, at Eben-Emael (Marnebel S.A.), Lixhe and Romontbos quarries (C.B.R.S.A.), in the Limburg and Liege Provinces (Belgium).

This species is also represented by numerous, but quantitatively, less abundant, isolated teeth in the Upper Campanian of the Hainaut and Limburg Provinces (Belgium).

For original reference, see: Leriche 1929: pp.: 206-207, figs.: 1-3.

## Genus Thaumas MÜNSTER, 1842

*S. alifera* (MÜNSTER, 1842), *S. draco* MÜNSTER, 1842), *S. fimbriatus* MÜNSTER, 1843 and *S. speciosa* (MEYER, 1856) are in fact representative fossil taxa of the Genus *Thaumas* MÜNSTER, 1842.

The Genus *Thaumas* MÜNSTER, 1842 is represented only by these four species, of which the geological range is restricted from the Lower Kimmeridigian to the end of the Lower Tithonian, and the geographical distribution apparently limited to the southern part of Germany (Baden-Würtemberg and Bayern).

## **Taxonomic problem**

For the entomologists, the Genus *Thaumas* HÜBNER, 1819 is a Genus of the Family Sphingidae LATREILLE, 1802 (Lepidoptera, Insecta).

This problem may be considered as resolved by the synonymisation of the Genus *Thaumas* MÜNSTER, 1842 with the Genus *Squatina* DUMERIL, 1806.

The problem remains, however, if the fossil ichthyologic Genus *Thaumas* MÜNSTER, 1842 may not be synonymized with the extant Genus *Squatina*.

#### Solution proposed

Such as for the multiple cases of confusion with pre-existing botanic or insect taxa, already mentioned in the *Géominpal Belgica* **5.2** and **5.3**, a possible respectful solution could be the simple adding of a short term precising the living group concerned: *Thaumas* MÜNSTER, 1842 could be replaced by *Piscithaumas* (MÜNSTER, 1842).

# Re-examination of the other fossil taxa of the Genus Squatina.

#### S. acanthoderma FRAAS, 1854

This taxon is based on one skeleton of the Upper Kimmerdigian from Nusplingen (Baden-Würtemberg, D).

After reexamination of the description and the figuration of the holotype of this taxon, the senior-author admits that it seems to be a synonym of *S. alifera* MÜNSTER, 1842 and considers that this taxon may be attributed to the Family Phorcynidaenov. Fam. of the Order Hemiscylliiformes nov. Ord.

For original reference, see: Fraas 1854: p.: 772 and pls.: 27-29.

#### S. marginata (ROGOVICH, 1860) or Hybodus marginata ROGOVICH, 1860

This taxon is based on isolated teeth of the Cenomanian from Kanev (Ukrania). The senior-author considers that this taxon is a representative of the Genus *Squatina* DUMERIL, 1806 (Family Squatinidae, Order Squatiniformes).

For original reference, see Bibliography: Rogovich 1860: p.: 62 and pl.: 3, figs.: 14-16.

## S. cranei WOODWARD, 1881

This taxon is based on one partial skeleton with teeth discovered in the Cenomanian of southern England. It is no more a *Squatina* but an Orectolobidae *sensu stricto*.

For original reference, see: Woodward 1881: p.: 144 and pl.: 36, fig.: 29-31.

# S. muelleri REUSS, 1846

This taxon is based on some isolated teeth discovered in a Turonian level of Bohême (Czechia). It is no more considered as a representative of the Genus *Squatina* but as an Orectolobidae *sensu stricto*.

For original reference, see: Reuss 1846: p.: 100 and pl.: 21, figs.: 18-20.

#### S. helophora (ROGOVICH, 1860) or Hybodus helophora ROGOVICH, 1860

This taxon is based on very badly preserved isolated teeth of the Priabonian (Uppermost Eocene) from the vicinity of Kiev (Ukrania).

The preservation of these reworked fossil remains does not allow specifying the systematic position of this taxon.

For original reference, see: Rogovich 1860: p.: 59 and pl.: 3, figs.: 14-16 and 19-20.

## S. subserrata (MÜNSTER, 1846) or Sphyrna subserrata MÜNSTER, 1846

This taxon is based on isolated teeth from the Miocene of the Wien Bassin. This taxon remains considered as a species of the Genus *Squatina*.

For original reference, see: Münster 1846: p.: 21 and pl.: 2, fig.: 17.

#### S. biforis (LE HON, 1871) or Scaldia biforis LE HON, 1871

This taxon is based on isolated teeth of the Belgian Pliocene. It is considered as a synonym of Squatina squatina.

For original reference, see: Le Hon 1871: p.: 7.

#### S. angeloides VAN BENEDEN, 1873

This taxon is based on vertebrae discovered in an unspecified level of the Terhaegen Lid of the Boom Clay Member of the Belgian Oligocene. It remains considered valid\* by the majority of the paleontologists.

\*The principal argument was that extant taxa of the Genus Squatina rarely cohabit in the same area at the same depth.

For original reference, see: Van Beneden 1873: p.: 384, no figuration.

This absence of figuration favoured the adoption of the designation *S. rupeliensis* for all the isolated teeth discovered in the diverse Belgian Oligocene deposits.

# S. danconai LAWLEY, 1876

This taxon is based on isolated teeth of the Zanclian (Lower Pliocene) of Toscania (Italia), and is considered as a synonym of *Squatina squatina*.

For original reference, see: Lawley 1876: p.: 37 and pl.: 1, fig.: 16.

#### S. alata PROBST, 1879

This taxon is based on isolated teeth of the Burdigalian of southern Germany, and is considered as a synonym of *S. subserrata* (MÜNSTER, 1846).

For original reference, see: See Probst 1879: p.: 177 and pl.: 3, figs.: 39-40.

#### S. carinata GIEBEL, 1848

This taxon is said to have been discovered in an Eocene level from the Netherlands. It must be considered as a nomen nudum.

For original reference, see:

Giebel 1848: p.: 298, no figuration and doubtful stratigraphic origin.

## S. caudata PROBST, 1879

This taxon is based on isolated teeth of the Burdigalian of southern Germany. It is a junior synonym of *S. subserrata* (MÜNSTER, 1846).

For original reference, see: Probst 1879: p.: 178 and pl.: 3, figs.: 41-42.

## S. fraasi PROBST, 1879

This taxon is based on isolated teeth of the Burdigalian of southern Germany. It is a junior synonym of *S. subserrata* (MÜNSTER, 1846).

For original reference, see: Probst 1879: p.: 177 and pl.: 3, figs.: 37-38.

#### S. beyrichi NOETLING, 1885

This taxon is based on one vertebra discovered in the Rupelian of Kalingrad (Russia).

For original reference, see: Noetling 1885: p.: 48 and pl.: 7, figs.: 2-7.

#### S. baumbergensis von der MARCK, 1885

This taxon is based on one skeleton discovered in the Upper Campanian of Westphalia (D). It is not a *Squatina* but an Orectolobidae *sensu stricto*.

# For original reference, see: von der Marck 1885: p.: 264 and pl.: 25, figs.: 1-5.

#### S. winkleri (DAIMERIES, 1888)

This taxon has no figuration and its origin is the same as this of *S. prima* (WINKLER, 1876), consequently it may be considered as a synonym of this last one.

#### S. crassa DAIMERIES, 1889

By the lack of figuration of its holotype, this badly known taxon remains frequently reported as discovered in different strata of the Lower Eocene (Ypresian) to the Middle Eocene (Lutetian) of Belgium.

Some specimens attributable to this taxon were discovered in the Lower Oligocene of Belgium and some others were mentioned and illustrated as fossils from the *Sint Niklaas Phosphorite Bed* (See *Géominpal Belgica* **5.3**).

After reexamination of the dentition of jaws of diverse species of the Genus *Orectolobus* BONAPARTE, 1834, the senior-author cannot be sure that, if valid, this taxon may be attributed to the Genus *Squatina*.

For original reference, see: Daimeries 1889: p.: 9, no figuration.

#### S. rupeliensis DAIMERIES, 1889

This taxon is based on isolated teeth discovered in the Boom Clay\* but considered as junior synonym of *S. angeloides* VAN BENEDEN, 1873.

\*Contrarily as mentioned in Cappetta 2006 (p.: 201, Eocene of Belgium).

For original reference, see: Daimeries 1889: p.: 10, no figuration.

## S. minor EASTMAN, 1911

This taxon is based on one skeleton discovered in the Lower Tithonic of Solnhofen, Bayern (D). It is not a Squatiniformes but an Orectolobiformes *sensu stricto*.

For original reference, see: Eastman 1911: p.: 403 and pl.: 3.

## S. crecelli WEILER, 1922

This taxon is based on isolated teeth from the Rupelian of the Mainz Basin (D), but it remains considered as a junior synonym of *S. angeloides* VAN BENEDEN, 1873.

For original reference, see: Weiler 1922: p.: 94 and pl.: 3, figs.: 23-25.

## S. decipiens DALINKEVICIUS, 1935

This taxon is based on common isolated teeth from the Cenomanian of Lithuania (Lietuva). It is not a *Squatina* but an Orectolobiformes *sensu stricto*.

For original reference, see: Dalinkevicius 1935: p.: 249 and pl.: 1, figs.: 10-17.

## S. frequens UNDERWOOD, 2002

This taxon is based on very common isolated teeth from the Kimmeridgian of southern England. The morphology of the apron of the dental crown of its teeth demonstrates that this taxon is not a Squatiniformes but an Orectolobiformes *sensu stricto*.

For original reference, see: Underwood 2002: p.: 314, and pl.: 4, figs.: 3-13.

#### Remark

Fossil teeth of the extant species *S. squatina* (LINNAEUS, 1758) were discovered in diverse Pliocene levels in the Belgian Pliocene and the Italian Pliocene.

## **Anatomical argument**

The anterior vertebrae of the vertebral column of the extant taxon are slightly flattened.

# 8.6. Conclusion and Natural History of the Order Squatiniformes

## **Conclusion Common criteria**

All the taxa attributed to the Order Squatiniformes are Chondrichthyes characterised by a flat morphology, of which all the species possess five pairs of gill slits, two dorsal fins without fin spines, first cervical oval-shaped vertebrae, dental crowns overlapping the top of their dental roots, presence of a cylindrical apron presenting a subcircular horizontal section, a hemiaulacorhyzid root, no lateral cusplets and smooth cutting edges.

# **Natural History of the Order Squatiniformes**

The first taxon attributable to the Genus *Squatina*, such as restricted in this Publication, has been discovered in diverse levels of the Maastrichtian (Upper Cretaceous) of Belgium and the Netherlands.

Their first populations are represented by numerous teeth of, at least, four stragraphical Maastrichtian levels presenting all the characteristics of shallow warm water deposits.

But its Genus *Squatina* was preceded by numerous populations of squatinid-like Chondrichthyes attributed to diverse generic taxa.

The oldest ones inhabited the central zone of the European Continent.

The teeth of the first squatinid taxa being so small\* all the field palaeontologists know that the chance to find some isolated teeth is virtually nil.

\*Smaller than 500µ.

Because of this missing link, it is only possible to presume that the original distribution area of this Order was, effectively, the central part of Europa.

If so, their anatomical and odontological characteristics allow suggesting that the Squatiniformes are the ancestors of all the primitive Orectolobiformes (Order *emend.*), such as their three extant generic taxa: *Orectolobus* BONAPARTE, 1834, *Sutorectus* REGAN, 1908 and *Eucrossorhinus* REGAN, 1908.

All these Genera were represented by specific taxa, inhabiting exclusively shallow sea bottoms in a warm water environment, unable to cross deep oceanic trenches.

They moved continuously from the central European coasts to the Middle East coasts. Then to the Indian Ocean and Pacific Ocean coasts to finish their course along the Australian coasts. None of them crossed the Great Eastern Pacific Barrier.

# 9. Order Orectolobiformes sensu APPLEGATE, 1974

# 9.1. Living representatives of the Order Orectolobiformes *sensu* APPLEGATE, 1974, with adjustments to 2012

# **9.2.** Systematics

## **Extant Families included in this Order**

With these adjustments, the order Orectolobiformes regroups seven Families. (sensu Applegate 2012)

The following enumeration of these seven Families seems to be the most representative\* of their very long evolution\*\*: Family Orectolobidae JORDAN & FOWLER, 1903, Family Brachaeluridae APPLEGATE, 1974, Family

Ginglymostomatidae GILL, 1862, 1986, Family Stegostomatidae GILL, 1862, Family Hemiscylliidae GILL, 1862, Family Parascylliidae GILL, 1862 and Family Rhincodontidae GARMAN, 1913.

\*Suggestion of the senior-author. \*\* Lower Jurassic to the present days.

Or eight Families, for researchers who, such as the senior-author, admit the Family Pseudoginglymostomatidae, DINGERKUS, 1986 as a valid taxon

# **Extant Genera included in these Families**

The Family Orectolobidae regroups the three following extant Genera: Genus *Orectolobus* BONAPARTE, 1834, Genus *Eucrossorhinus* REGAN, 1908 and Genus *Sutorectus* WHITLEY, 1939.

The Family Brachaeluridae APPLEGATE, 1974 regroups the two following extant Genera: Genus *Brachaelurus* OGILBY, 1908 and Genus *Heteroscyllium* REGAN, 1908.

The Family Ginglymostomatidae GILL, 1862 regroups the three following extant Genera: Genus *Ginglymostoma* MÜLLER & HENLE, 1837, Genus *Nebrius* RÜPPEL, 1837 and Genus *Pseudoginglymostoma* DINGERKUS, 1986.

The extant Genus *Ginglymostoma* is based on its single living species *Ginglymostoma cirratum* (BONNATERRE, 1788). The extant Genus *Nebrius* is based on its single living species *Nebrius ferrugineus* LESSON, 1831.

The Genus *Pseudoginglymostoma* DINGERKUS, 1986 is based on the extant taxon, formerly called, *Ginglymostoma brevicaudatum* GÜNTHER, 1837, but includes also two fossil taxa: *P. erguitaense* NOUBHANI & CAPPETTA, 1997 and *P. idiri* NOUBHANI & CAPPETTA, 1997, both discovered in levels of Upper Maastrichtian Age in the central part of Morocco.

The Family Pseudoginglymostomatidae DINGERKUS, 1986 is based on the extant taxon *Pseudoginglymostoma* brevicaudatum (GÜNTHER, 1837).

Representatives or not of the extant Genus *Pseudoginglymostoma*\*, the paleodistribution of its two fossil taxa help to understand the global paleodistribution of the Family Ginglymostomatidae.

\*See the remarks of Cappetta (2012: p.: 175) concerning the presence of small folds on the base of the dental crowns of these two fossil taxa.

The Family Stegostomatidae GILL, 1862 is based on the extant Genus Stegostoma Müller & HENLE, 1837.

The Family Hemiscylliidae GILL, 1862 regroups the two extant Genera: Genus *Hemiscyllium* MÜLLER & HENLE, 1837 and Genus *Chiloscyllium* MÜLLER & HENLE, 1837.

The Family Parascylliidae GILL, 1862 regroups the two extant Genera: Genus *Parascyllium* GILL, 1862 and Genus *Cirrhoscyllium* SMITH & RADCLIFFE, 1913.

The Family Rhincodontidae GARMAN, 1913 is based on the extant Genus Rhincodon SMITH, 1828.

## Problems

The validity of the Genera *Heteroscyllium* and *Cirrhoscyllium*, as well as the attribution of *Ginglymostoma brevicaudatum* to the Genus *Pseudoginglymostoma* DINGERKUS, 1986 remain subjected to permanent controversies.

## Genus Heteroscyllium

The Genus *Heteroscyllium* REGAN, 1908 is based on *Heteroscyllium colcloughi* OGILBY, 1908 which is generally considered as a second species of the Genus *Brachaelurus* OGILBY, 1908 of the Family Brachaeluridae APPLEGATE, 1974.

#### Genus *Cirrhoscyllium* (See Plate 31: fig.: 2, Plate 50: fig.: 2 and comments)

The Genus *Cirrhoscyllium* SMITH & RADCLIFFE, 1913 is based on *Cirrhoscyllium expolitum* SMITH & RADCLIFFE, 1913 and is generally considered as a synonym of the Genus *Parascyllium* GILL, 1862.

The three species attributed to this Genus: *Cirrhoscyllium expolitum* SMITH & RADCLIFFE, 1913, *Cirrhoscyllium formosanum* TENG, 1959 and *Cirrhoscyllium japonicum* KAMOHARA, 1943 could represent only three varieties

(populations) of the same species.

# Ginglymostoma brevicaudatum or Pseudoginglymostoma brevicaudatum

The attribution of an extant specific taxon to an extinct generic taxon is, of course, a controversial proposition for all the biologists, and insufficiently argumented for numerous paleontologists.

The fact that all the extant populations of *Ginglymostoma brevicaudatum* are inhabitants of a small part of southern Australia makes it difficult to believe that they are phylogenetically related to the mono-specific extinct Genus *Eostegostoma* HERMAN, 1977, only known from some Upper Eocene levels in central Europe.

# 9.3. Family Orectolobidae GILL, 1896

For the zoologists, this Family regroups the three following extant Genera: Genus *Orectolobus* BONAPARTE, 1834, Genus *Eucrossorhinus* REGAN, 1908 and Genus *Sutorectus* REGAN, 1908.

For the zoologists, the group of these three extant Genera of this Family is easily distinguishable by their possession of numerous flat and extended barbels surrounding their heads.

For the paleontologists, only some tenuous odontological details, irregularly present, allow proposing generic determinations of relative reliability.

## Genus Orectolobus BONAPARTE, 1834 (See Plates 22 to 24 and comments)

## **Systematics**

According to Rainer and Pauly 2010 and FishBase 2011, this Genus regroups the ten following extant species: *Orectolobus maculatus* (BONNATERRE, 1788), *Orectolobus ornatus* (DE VIS, 1883), *Orectolobus japonicus* REGAN, 1906, *Orectolobus wardi* WHITLEY, 1939, *Orectolobus halei* WHITLEY, 1940, *Orectolobus hutchinsi* LAST, CHIDLOW & COMPAGNO, 2006, *Orectolobus floridus* LAST & CHIDLOW, 2008, *Orectolobus reticulatus* LAST, POGONOSKI & WHITE, 2008 and *Orectolobus leptolineatus* LAST, POGONOSKI & WHITE, 2010.

## Generalities

The different species of this Genus are inhabitants of shallow waters in the temperate and tropical parts of the Pacific Ocean and the eastern part of the Indian Ocean.

Except for the species *Orectolobus japonicus*, all the other species may be encountered along the Australian and Indonesian coasts.

This Genus has no representative in the Atlantic Ocean, nor in the Pacific zones situated eastern from the Great Pacific Barrier.

For the zoologists, their principal morphological characteristic consists of their elongated dermal lobes surrounding their mouths.

The diverse populations of the species attributed to the Genus *Orectolobus* are ambush predators living principally on rocky bottoms or coral reefs.

For references, see Bibliography: Froese, Rainer, & Daniel Pauly. Eds. 2011: Orectolobus in FishBase.

## **Odontological characteristics of the Genus** Orectolobus

The lower jaw of all the extant species of the Genus *Orectolobus* presents a symphyseal tooth row. These teeth are the larger of their jaws and are perfectly symmetric.

The upper jaw of at least two\* extant species of this Genus presents a vestigial symphyseal tooth row. These teeth are represented by minute teeth reduced to a small acute and lightly sigmoid cuspid overlapping the top of a compressed and distorted hemiaulacorhyzid root.

\*O. ornatus an O. maculatus. For O. ornatus, see the jaw figured on: www.sciences-de-la-terre.com

This upper symphyseal tooth row is absent on the jaw of older individuals, where its original emplacement is replaced by a small diastema flanked by the two parasymphyseal tooth rows.

#### **Root characteristics**

All the dental roots of the living taxa of the Genus *Orectolobus* are hemiaulacorhyzid and present very short root lobes on the anterior teeth, which progressively become more elongated when nearing the commissural position.

#### **Crown characteristics**

All their teeth present a crown which overlaps the top of their root and a narrow, more or less elongated, apron with an oval-shaped transversal section.

The dental crown of the anterior teeth are monocuspid, these of the antero-lateral teeth possess a pair of unequally sized cuspids, these of the lateral teeth possess generally a second pair of unequally sized cuspids and the uppermost commissural teeth only elongated anterior and posterior cutting edges.

Both intern and extern faces of the dental crown of all the upper and lower anterior teeth are smooth, but the extern side of the upper commissural teeth presents a basal ornamentation constituted by very short but strongly marked costulae.

For figuration, see: Herman, Hovestadt-Euler & Hovestadt 1992: pls.: 19 and 20.

#### Spatio-temporal distribution of the Genus Orectolobus

Middle Eocene of central Europe and central Asia to the Present Times.

## Orectolobus maculatus (BONNATERRE, 1788)

#### Distribution

This species regroups diverse populations endemic to the southern and south eastern Australian coasts.

*Orectolobus maculatus* individuals live only in marine environments. No individuals were ever observed in brackish water environments.

#### **Depth record**

Individuals of *Orectolobus maculatus* may be encountered from the intertidal zone\*, to a depth of 120 metres or 150 metres, according to the source consulted.

\*Where some individuals may be found dead because they are unable to survive out of water, during a tidal interval.

Distribution map: see www.de.academic.ru

#### Mode of reproduction

Ovoviviparity

## Singularity

This species has a triennial reproductive cycle.

For references, see: Bonnaterre 1788, Compagno 1984, Herman, Hovestadt-Euler & Hovestadt 1992 and Huveneers 2006.

Orectolobus ornatus (DE VIS, 1883)

#### Distribution

This species is represented by numerous populations scattered along the southwestern, all the southern and all the eastern coasts of Australia. It is also present along all the coasts of Papua and New Guinea.

See Distribution map on: www.fishbase.org

#### **Depth record**

Individuals of this species inhabit littoral bottoms to bottoms of 100 metres depth.

## Mode of reproduction

#### Ovoviviparity

## Singularity

This species has a triennial reproductive cycle.

For references, see: Compagno 1984, Compagno 2001 and De Vis 1883.

## Orectolobus japonicus REGAN, 1906

## Distribution

This relatively rare species is represented by diverse populations inhabiting the major part of the northern Philippines Islands, all the Asian coasts from the more southern coasts of Vietnam to the northern coasts of Corea and the southern coasts of Japan.

See Distribution map on: www.nl.wikipedia.org

The specimens caught in the Philippines Islands are believed to be representatives of a distinct species.

## **Depth record**

Individuals of this species may be encountered in rocky environments and coral reefs, from littoral waters to a depth of circa 200 metres.

# Mode of reproduction

Ovoviviparity

For references, see: Compagno 1984, Compagno 2001 and Regan 1906.

# Orectolobus wardi WHITLEY, 1939

#### Distribution

The rare individuals reported to be *Orectolobus wardi* were caught on scattered places along all the northern coasts of Australia.

See Distribution map on: www.commons.wikimedia.org

#### **Depth record**

This species is only reported from littoral zones of 1 to 5 metres depth.

#### Mode of reproduction

Probably ovoviviparous.

For references, see: Compagno 1984, Compagno 2001 and Whitley 1939.

## Orectolobus halei WHITLEY, 1940

#### Distribution

The diverse populations of *Orectolobus halei* inhabit all the south-western, the southern and south-eastern coasts of Australia.

## See Distribution map on: www.commons.wikimedia.org

# **Depth record**

They are inhabitants of creviced stony bottoms, coral patches and coral reef environments comprised between littoral waters to *circa* 200 metres depth.

#### Mode of reproduction

Ovoviviparity

#### Singularity

Triennial reproductive cycle

For references, see: Compagno 1984, Compagno 2001, Kuiter 1993, Lieske & Myers 1992 and Whitley 1940.

## Orectolobus hutchinsi LAST, CHIDLOW & COMPAGNO, 2006

#### Distribution

The species *Orectolobus hutchinsi* is represented by small populations scattered along the southern more eastern part of Australia.

See Distribution map on: www.en.wikipedia.org or www.bie.ala.org.au

#### **Depth record**

The individuals of this recently described species may be encountered in littoral waters to a depth of circa 110 metres.

## Mode of reproduction

Ovoviviparity

#### Singularity

This species has a very slow rhythm of reproduction: biennial, or even, triennial.

For references, see: Compagno 1984, Compagno 2001 and Last, Chidlow & Compagno, 2006.

#### Orectolobus floridus LAST & CHIDLOW, 2008

## Distribution and depth record

There exists no distribution map for this taxon. The first individuals of *Orectolobus floridus* were caught on the southwestern coasts of Australia, between 40 and 85 metres depth.

See Distribution map on: www.en.wikipedia.org

## Mode of reproduction

Unknown

For references, see: Last & Chidlow 2008.

#### Orectolobus parvimaculatus LAST & CHIDLOW, 2008

#### Distribution and depth record

Endemic from the South-eastern Australian coasts, caught between 9 to 35 metres depth (2008 data)

See Distribution map on: <u>www.bie.ala.org.au</u>

# Taxonomical remark

Considering that their size is the principal, if not the single, criterion allowing a distinction between *Orectolobus* parvimaculatus LAST & CHIDLOW, 2008 and *Orectolobus*. maculatus (BONNATERRE, 1788), the second taxon

could represent the juvenile stage of the first taxon.

#### Mode of reproduction

Supposed aplacental viviparity

For references, see: Last & Chidlow 2008.

#### Orectolobus leptolineatus LAST, POGONORSKI & WHITE, 2010

## Distribution

Difficult to precise because only known from one locality of Australia.

#### **Depth record**

Difficult to precise because according to its inventors it was caught in upwelling waters.

#### Mode of reproduction

Supposed aplacental viviparity

For references, see: Last, Pogonorsky & White 2008.

## Orectolobus reticulatus LAST, POGONORSKI & WHITE, 2008

The few populations known of *Orectolobus reticulatus* were discovered in the north-eastern part of Australia in littoral waters to 10 metres depth.

See Distribution map on: www.bie.ala.org.au

## Mode of reproduction

Unknown.

For references, see: Last, Pogonorsky & White 2008.

#### **Historical anecdote**

It is this small part of the Australian subcontinent which was discovered by the famous English adventurer William Dampier\* on  $5^{th}$  January 1688, some 82 years before its official discovery and annexation by James Cook in 1770.

\*Reference: *Dampier's monkey, the South Seas Voyages of William Dampier* by Adrian Mitchell 2010. Ed. Wakefield Press. 545 p. ISBN: 9781862547599.

# Genus Eucrossorhinus REGAN, 1908

(See Plates 28 to 30 and comments)

## Systematics

This mono-specific Genus is based on its single species and generotype: *Eucrossorhinus dasypogon* (BLEEKER, 1867).

# Eucrossorhinus dasypogon (BLEEKER, 1867) or Crossorhinus dasypogon BLEEKER, 1867

## Distribution

The scattered populations of this species inhabit the coasts of eastern Indonesia, Papua, New Guinea, and northern Australia.

Genetic investigations are required to demonstrate that the populations inhabiting the coasts of Malaysia could represent another species.

## See Distribution map on: www.wikipedia.org

#### **Depth range**

Individuals of *Eucrossorhinus dasypogon* inhabit littoral bottoms to 40 metres depth, and may occasionally be encountered in deeper waters.

## Mode of reproduction

Ovoviviparity

For references, see: Bleeker 1867\*, Compagno 1984, Herman, Euler-Hovestadt & Hovestadt 1992 and Regan 1908.

\*BLEEKER, P., R. 1867: Crossorhinus dasypogon nov. sp. in Archives Néerlandaises des Sciences Naturelles. 2: 400, pl. 21, fig.: 1.

#### Spatio-temporal distribution of the Genus Eucrossorhinus

This extant Genus seems to have no fossil representatives.

#### Genus Sutorectus REGAN, 1908 (See Plates 25 to 27 and comments)

#### **Systematics**

This mono-specific Genus is based on its generotype and single species: Sutorectus tentaculatus (PETERS, 1864).

#### Distribution

This species, endemic to Australia, is represented by numerous small populations concentrated in small scattered zones of south-western and central southern Australia, from the vicinity of Geraldton Harbour to Cape Carnot.

See Distribution map on: www.wikipedia.org

## **Odontological characteristics of the Genus** Sutorectus

## **Dental root**

The dental root of all the teeth of the individuals of *Sutorectus tentaculatus* examined is hemiaulacorhyzid and presents a long and wide medio-intern protuberance flanked by two root lobes giving to the root a nearly perfect inversed U-form (anterior teeth) to a an elongated arched form (lateral and posterior teeth).

## **Dental crown**

The dental crown of all the teeth of the individuals of *Sutorectus tentaculatus* examined is monocuspid and presents a particularly protruded apron having strong morphological similarities with the apron of the fossil species '*Columbusia' roessingi* (CASE, 1987) considered as a ganopristid taxon by Cappetta (2002: fig.: 361, p.: 372).

Their dental crowns are proportionally wider than these of the Genera *Orectolobus* and *Eucrossorhinus*. The dental crowns of the lateral and posterior teeth present a strong extern basal ornamentation, constituted by short costulae.

The anterior teeth of the three Genera Orectolobus, Sutorectus and Eucrossorhinus have a very distinct general morphology.

For reference, see: Herman, Hovestadt-Euler & Hovestadt 1992: pls.: 51 to 54.

#### Distribution

The populations of *Sutorectus tentaculatus* inhabit small rocky or coraliferous areas scattered around the south-western coasts of Australia.

#### See Distribution map on: www.wikipedia.org

#### **Depth record**

The depth of its holotype is not specified, but supposed to be littoral.

#### Mode of reproduction

Ovoviviparity

For references, see: Whitley 1939, Compagno 1984, Herman, Euler-Hovestadt & Hovestadt 1992 and Peeters1864.

#### Spatio-temporal distribution of the Genus Sutorectus

This extant Genus seems to have no fossil representatives.

# 9.4. Family Stegostomatidae GILL, 1862

#### Genus Stegostoma MÜLLER & HENLE, 1837 (See Plates 39 to 41 and comments)

The extant mono-specific Genus *Stegostoma* is based on *Stegostoma fasciatum* (HERMANN, 1783). This Genus has for holotype *Eostegostoma angustum* HERMAN, 1977.

The species *Eostegostoma angustum* was represented by diverse European, northern African and northern American populations inhabiting shallow waters with violent sea bottom currents between the Lower Eocene and the Middle Eocene.

## Stegostoma fasciatum HERMANN, 1783

## Distribution

The first detail that a paleontologist will point out is that, in contrast with the single extant representative of the Genus *Nebrius*, the single extant representative of the Genus *Stegostoma* has no population living in the Atlantic Ocean\*.

\*See distribution map on Internet.

Its distribution may be summarized as follows: Diverse populations of this species may be encountered in all the north-western part of the Indo-Pacific Ocean, from the northern part of the Red Sea to southern Japan and to northern Australia.

New Caledonia is its oriental limit of distribution. It is rarely encountered along the north-eastern coasts of Africa, the southern coasts of the Arabian Peninsula and the northern coasts of New Guinea.

#### Singularity

The adult individuals have a very distinctive appearance and have a completely different pattern from these of the young individuals. The size record of this species seems to be 3.95 metres\*.

\*Australian diver friends' observation.

The coloured patterns of juvenile and adult individuals of *Stegostoma fasciatum* are so different that its adults and juveniles were, originally, considered as different species.

## Habitat and depth record

*Stegostoma fasciatum* is a common inhabitant of coral reefs and shallow sandy bottoms, but some individuals were caught at 80 metres\* depth.

\*Australian fishermen friends' data.

## Feeding habit

During the day they remain resting on sandy bottoms, but during the night they search for diverse molluscs, crustaceans, small fishes and even for sea snakes inhabiting coral reefs.

## Mode of reproduction

## Oviparity

The egg-capsules of this species are very long: up to 18 centimetres length.

For references, see Bibliography: Compagno 2002: pp.: 184-188, Dingerkus 1986, Dudgeon, Noad & Lanyon 2008, Goto 2001, Randall & Hoover 1995: p.: 20, Van der Elst & Borchert 1993: p.: 63.

#### **Possible ancestor**

The Genus *Eostegostoma* HERMAN *in* TAVERNE & NOLF, 1976 of the Lower Eocene of England and Middle Eocene of Belgium is considered as its first ancestor.

# 9.5. Family Ginglymostomatidae GILL, 1862

## **Systematics**

According to Compagno 1984 the Family Ginglymostomatidae regroups the two mono-specific extant Genera: *Ginglymostoma* MÜLLER & HENLE, 1837 and *Nebrius* RÜPPEL, 1837.

# **Odontological characteristics of the Family Ginglymostomatidae**

Their teeth are disposed in parallel rows and not imbricated. The base of their dental crown overlaps the top of their hemiaulacorhyzid root.

Their dental crowns present a principal cuspid adjoined by a variable number of lateral cusplets. They possess a wide apron presenting an oval-shaped horizontal section.

# **Biological characteristics of the Family Ginglymostomatidae**

All its living representatives have five pairs of gill slits and two dorsal fins without fin spines.

## Reproduction

The majority of the generic taxa of the Family Ginglymostomatidae are ovoviparous.

#### Genus Ginglymostoma MÜLLER & HENLE, 1837 (See Plates 34 to 37 and comments)

This Genus is presently represented only by its type species *Ginglymostoma cirratum* (BONNATERE, 1788), which has a very large distribution area (See on Internet).

## Distribution

The distribution of *Ginglymostoma cirratum* may be summarized as follows: Eastern Pacific: only along the western coasts of North and South America, from the Sea of Cortez to southern Peru.

In the western part of the Atlantic Ocean, it is represented by, more or less dense, populations from the most northern part of the coasts of the U.S.A. to the southern Brazilian coasts including the Caribbean Sea.

In the central part of the Atlantic Ocean, it is represented by a relatively isolated population in the Azores which presents some odontological singularities.

In the eastern part of the Atlantic Ocean, it is represented by populations, of irregular densities, from southern Angola to northern Morocco.

It is completely absent in all the Indo-Pacific Ocean and was never observed in the Mediterranean Sea.

## Ginglymostoma cirratum BONNATERRE, 1788

## Distribution

Ginglymostoma cirratum is a common inhabitant of shallow waters of the tropical and subtropical zones on the

continental shelf and insular coasts occupied by coral reefs, but also in mangrove channels, which allows supposing that members of this species support a light decrease of salinity.

#### **Depth record**

Adult males and females, as well as juvenile specimens may be found in less than one meter depth. Their depth record seems to be of a maximum of 80 metres.

## See Distribution map on: www.fr.wikipedia.org

## **Behaviour**

They are principally, if not exclusively<sup>\*</sup>, nocturnal solitary active animals, which contrasts with the habit of many of their populations to remain grouped during the day.

\*Depending on the population observed.

## Feeding

Their food consists of small crustaceans, middle-sized molluscs and diverse fishes. Poisonous caudal fin spines of the Dasyatidae were frequently observed deeply intruded in their jaws, but having for sole effect a sporadic production of abnormal teeth.

## Singularity

Some Ginglymostoma have been filmed grazing algae and corals, which is exceptional for Neoselachii.

#### Spatio-temporal distribution of the Genus Ginglymostoma

Early Paleocene to Present Times.

# Genus Nebrius RÜPPEL, 1837

(See Plate 38 and comments)

#### **Systematics**

According to FishBase 2010, this mono-specific Genus is represented by its single extant species *Nebrius ferrugineus* LESSON, 1831.

## Nebrius ferrugineus LESSON, 1831

#### Distribution

This Genus has a huge distribution. It is represented by numerous populations in quasi continuous distribution areas in all the Indian and Pacific Oceans and this, from the southern coast of South Africa, the Red Sea, the Arabian Peninsula to Pakistan, all the coasts of India, Maldives Islands, Indonesia, Malaysia, Borneo, Sarawak, Vietnam, Korea, China, Ryukyu (Japan), the Philippines Islands and all the northern Australian coasts.

It is also represented by some isolated populations in the central part of the Pacific Ocean. It was never signalized along the coasts of Pakistan\*, the Myanmar coasts and in any Pacific areas located eastern of the Great Pacific Barrier.

\*This absence results from the same cause as the one of the Genus *Squatina* (see above).

Individuals or groups of *Nebrius ferrugineus* inhabit coastal shallow waters and may be encountered in three different environments: coral reefs, sandy bottoms and sea grasses.

## Odontological characteristics of the Genus Nebrius

# Singularity

All the extant species attributed to this Genus are in possession of a lower symphyseal tooth row.

## Dental root characteristics of the Genus Nebrius

Their teeth are disposed in parallel rows and not imbricated. The base of their dental crown overlaps, if not conceals the top of their hemiaulacorhyzid root.

Their medio-intern root protuberance is relatively narrow and flanked by two root lobes nearly horizontally extended.

## Dental crown characteristics of the Genus Nebrius

Their dental crowns present a principal cuspid adjoined by numerous lateral cusplets, they possess a very wide apron presenting an oval-shaped horizontal section.

The intern side of the dental crown of all the taxa attributed to this Genus is absolutely smooth, but the extern side of their extremely wide apron, generally curved and tongue-shaped may present a variable number of central or basal callosities.

## **Depth record**

*Nebrius ferrugineus* inhabits the shallow coastal waters, preferring coral reefs, sandy bottoms and sea grasses. Their depth's record reported is about 80 meters.

They are nocturnal animals and very efficient predators, having a very high suction power, but during the day they remain in compact groups of numerous individuals resting in submarine caves with a sandy bottom.

#### Feeding

Nebrius ferrugineus feeds on diverse invertebrates, octopuses, small fishes and occasionally on sea snakes.

## Mode of reproduction

Its mode of reproduction is aplacental viviparous

## Singularity

*Nebrius ferrugineus* is the only oophagous species of the Order Orectolobiformes, eating the other eggs in the uterus of their mother.

## Spatio-temporal distribution of the Genus Nebrius

Beginning of the Paleogene to Present Times.

For references, see: Compagno 1984, Cappetta 2012 and Herman, Hovestadt-Euler & Hovestadt 1997.

# 9.6. Family Hemiscylliidae GILL, 1862

## **Systematics**

According to FishBase 2012, this Family regroups the two extant Genera: Genus *Hemiscyllium* MÜLLER & HENLE, 1838 and Genus *Chiloscyllium* MÜLLER & HENLE, 1837 and the four extinct Genera: Genus *Mesiteia* GORJANOVIC-KRAMBERGER, 1885, Genus *Acanthoscyllium* CAPPETTA, 1980, Genus *Almascyllium* CAPPETTA, 1980 and Genus *Navia* BERNARDEZ, 2002.

The extant different taxa of this Family are exclusive inhabitants of some tropical Indo-Pacific shallow waters.

This Family has a temporal range extending from the Cenomanian Stage to the Recent Times.

# Extant taxa included in this Family

#### Genus Hemiscyllium MÜLLER & HENLE, 1838 (See Plates 46 to 49 and comments)

#### **Systematics**

According to FishBase 2012 and the last discoveries, the Genus *Hemiscyllium* regroups the eight following extant species: *H. ocellatum* (BONNATERRE, 1788), *H. freycineti* (QUOY & GAIMARD, 1824), *H. trispeculare* RICHARDSON, 1843, *H. strahani* WHITLEY, 1967, *H. galei* ALLEN & ERDMANN, 2008, *H. henryi* ALLEN &

ERDMANN, 2008, *H. michaeli* Allen & DUDGEON, 2010 and *H. halmahera* Allen, ERDMANN & DUDGEON, 2013.

According to Cappetta (2012: p.: 158), the first taxa attributed to this extant Genus are of Cenomanian Age.

# Odontological characteristics of the Genus Hemiscyllium

## Placement

Their teeth are arranged in parallel rows.

## **General morphology**

The width of their anterior teeth equals their height, the lateral and posterior teeth are wider than high.

## **Dental root characteristics**

The base of their dental crown overlaps the top of their flat hemiaulacorhyzid dental root. Their dental root possesses a well-developed medio-intern protuberance adjoined by two short lateral radicular lobes.

### **Dental crown characteristics**

Their dental crown presents a relatively short cuspid adjoined by two rounded and, more or less, elongated extensions. It has an arched apron presenting an elongated oval transversal section.

The height of their apron equals half of the width of the crown.

# Systematic interest of the extern morphology

The recent\* morphological observations of Dr. Goto 2002 concerning the diverse species attributed to the Genus *Hemiscyllium* allow considering it as a *polytomyc group*, which means that the phylogenetic relationships existing between the type species of this Genus and the other species attributed to this Genus could not be resolved only by morphological considerations.

\*See Bibliography: Goto 2002.

Future analysis of their mitochondrial DNA could help to resolve this problem, but thorough anatomical investigations\* also.

\*Particularly of their pectoral and pelvic girdles.

## Hemiscyllium ocellatum (BONNATERRE, 1788)

## **Distribution maps**

For its aspect and general distribution, see Internet: *Hemyscyllium ocellatum* images. Source: <u>www.nl.m.wikipedia.org</u> and for its distribution in the Australian waters, see Source: <u>www.australianmuseum.net.au</u>

The distribution of this species may be summarized as follows: All the coasts of Papua and New Guinea, nearly all the eastern coasts of Australia, the northern and western coasts of Australia and the coasts of the Salomon Islands.

In Australian waters, their diverse populations have very small territories. In fact this species may be considered as an endemic taxon of the Australian subcontinent. Its direct ancestors must be researched in the Australian uppermost Cenozoic levels.

# Habitat and depth record

Individuals of this species are found in shallow waters and are often seen in water just deep enough to cover their bodies.

They prefer intertidal pools and coral reefs, but some specimens can be encountered to a maximum depth of 50 metres.

#### Mode of reproduction

## Oviparity

## Singularity

#### Crawling out of the water.

This species can survive for 15 to 20 minutes out of the water.

## Observations of MARTIN, R., A. 2009 of the ReefQuest Centre for Shark Research:

## Why do sharks expose their dorsal fins? Citation:

As an adaptation for navigating in its complex reef environment, Hemyscyllium ocellatum moves by seemingly walking, bending its body from side-to-side and pushing off of the substrate with its paddle-shaped pectoral and pelvic fins.

The shark only swims to escape from a threat, and then not very far. The cartilaginous supports of the Hemiscyllium shark's paired fins are reduced and separated when compared to other sharks, allowing them to be rotated for use as limbs.

This mode of locomotion even enables the shark to crawl out of the water to access isolated tidal pools.

The gait of Hemyscyllium ocellatum is convergently similar to those of the primitive tetrapods such as salamanders, suggesting that the movements needed for walking on land may predate, and facilitated the evolution of the first terrestrial vertebrates.

For other references, see: Compagno 2002: pp.: 181-182, Goto 2001, Goto, Nishida & Nakaya 1999, Peach 2002, Renshaw, Kerricks & Nilsson 2002, Wise Mulvey & Renshaw 1998 and West & Carter 1990.

## Hemiscyllium freycineti (QUOY & GAIMARD, 1824)

## Distribution

The diverse populations, represented by highly variable concentrations of individuals, are dispersed along the southern and the northern coasts of New Guinea and Papua. Along the central part of the northern coasts of this Island, *H. freycinetti* has not yet been mentioned.

#### See: www.commons.wikimedia.org

This species is also, sporadically, signalized in Iran Jaya and western Indonesia.

#### **Depth record**

All the catches of individuals or groups of *Hemiscyllium freycineti* are reported from the littoral zone to a depth of maximum 55 metres.

## Feeding habit

The food selected by this species is similar to the food of all the other species of the Genus *Hemiscyllium*: a large predominance of small invertebrates and some very small teleostean fishes.

#### Mode of reproduction and singularity

Oviparity. Mating is realized in less than two minutes.

For references, see: Compagno 1984, Compagno 2001, Cornish 2005, Devados 1986, Quoy & Gaimard 1824 and West & Carter 1990.

## Hemiscyllium trispeculare RICHARDSON, 1843

#### Distribution

*H. trispeculare* is represented by numerous, and frequently dense, populations dispersed in coral reef environments along all the northern coasts of Australia. See: <u>www.fr.academic.ru</u>

#### **Depth record**

All the catches of individuals or groups of *Hemiscyllium trispeculare* are reported from the littoral zone to a depth of maximum 50 metres.

# Mode of reproduction

Oviparity

For references, see: Compagno 1984, Compagno 2001, and Richardson 1843.

## Hemiscyllium strahani WHITLEY, 1967

#### Distribution

The populations of *H. strahani* have limited distribution areas dispersed along the northern and southern coasts of Papua.

Source: www.fr.wikipedia.org

#### **Depth record**

All the catches of individuals or groups of *H. strahani* are reported from the intertidal zone to 20 metres depth.

#### Mode of reproduction

Supposed oviparous

For references, see: Compagno 1984, Compagno 2001 and Whitley 1967.

## Hemiscyllium galei ALLEN & ERDMANN, 2008

#### Comments

*Hemiscyllium galei* is one of the three recently discovered species of the Genus *Hemyscyllium*. This species was discovered together with *Hemiscyllium henryi* and described in 2008 by Allen and Erdman without any anatomical argumentation.

*H. galei* is, presently, only known from depths of 2 to 4 metres in coral reef platforms of one bay\* in western Papua, Indonesia.

\*The Cenderawasih Bay.

This new species can only be distinguished from its relatives, such as *H. freycineti* by different colour patches patterns.

## Distribution

The dispersal area of the rare populations of Hemiscyllium galei, presently known, is the Gulf of Papua.

#### See: www.en.wikipedia.org

#### **Depth record**

*H. galei* individuals are only reported as inhabitants of the intertidal zone, or more precisely of fringe reefs or shallow patch reefs of 2 to 4 metres depth.

# Mode of reproduction

Unknown

#### Singularity

Crawling on the bottom, between the patch reefs

For references, see: Allen & Erdmann 2008, Compagno 1984 and Compagno 2001.

#### Hemiscyllium henryi ALLEN & ERDMANN, 2008

The sole population of *H. henryi* was discovered in 2008, in western Papua.

## Distribution

No distribution map is available.

## **Depth record**

This species is supposed to live between 3 and 30 metres depth in this restricted area.

#### Mode of reproduction

Unknown

For references, see: Allen & Everdmann 2008.

## Hemiscyllium michaeli ALLEN & DUDGEON, 2010

#### Distribution

The holotype of Hemiscyllium michaeli was discovered in shallow waters in the Milne Bay (eastern Papua).

## **Depth record**

The individuals of this species are inhabitants of coastal reefs and live between 2 to 20 metres depth.

## Mode of reproduction

Unknown

For original reference, see: Allen & Dudgeon 2010.

#### Hemiscyllium halmahera ALLEN, ERDMANN & DUDGEON, 2013

This species is based only on two specimens collected in 2013, off the coast of Halmahera Island, differing from *Hemiscyllium galei* inhabiting West Papua only by differences in its pattern of spots.

## Distribution

No distribution map is available.

Dr. Allen's team caught two specimens of *Hemiscyllium halmahera* near the island Ternate, in the Maluku Islands, Indonesia.

# **Depth record**

This species is supposed to live between 3 and 30 metres depth in this restricted area.

#### Mode of reproduction

Unknown

#### Remark

According to many ichthyologists, *Hemiscyllium halmahera* is most similar in general appearance to *Hemiscyllium galei* discovered in Cenderawasih Bay, West Papua.

For references, see: Allen, Erdmann & Dudgeon 2008 and Allen, Erdmann & Dudgeon 2013.

## Natural History of the Genus Hemiscyllium

#### Depth range and Geographical distribution of its living representatives (See details species per species)

#### **Depth records**

*H. ocellatum* (BONNATERRE, 1788): 0 to 50 metres, *H. freycineti* (QUOY & GAIMARD, 1824): 0 to 55 metres, *H. trispeculare* RICHARDSON, 1843: 0 to 50 metres, *H. strahani* WHITLEY, 1967: 0 to 20 metres, *H. galei* ALLEN & ERDMANN, 2008: 2 to 4 metres, *H. henryi* ALLEN & ERDMANN, 2008: 3 to 30 metres, *H. michaeli* ALLEN & DUDGEON, 2010: 3 to 30 metres and *H. halmahera* ALLEN, ERDMANN & DUDGEON, 2013: 3 to 30 metres.

#### Conclusion

All the extant species of this Genus have individuals inhabiting coastal, if not intertidal, waters and other individuals able to live in waters of 20 to 55 metres.

To ensure the survival of each of their taxa, the *Hemiscyllium* depend on the continuity of their dispersal area. All major tectonic events may induce a definitive separation of one of their populations.

## Geographical distribution (Central point)

*H. ocellatum* (BONNATERRE, 1788): northern Australia and southern New Guinea - Papua (endemic), *H. freycineti* (QUOY & GAIMARD, 1824): northern and southern New Guinea - Papua (endemic), *H. trispeculare* RICHARDSON, 1843: northern Australia (endemic), *H. strahani* WHITLEY, 1967: western Papua (endemic), *H. galei* ALLEN & ERDMANN, 2008: southern Papua (endemic), *H. henryi* ALLEN & ERDMANN, 2008: northern Australia (endemic), *H. henryi* ALLEN & ERDMANN, 2008: northern Australia (endemic), and *H. halmahera* ALLEN, ERDMANN & DUDGEON, 2010: northern and southern New Guinea - Papua (endemic) and *H. halmahera* ALLEN, ERDMANN & DUDGEON, 2013: Indonesia (endemic).

#### Conclusion

In comparison with the extant species of the Genus *Chiloscyllium*, all the extant species of the Genus *Hemiscyllium* have very restricted dispersion areas.

All these areas are situated in the vicinity of the Australian continent, which may confirm the hypothesis that they have a common ancestor which lived in this area and not in Europe.

This proposal implies the revision of the generic attribution of all the fossil European taxa, classically attributed to the Genus *Hemiscyllium*.

## Possible ancestor of the Genus Hemiscyllium

All the anatomical and odontological characteristics of its eight extant species demonstrate clearly its narrow phylogenetic relationship with the Genus *Chiloscyllium* MÜLLER & HENLE, 1837 and justify its merging into one Family: Family Hemiscylliidae GILL, 1862.

Considering the fact that the two Genera *Hemiscyllium* and *Chiloscyllium* are easily distinguishable by the biologists\* and the paleontologists\*\*, the present problem is to find the ancestor of this Family.

\*Biological considerations: See Bibliography: Compagno 1984, Compagno 2001, Compagno 2005 and Dingerkus & De Fino 1983.

\*\*Odontological considerations: See Bibliography: Herman, Hovestadt-Euler & Hovestadt 1992.

The reassessment of the Family Hemiscylliidae GILL, 1862 will be suggested in the Chapter: New systematics proposals.

#### Genus Chiloscyllium MÜLLER & HENLE, 1837 (See Plate 42: fig.: 2, Plates 43 and 44 and comments)

#### **Systematics**

According to FishBase 2012 and the last discoveries, the Genus *Chiloscyllium* regroups the eight following extant species: *C. indicum* GMELIN, 1789, *C. plagiosum* (BENNETT, 1830\*), *C. griseum* MÜLLER & HENLE, 1838, *C.*  punctatum Müller & Henle, 1838, C. hasseltii Bleeker, 1852, C. arabicum Gubanov, 1980, C. caerulopunctatum Pellegrin, 1914 and C. burmensis Dingerkus & De Fino, 1983.

\*Contested attribution.

The oldest representatives of this extant Genus were discovered in Lower Selandian levels in Belgium.

## Odontological characteristics of the Genus Chiloscyllium

#### **Placement of its teeth**

Their teeth are arranged in parallel rows.

## General morphology of its teeth

The width of their anterior teeth equals their height, the lateral and posterior teeth are wider than high.

## **Dental root characteristics**

The dental root of the anterior, lateral and posterior teeth is hemiaulacorhyzid, but their upper commissural teeth present a root which could be considered as anaulacorhyzid.

All their dental roots present a well-developed medio-intern protuberance and two lateral radicular lobes.

#### **Dental crown characteristics**

Their dental crown overlaps the top of their dental root, and possesses a rounded or very lightly arched apron presenting a large oval-shaped transversal section.

The dental crown of their anterior teeth presents an elongated and narrow cuspid adjoined by one pair of short lateral cusplets.

The dental crown of their lateral and posterior teeth presents a large, low and massive cuspid without lateral cusplets.

The extern and intern sides of the anterior, lateral and posterior teeth are absolutely smooth, but the intern side of the commissural teeth presents some vertical large swellings.

#### Remark

The absence of a pair of short lateral cusplets and the morphology of their apron are the two odontological characteristics that allow differentiating their species from the extant species of the other Genus of the Family Hemiscylliidae: the Genus *Hemiscyllium* MÜLLER & HENLE, 1838.

## Biological characteristics of the Genus Chiloscyllium

All the extant taxa of the Genus *Chiloscyllium* possess five pairs of gill slits, two dorsal fins without spines and their cervical vertebrae, as well as the other vertebrae, present a transversal circular section.

## **Surprising fact**

In 2002\*, Doug Sweet, Curator of fishes at the Belle Isle Aquarium in Detroit signalized that two *Chiloscyllium plagiosum* (BENETT, 1830) were *born* at the Belle Isle Aquarium in Detroit (Michigan State, U.S.A.), and hatched 15 weeks after being laid.

\*See: SWEET, D. 2002: Shark gives virgin birth in Detroit. National Geographic. September 2002.

One suggestion was that *the Belle Isle bamboo shark* was a hermaphrodite, in possession of male and female sexual organs, and able to fertilize its own eggs.

But what a simple examination of its sexual organs could have demonstrated was, of course, not realised and never confirmed.

The logical explanation for this surprising birth is that the female shark had been fertilized a long time before.

For special references, see Bibliography: Parthenogenesis.

#### Conclusion

The *parthogenesis ability* of these *Chiloscyllium* was, of course, a deviant interpretation of the scientific term *parthogenesis* meaning that an individual has the possibility to reconstruct its whole anatomy from a part of its body and without mating.

The use of this term must be strictly reserved for taxa having this capacity, which means only some Phylla of Invertebrata.

It is possible that females of other taxa of the Family Hemiscylliidae have the same possibility to conserve fertilised eggs in their uterus for a certain time.

#### Chiloscyllium indicum GMELIN, 1789

## Distribution

This species is represented by numerous dense populations along the coasts of Pakistan, western coasts of India, the major part of the coasts of Indonesia, Myanmar to northern China. But, it is strangely absent between the northeastern coasts of India to the western coasts of Burma.

## Source: www.nl.wikipedia.org

This phenomenon affects also some populations of the Genus *Squatina* and other species of the Genus *Chiloscyllium*. One plausible explanation has been proposed in the Chapter: Order Squatiniformes. In this region shallow areas do not exist.

# Habitat and Depth record

Individuals of *C. indicum* may be encountered from the intertidal zone to 20-25 metres depth, on sandy or muddy bottoms.

## Mode of reproduction

Oviparity

For references, see: Compagno 1984, Compagno & Niem, 1998, Compagno 2001 and Gmelin 1789.

#### Chiloscyllium plagiosum (BENNETT, 1830\*)

#### Distribution

This species is represented by numerous dense populations dispersed along the same Indo-Pacific coasts as these frequented by *C. indicum* but also along all the coasts of the Philippines Islands and some parts of New Guinea.

Source: www.commons.wikimedia.org

#### Habitat and depth record

The diverse populations of *Chiloscyllium plagiosum* are principally inhabitants of sandy and muddy bottoms of coastal waters on rocky bottoms and coral reefs.

But, some of their populations support brackish waters and, locally, freshwater of some bays where the mouth of a river reaches marine waters.

#### Mode of reproduction

## Oviparity

#### Singularity

The fertilized eggs may remain a long time in the uterus of the female before being laid.

For references, see: Bennett 1830, Chen & Liu 2006, Compagno 1984 and Compagno 2001.

#### Chilioscyllium griseum Müller & Henle, 1838

#### Distribution

*Chilioscyllium griseum* is represented by a very high number of populations along the eastern and western coasts of India, the coasts of Myanmar, all the coasts of Thailand and Vietnam, the coasts of the western China Sea, the coasts of Indonesia, the coasts of Malaya and the central part of the Philippines Islands, New Guinea and some other small populations of the western Pacific Ocean.

Only the attribution of these small populations to Chilioscyllium griseum remains controversial.

Source: www.zh.m.wikipedia.org

## **Depth record**

Individuals of this species may be encountered from littoral waters to a depth of *circa* 80 metres.

#### Mode of reproduction

Oviparity

For references, see: Compagno 1984, Compagno 2001 and Müller & Henle 1837.

## Chilioscyllium punctatum Müller & Henle, 1838

## Distribution

*Chilioscyllium punctatum* is represented by a very high number of populations occupying nearly the same areas as the populations of *C. griseum*.

If, apparently absent in the Philippines Islands, this species has colonized the southern coasts of New Guinea and the northern coasts of Australia.

Source: www.en.academic.ru

#### **Depth record**

Individuals and small groups of *C. punctatum* may be encountered from intertidal poles to a depth of *circa* 90 metres.

## Mode of reproduction

Oviparity

## Singularity

Individuals of this species are able to survive out of the water, for more than twelve hours.

For references, see: Compagno 1984, Compagno 2001 and Müller & Henle 1837.

## Chilioscyllium hasseltii BLEEKER, 1852

#### Distribution

The diverse populations of *C. hasseltii* are concentrated in a very large area including all the coasts of Indonesia, Myanmar, former Indochina and the western coasts of Borneo Island, where they are inhabitants of rocky or reef bottoms.

Source: www.nl.wikipedia.org

#### **Depth record**

This species lives in tidal zones to a depth of maximum 15 metres.

#### Mode of reproduction

#### Oviparity

For references, see: Bleeker 1852, Breder & Rosen 1966, Compagno 1984 and Compagno 2001.

## Chilioscyllium arabicum GUBANOV, 1980

#### Remark

Before the description of this species, its individuals were generally considered as Chilioscyllium griseum.

## Distribution

The numerous, but very homogenous, populations of *C. arabicum* occupy all the coasts of the Persian Gulf, the Oman Gulf, Pakistan and western India.

Their individuals are inhabitants of rocky bottoms, coral reefs, mangroves and river-mouths.

#### Source: www.fr.academic.ru

#### **Depth record**

Individuals of *C. arabicum* are commonly encountered from the littoral to 15 metres depth, but some specimens were caught at nearly 120 metres depth (Fishermen friends' information).

## Mode of reproduction

Oviparity. Gestation: 12 months.

For references, see: Compagno 1984, Dingerkus & De Fino 1983, Gubanov 1980 and Randall & Hoover 1995.

## Chiloscyllium caerulopunctatum PELLEGRIN, 1914

#### Distribution

The diverse, more or less dense and numerous, populations of *C. caerulopunctatum* occupy a huge area including the western Indian coasts\*, all the Chinese coasts, the coasts of Myanmar, Indonesia and the Philippines Islands and the coasts of New Guinea.

\*The attribution of the populations inhabiting the western Indian coasts to *C. caerulopunctatum* requires further investigations, to be sure that none of them was in fact a representative of *C. arabicum*.

Source: www.fr.academic.ru

#### **Depth record**

Most of the catches were realized from the littoral to a depth of 12 metres.

#### Mode of reproduction

Oviparity

For references, see: Compagno 1984, Dingerkus & De Fino 1983 and Pellegrin 1914.

## Chilioscyllium burmensis DINGERKUS & DE FINO, 1983

#### Distribution

*Chiloscyllium burmensis* is an extremely rare species. It was caught in 1963 off the coast from Rangoon (Burma) at a depth of 29 to 33 metres. It seems that, except for its holotype, no other specimen has been observed since 1963.

Source: www.nl.wikipedia.org

## Mode of reproduction

Unknown, presumed oviparity.

For references, see: Dingerkus & De Fino 1983.

## Natural History of the Genus Chiloscyllium

Represented by some European fossil\* taxa\*\*, the Natural History of this Genus presents, after the Eocene-Oligocene Transition\*\*\* a constant colonization of more eastern areas, from central Europe to the western Indian Ocean, the central and eastern Indian Ocean, the western Pacific Ocean, where one branch colonized its central and northern part and the other branch colonized its central part to Australia.

\*According to Cappetta (2006: p.: 312 and 2012: p.: 158), who did not mention H. tailledisensis ADNET, 2002.

\*\*The three fossil taxa: *H. bruxelliensis* HERMAN, 1977 (Ypresian and Lutetian of Belgium), *H. hermani* MÜLLER, 1989 (Upper Campanian of northern Germany) and *H. tailledisensis* ADNET, 2002 (Ypresian and Lutetian of southwestern France), generally considered as representatives of the Genus *Hemiscyllium* seem to represent primitive *Chiloscyllium*, or even a Cretaceous ancestor of the Genus *Chiloscyllium*.

\*\*\*The Eocene-Oligocene Transition was responsible for climatic changes so drastic, that central European marine waters remained definitely too cold for all the representatives of the Order Orectolobiformes. See Bibliography: Herman & Van Waes 2012: *Géominpal Belgica* 5(1) and Herman & Van Waes 2013: *Géominpal Belgica* 5(2) and *Géominpal Belgica* 5(3).

The distribution area of the populations of *C. arabicum* includes all the coasts of the Gulf of Iran to the Indian coasts. *C. burmensis* constitutes an isolated taxon registered in a more eastern area, i.e. in only one bay of Burma.

A more eastern expansion was realized by the populations of *C. indicum*, which includes many more coasts of the Indian Ocean and the Pacific Ocean than the populations occupied by *C. arabicum*.

In the north-eastern direction *C. griseum* occupies all the Indian, Indonesian, the Philippines Islands, Chinese coasts and the coasts of New Guinean.

The distribution area of the populations of *C. hasseltii* includes all the coasts of former Indo-China, Indonesia and western Borneo.

The distribution area of the populations of *C. plagiosum* is approximately the same as this of *C. hasseltii*, but includes also all the southern coasts of Japan (northern expansion).

The distribution area of the populations of *C. caerulopunctatum* is nearly the same as this of *C. hasseltii* but without the western coast of India.

And finally, in the south-eastern direction, the Genus *Chiloscyllium* is represented by the numerous populations of *C. punctatum*, of which some have colonized the northern Australian coasts.

## Possible ancestor of the Genus Chiloscyllium

The ancestor of the Genus *Chiloscyllium* must have been in possession of teeth presenting a dental crown with an apron, which is the principal characteristic that allows recognizing a member of the Order Orectolobiformes (*sensu* Appelgate 1972).

But the dental crown may have had a simpler constitution, such as the absence of the pair of short lateral cusplets adjoined to their cuspid.

This hypothetical dental morphology is precisely this one presented by the diverse extant and extinct specific taxa of the Genus *Hemiscyllium* MÜLLER & HENLE, 1838, the second Genus included in the Family Hemiscylliidae APPLEGATE, 1974.

# 9.7. Family Brachaeluridae Applegate, 1974

## **Systematics**

Because the odontological characteristics of the extant representatives of this Family correspond with these of

the Order Orectolobiformes (*sensu* APPLEGATE, 1974), the senior-author follows the systematics proposed by Applegate in 1972.

This mono-generic Family is based on the Genus Brachaelurus OGILBY, 1907.

## Genus Brachaelurus OGILBY, 1908

#### Systematics divergence

For the biologists\* who admit the validity of the Genus *Cirrhoscyllium* SMITH & RADCLIFFE, 1913, regrouping the three following extant taxa: *Cirrhoscyllium colcloughi* (OGILBY, 1908), *Cirrhoscyllium japonicum* KAMOHARA, 1943 and *Cirrhoscyllium formosanum* TENG, 1959, the extant Genus *Brachaelurus* is only represented by its generotype *Brachaelurus waddi* (BLOCH & SCHNEIDER, 1801).

\*In 2013, this subject remained a controversial problem for the biologists. In absence of fossil teeth attributable to this Genus, this problem does not concern the palaeontologists.

As fossil teeth attributable to the Genus *Brachaelurus*, Cappetta (2012: p.: 165) mentioned: *B. roklumensis* THIES, 1983 from the Middle Barremian (lowermost Middle Cretaceous) of northern Germany, *B. templeuvensis* MOREAU & MATHIS, 2000 from the Thanetian (Upper Paleocene) of northern France and *B. hornestowensis*\* CASE, BORODIN & LEGGET, 2001 from the Upper Maastrichtian (End Cretaceous) of New Jersey (U.S.A.).

\*Once more the evident fact that small benthic sharks could not cross oceanic trenches is forgotten. The taxon *B*. *hornestowensis* requires a revision of its systematics position.

The species *Brachaelurus alvarezi* BERNARDEZ, 2002 from the Lower Turonian of northern Spain representing a possible link between the European Middle Cretaceous fossil representatives of this Genus and the European Paleocene fossil representatives of this Genus is not mentioned, simply, because considered as *nomen nudum*.

# **Odontological characteristics of the Genus** *Brachaelurus*

## Generalities

The teeth of the two extant species of this Genus are arranged in parallel rows.

The width of their anterior teeth is equal to their height; the width of their other teeth is superior to their height.

## **Dental root characteristics**

The dental root of all the teeth of the specimens examined is hemiaulacorhyzid. They possess a wide and massive medio-intern protuberance flanked by two massive root lobes. The base of the anterior, the lateral, posterior and commissural teeth is obviously arched.

## **Dental crown characteristics**

The dental crown of the anterior and lateral teeth presents one pair of large cusplets, acuminated (anterior teeth) or pointed (lateral teeth). These cusplets decrease progressively in size from the posterior to the commissural teeth, on which they are virtually unextant.

The extern and intern sides of all the crowns of these two species are absolutely smooth.

## Biological characteristics of the Genus Brachaelurus

All the extant taxa of this Genus possess five pairs of gill slits, two dorsal fins without fin-spines and a vertebral column constituted only by cylindrical vertebrae. They are ovoviviparous.

## Brachaelurus waddi (BLOCH & SCHNEIDER, 1801) or Squalus waddi BLOCH & SCHNEIDER, 1801

## **Distribution and Habitat**

This species has only been encountered along the Australian coasts, and more precisely and with certitude, only from South Queensland and New South Wales.

It is a typical inhabitant of rocky coasts and coral reefs, able to survive during a short emersion. Its food consists of cnidaria, small decapods, small cephalopods and very small fishes.

#### See Distribution map on: www.de.m.wikipedia.org

#### **Depth record**

Individuals of this species may be encountered from the intertidal zone to circa 150 metres depth.

## Mode of reproduction

Ovoviviparity.

## Singularity

The individuals of this species are able to survive for more than twelve hours out of the water. They were supposed to be blind by diverse authors. In fact they are not blind, but they immediately close their eyes when taken out of the water.

For references, see: Applegate 1972, Bloch & Schneider 1801, Compagno 1984 and Compagno 2001.

#### Brachaelurus colcloughi OGILBY, 1906

#### Distribution

The poorly known populations of this species are scattered along the eastern and northern coasts of Australia. Only one small population is known (2001) from the more northern part of New South Wales (Australia).

Source: <u>www.bie.ala.org.au</u>

#### **Depth record**

The individuals of this species are inhabitants of coastal, but never intertidal, zones and were encountered to depths of more than 200 metres.

## Mode of reproduction

#### Ovoviviparity

For references, see: Applegate 1972, Compagno 1984, Kyne, Compagno, Stead, Jackson & Bennett 2011 and Ogilby 1906.

#### Spatio-temporal distribution of the Genus *Brachaelurus*

According to Cappetta (2012: p.: 165), the oldest isolated teeth, attributable to this Genus, were discovered in levels from the Barremian (Lower Cretaceous) of Europe (France) and later in the Near-East and North America.

Once more, the extant taxa of this Genus being coastal nectic animals, the validity of the attribution of the North American species to this Genus is geologically not conceivable.

## Validity of their attribution to the Genus Brachaelurus

The extant representatives attributed to the Genus *Cirriscyllium* being inhabitants of China, Formosa and Australia, it seems plausible that the European fossil remains are effectively representatives of the Genus *Brachaelurus*.

#### Genus *Cirrhoscyllium* OGILBY, 1908 (See Plate 31: fig.: 2, Plate 50: fig.: 2 and comments)

The type species of the extant Genus *Cirrhoscyllium* is *Cirrhoscyllium expolitum* SMITH & RADCLIFFE, 1913, but this Genus must be considered\* as a synonym of the extant Genus *Brachaelurus* OGILBY, 1906.

\*According to FishWise 2012.

## Cirrhoscyllium expolitum SMITH & RADCLIFFE, 1913

Thanks to the help of Dr. Compagno (July 1977, San Francisco, California, U.S.A.), the senior-author had the

possibility to illustrate two teeth of the holotype of this species with some SEM photographs.

# See Bibliography: Herman, Hovestadt-Euler & Hovestadt 1992: Plate 26.

The only odontological differences observed between this anterior tooth and the anterior teeth of *Parascyllium variolatum* (DUMERIL, 1853) were the presence of some obvious very small folds on the lower part of the extern side of their crown and the virtual inexistence of the apron.

## Genus Heteroscyllium REGAN, 1906

## Heteroscyllium colcloughi (OGILBY, 1908) or Brachaelurus colcloughi OGILBY, 1908

If distinct of the extant Genus *Brachaelurus* OGILBY, 1906, this extant Genus is only represented by its generotype *Heteroscyllium colcloughi*, which still remains a very poorly known species.

# 9.8. Family Parascylliidae GILL, 1862

## **Systematics**

According to Cappetta 2006 (p.: 399), the Family Parascylliidae regroups two extant Genera: Genus *Parascyllium* GILL, 1862 and Genus *Cirrhoscyllium* SMITH & RADCLIFFE, 1913 and one extinct Genus: Genus *Pararhincodon* HERMAN *in* CAPPETTA, 1976, considered as its ancestor.

In 1974, Applegate already considered these two Genera as the more primitive orectoloboid\* sharks.

\*Former conception suggesting that the Orectolobidae included all the taxa presently regrouped in the Phorcynidae nov. Fam.

This phylogenetical proposal seems to have been accepted by Cappetta since 2006 (p.: 399).

# **Odontological characteristics of the Family Parascylliidae**

The teeth of the members of the Family Parascylliidae present a low heterodonty. Their dental crown presents one principal cuspid, lateral cusplets and, proportionally, large and massive root lobes.

# **Biological characteristics of the Family Parascylliidae**

The Parascylliidae possess five pairs of gill slits. They are slender, supple and rapid small sharks without dorsal fin spines. All their vertebrae, cervical and following ones, present a circular section and *centrae* without radii.

#### Mode of reproduction

As far as known, the members of the Family Parascylliidae are oviparous.

## Genus Parascyllium GILL, 1862

(See Plate 51, Plate 52 and comments)

#### **Systematics**

The extant Genus *Parascyllium* GILL, 1862 includes the five following species: *P. variolatum* (DUMERIL, 1853), *P. collare* RAMSAY & OGILBY, 1888, *P. ferrugineum* McCULLOCH, 1911, *P. sparcimaculatum* GOTO & LAST, 2002 and *P. elongatum* LAST & STEVENS, 2008.

Four of the extant species attributed to the Genus *Parascyllium* are inhabitants of the eastern Indian Ocean and the fifth, *P. collare*, of the South West Pacific Ocean.

Their diverse populations may be encountered in shallow waters and inhabit all kinds of sea bottoms.

# Odontological characteristics of the Genus Parascyllium

The dental crown of the teeth of all the extant species of this Genus overlaps the top of the dental root.

The teeth of all the extant taxa of this Genus are singularly laterally compressed, the height of their anterior teeth may be three times the size of their width (*P. variolatum*, *P. collare* and *P. ferrugineum*), their apron is quite inexistent and the base of their teeth is nearly flat.
#### Dental root characteristics of the Genus Parascyllium

The dental root of the teeth of the extant species of this Genus is generally hemiaulacorhyzid, but anterior teeth may be holaulacorhyzid, a principal odontological characteristic of all the extant taxa of the Super Order Scyliorhinomorphii HERMAN & VAN WAES, 2012.

Their nearly flat dental roots present a very short medio-intern protuberance flanked by two massive and short root lobes.

#### Dental crown characteristics of the Genus Parascyllium

The dental crown of the teeth of all the extant taxa of this Genus presents a narrow and elongated cuspid adjoined by one pair of rounded large lateral cusplets.

The intern side of all their dental crowns is absolutely smooth, but the base of their dental crowns may present some massive folds (e.g.: *P. collare*). These folds are absent on the crowns of *P. ferrugineum*.

#### Biological characteristics of the Genus Parascyllium

## Anatomical characteristics

The five extant species attributed to this Genus possess five pairs of gill slits, two dorsal fins without fin spine and a vertebral column constituted exclusively by vertebrae presenting a cylindral centrum.

#### **Ecological characteristics**

Their representatives may be encountered in coastal waters but never in the intertidal zone, which means that they are unable to survive in anoxic, or even hypoxic, environments.

#### Mode of reproduction

All the populations of the three commonest species are oviparous. Oviparity is the most primitive reproduction system for all the Vertebrata, but also for the Chondrichthyes.

## For illustrations, see:

Cappetta 2012: p.: 164, fig.: 151) and Herman, Hovestadt-Euler & Hovestadt 1992: Plates 21 to 25.

## Habitat, Distribution and Biology

These are little-known, rare to common, bottom sharks of often deep temperate and tropical, continental waters of the western Pacific, occurring from littoral waters to at least 183 metres depth.

The Genus *Parascyllium* is confined to Australian waters while the Genus *Cirrhoscyllium* occurs in the China Sea north to Japan and Taiwan Island.

They are found on muddy, sandy or rocky bottoms, and can apparently change colour in function of the bottom type.

At least some of the species are oviparous, depositing eggs in elongated, flattened egg cases on the bottom.

#### Remark

According to Applegate (1974), the senior-author considers also the two Genera: Genus *Cirrhoscyllium* and Genus *Parascyllium* as members of one distinct Family: the Family Parascylliidae APPLEGATE, 1974.

These sharks are distinguishable from the other former primitive\* Orectobidae by their teeth, with strong labial root lobes (variably reduced in other orectoloboids), low basal edges (expanded in most other orectoloboids) and by their cylindrical vertebral centrae with simple wedge-shaped intermedialia but no radii.

\*Primitive Orectobidae sensu Gill 1896.

#### Geological range of the Genus Parascyllium

Scientific literature allows suggesting that this Genus has existed since the Middle Eocene to the Present Times.

According to Cappetta (2012: p.: 164), isolated teeth of the oldest representative of this Genus were discovered by Dr. S. Adnet in the Lutetian of the Basin of Aquitaine (France).

#### Parascyllium variolatum (DUMERIL, 1853)

## Distribution

The diverse populations of this common species are dispersed along the southern west coasts of the south-western part of Australia, the northern coasts of Tasmania and the coasts of the Islands of the Bass Strait.

#### See distribution map on: www.wikimedia.org

According to FishBase and fishermen friends, the individuals of its diverse populations may be encountered on sandy bottoms, between coral reefs and on bottoms covered by various sea grasses.

#### **Depth record**

The populations of *Parascyllium variolatum* live from the coastal zone\* to a maximum depth estimated at 180 metres.

\*Apparently, never observed in the intertidal zone.

#### Mode of reproduction

Oviparity.

For references, see: Compagno 1984 and Duméril 1853.

## Parascyllium collare RAMSAY & OGILBY, 1888

## Distribution

The diverse populations of *Parascyllium collare* occupy all the south-eastern coasts of Australia from Hicks Point (South) to Fraser Island (North), on diverse sea bottoms, including small coral patches, but none of them was signalized in the Great Coral Reef Barrier.

See distribution map on: www.commonswikimedia.org

#### **Depth record**

The individuals of this species may be encountered between 20 and 190 metres depth\*, but they are particularly frequent between 50 and 120 metres depth\*.

\*2012 data from divers and fishermen.

#### Mode of reproduction

#### Oviparous

For references, see: Compagno 1984 and Ramsay & Ogilby 1888.

#### Parascyllium ferrugineum McCulloch, 1911

## Distribution

The numerous populations of *Parascyllium ferrugineum* are dispersed along all the southern coasts of Australia, all the coasts of Tasmania and some coasts of the Islands of the Bass Strait.

See distribution map on: www.commonswikimedia.org

## **Depth record**

The individuals of the diverse populations of *Parascyllium ferrugineum* may be encountered from the coastal zone to a depth of circa 150 metres, but never in the intertidal zone.

#### Mode of reproduction

#### Oviparous

For references, see: Compagno 1984 and McCulloch, 1911.

#### Parascyllium sparcimaculatum GOTO & LAST, 2002

## Distribution

The individuals of *Parascyllium sparcimaculatum* are common inhabitants of some sandy bottoms of the southern western part of Australia.

See distribution map on: www. commonswikimedia.org

#### **Depth record**

Individuals of *Parascyllium sparcimaculatum* are inhabitants of the coastal zone to a depth of circa 180 metres. It seems that they never penetrate the intertidal zone.

#### Mode of reproduction

Presumed oviparous.

For principal references, see: Compagno 1984 and Goto & Last, 2002.

## Parascyllium elongatum LAST & STEVENS, 2008

#### Distribution

This species is only known by its holotype, a juvenile female discovered, in 1990, in the stomach of a carcharhinid shark *Galeorhinus galeus* (LINNAEUS, 1758).

See Distribution map on: www.wikimedia.com

#### **Depth record**

The Galeorhinus galeus was caught at circa 50 metres depth off the coast of Chatham Island (Western Australia).

#### Mode of reproduction

Unknown, presumed oviparous.

For references, see: Compagno 1984 and Last & Stevenens, 2008

## Remark

The validity of these two last taxa, endemic to Australia, has no implication for this study.

## Genus Cirrhoscyllium SMITH & RADCLIFFE, 1913

(See Plate 31: fig.: 2, Plate 50: fig.: 2 and comments)

## **Systematics**

This Genus regroups the three following extant taxa: *Cirrhoscyllium expolitum* SMITH & RADCLIFFE, 1913, *Cirrhoscyllium japonicum* KAMOHARA, 1943 and *Cirrhoscyllium formosanum* TENG, 1959.

The three extant species attributed to the Genus *Cirrhoscyllium* are inhabitants of waters comprised between 100 and 200 metres depth.

They are presently known from restricted areas of the Chinese and Japanese coasts where they inhabit all kinds of sea bottoms.

In 1996, Dr. Goto and Dr. Nakaya definitely demonstrated the validity of these three species.

#### Cirrhoscyllium expolitum SMITH & RADCLIFFE, 1913

#### Distribution

The diverse and relatively dense populations constituting this species inhabit principally sandy bottoms of the China Sea and the Philippines. Its holotype was caught, in 1911, between northern Luzon (the Philippines) and China.

## Source: www.zh.m.wikipedia.org

## **Depth record**

The individuals of this species may be encountered from the littoral zone to a depth of *circa* 220 metres.

## Mode of reproduction

## Presumed Oviparity

For references, see: Compagno 1984, Compagno 2001 and Compagno & Niem 1998.

## Cirrhoscyllium japonicum KAMOHARA, 1943

#### Distribution

The populations of Cirrhoscyllium japonicum inhabit the western North Pacific coasts, Shikoku Island (Japan).

See distribution map on: www.artesdepesca.blognet.com

#### **Depth record**

Originally signalled from the continental shelf on bottoms comprised between 183 to 190 metres, individuals of this species are presently reported as inhabitants of sandy bottoms ranging from 250 to nearly 300 metres.

#### Mode of reproduction

Oviparity

For references, see: Breder & Rosen 1996, Compagno 2001 and Goto & Nakaya 1996.

## Cirrhoscyllium formosanum TENG, 1959

#### **Taxonomic remark**

Internet proposes images of one species *Cirrhoscyllium formosanum*, Family Orchideaceae de JUSSIEU, 1789, (Order Orchidales, Plantae), but this proposal is absolutely erroneous.

#### Distribution

The populations constituting this species have a distribution area limited to the coasts of Taiwan.

See distribution map on: www.artesdepesca.blognet.com

#### **Depth record**

The most frequent reports of catches of individuals of this species allow supposing that their populations are inhabitants of a depth comprised between 80 and 140 metres.

#### Mode of reproduction

#### Oviparity

For references, see: Breder & Rosen 1996, Compagno 2001 and Goto & Nakaya 1996 and Teng 1995.

## 10. Re-examination of the Order Orectolobiformes sensu APPLEGATE, 1974

All the extant and extinct generic or specific taxa attributable to this Order present the same following characteristics.

## **10.1. Odontological data of the Order Orectolobiformes** (*sensu* APPLEGATE, **1974**)

#### **Dental root**

Their dental root is hemiaulacorhyzid and presents a medio-intern protuberance, more or less developed adjoined by a pair of lateral root lobes, arched (anterior teeth) or more or less anterio-posteriorily elongated (lateral to commissural teeth).

#### **Dental crown**

Their dental crown presents one apron. It may be very narrow and subcylindrical (squatinoid type) to wide or very wide.

In the first case, it presents a subcircular horizontal section. In the second case, it presents an oval-shaped horizontal section.

The morphology of this apron, the ornamentation of the crown and the number and morphology of the lateral cusplets allow distinguishing, relatively easily, their numerous representatives.

## **10.2. Principal Biological data of the Order Orectolobiformes** (*sensu* APPLEGATE, **1974**)

## **General morphology**

All the extant generic or specific taxa attributable to this Order, present five pairs of gill slits and two dorsal fins without fin spines.

## **Reflection concerning the risk-perception capacity of some Orectolobiformes**

## **Ecological data furnished by extant representatives**

The majority of these benthic Chondrichthyes does not frequent the intertidal zone, nor did their ancestors. They were only surprised by exceptional events, such as tsunamis, typhoons, methane gas emanations and Dinoflagelelleta blooms.

Only those able to survive for a prolonged time in hypoxic or anoxic environments colonized the intertidal zones: the extant representatives of the three Genera: *Hemiscyllium* MÜLLER & HENLE, 1837, *Chiloscyllium* MÜLLER & HENLE, 1837 and *Brachaelurus* OGILBY, 1907.

Some morphological studies\* allow supposing that the Genus *Brachaelurus* has a narrow phylogenetic relation with the Family Orectolobidae (*sensu stricto*).

\*See Bibliography: Goto 2001.

## Paleontological data

Fossil teeth attributable to ancestors of the extant Genera *Hemiscyllium* and *Chiloscyllium* have been discovered in strata ranging from Upper Cretaceous to Pliocene Age.

Fossil teeth attributable to representatives of the Genus *Brachaelurus* have been discovered in some Upper Cretaceous levels in Europe and, more recently, in Pliocene sediments in Chile and Peru.

The examination of all the fossils of the diverse Invertebrata discovered in the same strata allows suggesting that their original paleoenvironment was also coastal or littoral, but never intertidal.

## Conclusion

The perception, or the understanding, of the possible risk to be trapped in intertidal zones seems to be a very an-

cient protective acquisition of these generic taxa of the Order Orectolobiformes (sensu Applegate 1972).

During the Eocene-Oligocene Transition, the re-occurrence of alterning glacial and interglacial phases inducing repetitive global sea-level changes, all the benthic littoral forms of life were again confronted with biological conditions that had disappeared since the Permo-Triassic Transition.

Generic taxa including populations living in cooler waters\* had more chance to support these phenomena.

\*Such as the Genus Squatina.

Consequently, the majority of the generic taxa of the Orectolobiformes (*sensu* Applegate 1972) abandoned the northern European areas and moved in eastern and southern directions.

In the uppermost Eocene of the English-Belgian-French Basin, the Order Orectolobiformes (*sensu* Applegate 1972) was only represented by dense populations of the two Genera *Squatina* DUMERIL, 1806 and *Nebrius* RÜPPEL, 1837.

## **Reflection concerning the performances of some Orectolobiformes**

## Ecological data furnished by extant representatives

## 1. Respiratory performances

The extant representatives of the three Genera *Hemiscyllium* MÜLLER & HENLE, 1837, *Chiloscyllium* MÜLLER & HENLE, 1837 and *Brachaelurus* OGILBY, 1907 present a very high capacity to survive out of the water.

This very complex adaptation, supposing high intern thermo-regulation capacities and significant respiratory modifications has surely required a certain time.

The strong similarities of their odontological\*, morphological and structural characteristics existing between their extant representatives and their extinct representatives are the sole arguments that paleontologists may advance to suppose that these biological modifications were not realized before the Eocene-Oligocene Transition.

\*The histology of their teeth.

## 2. Moving performances

The individuals of the diverse populations of *Hemiscyllium ocellatum* (BONNATERRE, 1788) have developed a system of moving similar to that of the salamander (*Salamandra salamandra LINNAEUS*, 1758, Amphibia).

Their strongly calcified pectoral and pelvic girdles allow them to walk on the sea bottom, between rocks or coral patches.

This capacity, combined with their ability to survive out of the water during a longer time than an intertidal period, has given to this species the possibility to move easily from one isolated water place to another one.

#### 3. New risk

This attempt to colonize some temporarily emerged parts of the marine environments, had its price: the risk to be captured by unknown predators, such as this individual of *Hemiscyllium ocellatum* (BONNATERRE, 1788), captured\* by an eagle of the species *Haliaeetus leucogaster* (GMELIN, 1788).

\*See on Internet: <u>www.vistaalmar.es</u> the surprising photograph realized by Michael Fogg on the reefs of Montgomery (Kimberley, northwestern Australia).

## Paleontological data

In absence of fossil skeletons, it is not possible to precise when the strengthening of their pectoral and pelvic girdles started, but the perfectly coordinated moving of their pectoral and pelvic fins allows supposing that their hyper-calcification happened during a short time, and was, maybe concomitant.

# 10.3. Biological data detectable on fossil skeletons of the Order Orectolobiformes (*sensu* APPLEGATE, 1974)

All the skeletons attributable to this Order, present five pairs of gill slits and two dorsal fins without fin spines.

## 10.4. Fossil representatives of the Order Orectolobiformes *sensu* CAPPETTA, 2002 and Orectolobiformes considered as *incertae sedis*.

## Remarks

The best and the most complete source of illustrations of the teeth of all the extinct taxa of the Order Orectolobiformes *sensu lato* is the revised Handbook of Palaeoichthyology – Vol. 3E. 2012. 512 p., 438 figs. Author: Henri Cappetta. Editor: Dr. Fritz Pfeil Verlag. München.

Illustrations concerning orectolobid taxa, see: Cappetta 2012: figs.: 141 to 172.

#### Generalities

In its two classic conceptions (Cappetta 2006 and Cappetta 2012), this Order regrouped thirty-six Genera\* and ninety-one nominal specific fossil taxa\*.

\*Including the taxa suppressed without argumentation.

Nineteen of these fossil Genera are mono-specific. Five taxa are based on skeletons, eighty-six taxa are based on isolated teeth. Some of them are of dubious validity.

The following lines regroup all the data already published and the personal observations of the senior-author, collected between 1968 and 2012.

These last ones allow the formulation of new systematics proposals. These proposals will be presented after a reexamination of all the Generic and specific taxa of this Order (former conception).

## Genus Orectolobus BONAPARTE, 1834

Only one fossil species was attributed to the extant Genus *Orectolobus*: *O. gippslandicus* (CHAPMAN & CUDMORE, 1924).

## Orectolobus gippslandicus (CHAPMAN & CUDMORE, 1924) or Squatina gippslandicus CHAPMAN & CUDMORE, 1924

This species is based on isolated teeth discovered in the Upper Rupelian (Victoria State, Australia).

For references, see:

Chapman & Cudmore, 1924: p.: 136, pl.: 11, fig.: 47, Pledge 1985 and Kemp 1991.

## Genus Ginglymostoma Müller & Henle, 1837

#### **1.** Fossil representatives of this Genus

According to Cappetta (2006: 308-309), sixteen fossil taxa represent ancient populations of this Genus: *G. angolensis* DARTEVELLE & CASIER, 1943, *G. botmaense* NOUBHANI & CAPPETTA, 1997, *G. cristata* (PROBST, 1878), *G. cuspidata* CASE, BORODIN & LEGGETT, 2001, *G. dartevellei* CASIER, 1946, *G. delfortrei* DAIMERIES, 1889, *G. erramii* NOUBHANI & CAPPETTA, 1997, *G. khouribgaense* NOUBHANI & CAPPETTA, 1997, *G. maghrebianum* CASIER, 1947, *G. malembeense* DARTEVELLE & CASIER, 1943, *G. maroccanum* NOUBHANI & CAPPETTA, 1997, *G. pectinatum* NOUBHANI & CAPPETTA, 1997, *G. serra* (LEIDY, 1877), *G. sokotense* WHITE, 1934 and *G. subafricanum* ARAMBOURG, 1952.

## 2. Material examined

*G. angolensis* DARTEVELLE & CASIER, 1943, numerous perfectly preserved teeth from the Lutetian of Cabinda, Atlantic coast of Africa (Collections M.R.A.C., Tervueren, Belgium), *G. botmaense* NOUBHANI & CAPPETTA, 1997, numerous perfectly preserved teeth from the Maastrichtian of the Ouled Abdoun Basin, Morocco (I.R.S.N.B. Collections and Private Belgian and French Collections), *G. chenanei* NOUBHANI & CAPPETTA, 1997, numerous perfectly preserved teeth from the Thanetian of the Ganntour Basin, Morocco (Collections)

I.R.S.N.B., Belgium and Private French Collections), G. cristata (PROBST, 1878), twelve reworked teeth from the Lower Miocene of the Bade-Würtemberg, Germany (Private Collections), G. cuspidata CASE, BORODIN & LEGGETT, 2001, six perfectly preserved teeth from the Upper Maastrichtian of New Jersey, U.S.A., (Private Collections), G. dartevellei CASIER, 1946, types and other teeth (Collections M.R.A.C., Tervueren, Belgium), from the Danian of Cabinda, G. delfortrei DAIMERIES, 1889, teeth never seen by the senior-author, from the Miocene of the Aquitanian Basin, France, G. erramii NOUBHANI & CAPPETTA, 1997, six teeth from the Upper Maastrichtian of the Ganntour Basin, Morocco, (Collections I.R.S.N.B., Belgium Private French Collection), G. khouribgaense NOUBHANI & CAPPETTA, 1997, twelve teeth from the Upper Maastrichtian of the Ouled Abdoun Basin, Morocco, (Private French Collection), G. maghrebianum CASIER, 1947, types in repository in the I.R.S.N.B. Collections, but not retrieved, from the Lower Eocene of Tunisia, G. malembeense DARTEVELLE & CASIER, 1943, types and other teeth (Collections M.R.A.C., Tervueren, Belgium), from Cabinda, G. maroccanum NOUBHANI & CAPPETTA, 1997, forty teeth (Private Collection) from the Thanetian and sixty teeth (Private Collection) from the Ypresian of the Ouled Abdoun Basin, Morocco, G. pectinatum NOUBHANI & CAPPETTA, 1997, eight teeth (Private Collection) from the Upper Maastrichtian of the Meskala Basin, Morocco, G. serra (LEIDY, 1877), six teeth from the Miocene\*, but reworked from the Upper Eocene of South Carolina, U.S.A., G. sokotoense WHITE, 1934, figuration, from the Thanetian of the Sokoto Basin, Nigeria, and G. subafricanum ARAMBOURG, 1952, four teeth (L. Dubertret Collection) from the Danian of the Ganntour Basin, Morocco.

\*Reconsideration of the age of the discovery level by American colleagues.

## Conclusions

## 1. Paleogeographical and stratigraphical distribution of the Genus Ginglymostoma

Maastrichtian to uppermost Eocene from diverse eastern and western Atlantic geological Formations.

## 2. Paleoecological distribution of the Genus Ginglymostoma

Considering the other vertebrate and invertebrate remains associated to these fossil teeth in all the diverse type localities, it seems obvious that the extinct populations of this Genus inhabited similar ecological niches as their extant representatives.

## 3. Natural History of the Genus Ginglymostoma

## **1.** Distribution of its extant representatives

#### **Objective data**

The single representative species of this extant Genus, *Ginglymostoma cirratum* (BONNATERRE, 1788), is represented by four main groups of more or less dense populations occupying shallow bottoms of the eastern Atlantic Ocean\*, one inhabiting nearly all the eastern coasts of the American Continent, from the boundary between Canada and U.S.A. to the southern coasts of Brasil and a fourth group of populations inhabiting nearly\*\* all the eastern coasts of the American Continent from the Sea of Cortez to the southern boundary of Peru.

\*One small group scattered along the northern coasts of Spain and one huge group occupying all the western coasts of Africa, from North Morocco to North Angola.

\*\*The Genus *Ginglymostoma* is absent from the eastern coast of the Yucatan Peninsula (Mexico) to the Dutch Guyana coast.

#### Source: <u>www.fr.academic.ru</u>

#### 2. Distribution of its extinct representatives

As far as known, the Eocene paleogeographical distribution of its extinct representatives covered the British-French-Belgian Basin, the northern African Basin, the Angola Basin and the central part of the North American Continent.

Such a large Cenozoic paleodistribution could explain the actual distribution of the Genus *Ginglymostoma*, but gives no explanation for the problem represented by its crossing of the North Atlantic trenches.

Genetic investigations of these diverse extant populations will surely demonstrate that their affinities require reconsiderations.

For the Eocene European, North African and western African representatives of this Genus, the Jurassic Genera *Phorcynis* THIOLLIERE, 1852, the Cretaceous Genus *Paraginglymostoma* HERMAN, 1982, the Paleocene Genus *Hologinglymostoma* NOUBHANY & CAPPETTA, 1997 and the Eocene Genus *Protoginglymostoma* HERMAN, 1977 seem to be possible ancestors.

#### 3. Conclusion

The oldest representatives surely attributable to this Genus are: *G. africanum* LERICHE, 1927, from the Thanetian of Cabinda and Morocco, *G. angolense* DARTEVELLE & CASIER, 1943 from the Ypresian (Cabinda) and the Lutetian (Morocco, Guinea Bissao and Togo).

For references, see: Cappetta 2012, Dartevelle & Casier 1943 and Leriche 1927.

## Genus Nebrius RÜPPEL, 1837

## **1.** Fossil representatives of this Genus

According to Cappetta 2006 (p.: 338), four or five extinct species represent ancestral populations of this Genus: *N. thielensi* (WINKLER, 1873) present and abundant in the Lower, Middle, Upper and Uppermost Eocene of the Anglo-Belgian-French Basin, *N. obliquus* (LEIDY, 1877) present and abundant from the Eocene of New Jersey, U.S.A., *N. bequaerti* (LERICHE, 1920) from the Danian of Landana, Cabinda, *N. blanckenhorni* (STROMER, 1905) from the Bartonian\* of Wadi Ramlich, Egypt and *N. priemi*\*\* GEMMELLARO, 1912 from the Lutetian of Sicilia, Italy.

\*Its precise geological age is not sure. \*\*Of dubious validity because based on only one badly preserved tooth.

## 2. Geological range

Early Paleocene to Recent Times.

## 3. Natural History of the Genus *Nebrius*

## Distribution of its extant representatives

The geographical distribution of the extant populations of its single representative may be summarized as follows: It includes all the coasts of the Red Sea, of the eastern side of Africa, the southern Arabian Peninsula, of the Persian Gulf, of India and Ceylan, and of the western coasts of the Pacific Ocean from northern Australia to southern Japan. For more details, consult the source below.

#### Source: www.en.academic.ru

## Distribution of its extinct representatives

The paleogeographical distribution of all the extinct European and African representatives of the Genus *Nebrius* explains perfectly its present distribution and depth range.

## Conclusion

Such as for many fossil taxa attributed to the Genus *Ginglymostoma* MÜLLER & HENLE, 1837 a careful odontological re-examination of all the North American taxa attributed to the extant Genus *Nebrius* could be interesting for a better understanding of their dispersion.

These Chondrichthyes being benthic inhabitants of shallow waters had no possibilities to cross the Atlantic Ocean after the Upper Jurassic Period and surely not at the Upper Cretaceous Period.

Their single possibility to colonize northern American territories was to progress along the continental mass that formed Africa and South America. But its extant populations have a large and understandable distribution.

The most representative fossil taxon of this Genus is *Nebrius thielensi* (WINKLER, 1874) from which isolated teeth are some of the most common fossils collectable in all the Lower to the Uppermost Eocene levels of the English-French-Belgian Basin.

For references, see: Bourdon 2007, Compagno 1984, Herman, Hovestadt-Euler & Hovestadt 1993, Herman, Hovestadt-Euler & Hovestadt 1997 and Seposky 2002.

## Genus Chiloscyllium Müller & Henle, 1837

According to Cappetta (2006: pp.: 291-292 and 2012: pp.: 156-158) the eleven following extinct taxa are attributable to this extant Genus: *C. humboldti* (REUSS, 1845), *C. humboldti* (REUSS, 1845), *C. minutum* (DAIMERIES, 1888), *C. broenimanni* CASIER, 1958, *C. daimeriesei* (HERMAN, 1973), *C. greeni* (CAPPETTA, 1973), *C. missouriense* CASE, 1979, *C. gaemersi* MÜLLER, 1989, *C. meretiae* WERNER, 1989, *C. meraense* NOUBHANI & CAPPETA, 1997, *C. salvani* NOUBHANI & CAPPETA, 1997 and *C. arbizui* BERNARDEZ, 2002.

#### Chiloscyllium humboldti (REUSS, 1845) or Scyllium humboldti REUSS, 1845

This species is based on isolated teeth discovered in a Turonian level (Upper Cretaceous) of Bohemia (Czech Republic).

For original reference, see: Reuss 1845: p.: 4, pl.: 4, figs.: 4 to 8.

## Chiloscyllium minutum (DAIMERIES, 1888) or Rhina minutum DAIMERIES, 1888

This species is based on hundreds of perfectly preserved isolated teeth discovered in the basal gravel of the Tuffeau de Lincent (European Upper Paleocene) at Orp-le-Grand - Maret (Waloon Brabant Province, Belgium). Concerning its validity: see Cappetta 2006 (pp.: 62-63).

For original reference, see: Daimeries: p.: 43. No figuration

## Chiloscyllium broenimanni CASIER, 1958

This species is based on isolated teeth discovered in a western Atlantic Upper Cretaceous level of non-specified Age in La Trinidad.

For original reference, see: Casier 1958: p.: 56, pl.: 3, figs.: 12 to 14.

## Chiloscyllium daimeriesei (HERMAN, 1973) or Ginglymostoma daimeriesei HERMAN, 1973

This species is based on hundreds perfectly preserved isolated teeth discovered in the Sands of Orp-le-Grand Formation of Selandian Age (European Paleocene). Concerning its validity: see Cappetta 2006 (pp.: 62-63).

For original reference, see: Herman 1973: p. 193, pl.: 1, figs.: 6 to 9.

#### Conclusion

The senior-author agrees that this taxon is a synonym of Chiloscyllium minutum (DAIMERIES, 1888).

## Chiloscyllium greeni (CAPPETTA, 1973) or Brachaelurus greeni CAPPETTA, 1973

This species is based on isolated teeth discovered in the Carlile Shales Formation of Turonian Age (Upper Cretaceous) of South Dakota (U.S.A.).

For original reference, see: Cappetta 1973: p.: 507: fig.: 2, pl.: 1, figs.: 36 to 41.

#### Chiloscyllium missouriense CASE, 1979

This species is based on isolated teeth discovered in the Judith River Formation of Campanian Age (Upper Cretaceous) of the Blaine County (Montana, U.S.A.).

For original reference, see: Case 1979: p.: 224, p.: 225: fig.: 1, pl.: 1.

#### Chiloscyllium gaemersi Müller, 1989

This species is based on isolated teeth discovered in an Upper Campanian level (Upper Cretaceous) of north-western Germany.

For original reference, see: Müller 1989: p.: 38, pl.: 8, figs.: 1 and 3 to 5.

#### Chiloscyllium meretiae WERNER, 1989

This species is based on isolated teeth discovered in an Upper Campanian level (Upper Cretaceous) of the Bahariya Basin (Egypt).

For original reference, see: Werner 1989: p.: 23: fig.: 8, pl.: 8, figs.: 1 to 6.

#### Chiloscyllium meraense NOUBHANI & CAPPETA, 1997

This species is based on isolated teeth discovered in an Upper Ypresian level (Lower Eocene) of the Ouled Abdoun Basin (Morocco). In July 1971, the senior-author had collected a lot of teeth of this taxon.

For original reference, see:

Noubhany & Cappetta 1997: p.: 20, pl.: 1, figs.: 5 to 8 and pl.: 2, figs.: 1 to 7.

#### Chiloscyllium salvani NOUBHANI & CAPPETA, 1997

This species is based on perfectly preserved isolated teeth discovered in only one Thanetian level of the Ouled Abdoun Basin (Morocco). In July 1971, the senior-author had collected a lot of teeth of this taxon.

For original reference, see: Noubhany & Cappetta 1997: p.: 19, pl.: 1, figs.: 1 to 4.

#### Chiloscyllium arbizui BERNARDEZ, 2002

This species is based on perfectly preserved isolated teeth discovered in the Lower Turonian (Upper Cretaceous) of Asturias (Spain).

Even if considered as *nomen nudum* (Cappetta 2006: p.: 24) this species represents a distinct population of the Genus *Chiloscyllium* also present in the lower and middle Turonian levels of Bettrechies (northern France).

For original reference, see: Bernardez 2002: p.: 213, pl.: 6, fig.: 7 and pl.: 8, figs.: 1 and 2.

#### Reflection concerning the American fossil taxa attributed to the Genus Chiloscyllium

The three American specific taxa attributed to the Genus *Chiloscyllium: C. broenimanni* CASIER, 1958, *C. greeni* (CAPPETTA, 1973) and *C. missouriense* CASE, 1979 may be considered as potential ancestors of the common ancestral source of the Family Hemiscylliidae such as defined by the biologists, but are surely not representatives of the Genus *Chiloscyllium* such as defined by the biologists.

It is difficult to admit that populations of the Genus *Chiloscyllium* or of the Genus *Hemiscyllium*, presently, represented by species unable to colonize sea bottoms deeper than 100 metres crossed the North Atlantic Ocean after the Jurassic Period, when trenches of thousands of metres depth succeeded to trenches of similar depth.

The senior-author considers consequently that the generic status of these North American taxa requires further re-examinations.

#### Genus Hemiscyllium MÜLLER & HENLE, 1838

According to Cappetta (2006: p.: 312 and 2012: p.: 158), the three following extinct taxa are attributable to this extant Genus: *H. bruxelliensis* HERMAN, 1977, *H. hermani* MÜLLER, 1989 and *H. tailledisensis* ADNET, 2000.

## Hemiscyllium bruxelliensis HERMAN, 1977

This species is based on perfectly preserved isolated teeth discovered in two different levels of the Brussels

Sands Formation (Middle Lutetian) in diverse localities of the Brussels Regio and the Flemish Brabant Province (Belgium).

For original reference, see: Herman 1977: p.: 132: fig.: 3, pl.: 1, figs.: 1 and 2.

#### Hemiscyllium hermani Müller, 1989

This species is based on isolated teeth discovered in the Baumberge Schichten Formation (Upper Campanian, Upper Cretaceous) of Westfalia (northern Germany).

For original reference, see: Müller 1989: p.: 35, pl.: 7, figs.: 2 to 7.

## Hemiscyllium tailledisensis ADNET, 2000

This species is based on isolated teeth discovered in the Lower Ypresian of the Aquitaine Basin (southern France). Even if considered as *nomen nudum* (Cappetta 2006: p.:225), this species is also present in the Lower Ypresian of the English Basin.

For original reference, see: Adnet 2000: p.: 63, pl.: 17, figs.: 5 to 7.

## Genus Phorcynis THIOLLIERE, 1854

This Genus is represented by the three following species: *P. catulina* THIOLLIERE, 1852, *P. minus* (WOODWARD, 1889) and *P. jurassicus* (WOODWARD, 1912), all based on skeletons.

## Odontological characteristics of the Genus Phorcynis

## **Dental root**

The dental root of the Genus *Phorcynis* presents an anaulacorhyzid\* root, a medio-intern protuberance with a central orifice on its top and two short root lobes.

\*Looking like what E. Casier defined in 1947 as secondary anaulacorhyzid step.

#### **Dental crown**

The dental crown of the Genus *Phorcynis* presents an elongated crown with an extern side nearly flat to lightly convex, presenting a marked ridge near its posterior cutting edge.

The dental crown possesses a narrow and elongated cuspid and a posterior cusplet, presents a wide tongueshaped apron and some short parallel basal costulae on its posterior extern side.

#### Main sources of information

Personal observations (1972) of the holotype P.11211 of the B.M.N.H. (London, England, Great Britain), and description furnished by Cappetta in 2012: pp.: 181-182 and p.:183, fig.: 172.

#### Biological characteristics of the Genus Phorcynis

The skeleton of the rare individuals of this extinct Genus demonstrate that they were in possession of five pairs of gill slits and of two dorsal fins without spines.

The invertebrates discovered in the same levels confirm that the environment was this of very shallow and warm marine waters.

#### Conclusion

The odontological and biological characteristics of the Genus *Phorcynis* THIOLLIERE, 1854 allow considering this taxon as the generotype of a new Family: Family Phorcynidae nov. Fam.

#### Phorcynis catulina THIOLLIERE, 1854

This species is based on its holotype: a very well preserved skeleton discovered in the Kimmeridgian (Middle

Upper Jurassic) at Cérin (Charente-Maritime Department, France).

Other skeletons, later discovered in the Upper Tithonian limestones of Solnhofen (Bayern, Germany) have been attributed to the same species.

## Phorcynis minus (WOODWARD, 1889) or Palaeoscyllium minus WOODWARD, 1889

This species is based on a well preserved skeleton discovered in the Lower Tithonian limestones of Solnhofen (Bayern, Germany).

The senior-author considers that this taxon could be the direct ancestor of *Phorcynis catulina* THIOLLIERE, 1854, or that it represents a juvenile individual of this species.

For original reference, see: Woodward 1889: p.: 339, pl.: 16, fig.: 14.

## Phorcynis jurassicus (WOODWARD, 1912) or Crossorhinus jurassicus WOODWARD, 1912

This species is based on a very well preserved skeleton discovered in the Upper Tithonian limestones of Solnhofen (Bayern, Germany).

Its attribution to the extant Genus *Crossorhinus* MÜLLER & HENLE, 1837 by Woodward signifies that its inventor had realized its direct phylogenetic relationship with the most primitive extant Genera of the Family Orectolobidae (*sensu stricto*).

The senior-author proposes the Genus *Phorcynis* as generotype of the Family Phorcynidaenov. Fam.

For original reference, see: Woodward 1912: p.: 231, pl.: 3, fig. 1.

## Genus Parascyllium GILL, 1862

As far as known, this extant Genus has no fossil representative.

## Genus Plicodus WINKLER, 1874

This mono-specific Genus is represented only by its holotype P. thielensi WINKLER, 1874.

*P. thielensi* is based isolated teeth discovered in the Brussels Sands Formation (Middle Lutetian) of the Brussels Regio (Belgium).

The senior-author agrees completely with the suggestion that the Genus *Plicodus* is a synonym of the Genus *Nebrius* RÜPPEL, 1837.

For original reference, see: Winkler 1874: p.: 7.

## Genus Acrodobatis LEIDY, 1877

This Genus is only represented by some teeth discovered in an imprecise level of contested age in the U.S.A. Its type species is *Acrodobatis serra* LEIDY, 1877.

According to Cappetta 2006 (p.: 272), its type set is a mixture of teeth reworked from the upper Eocene, attributable to two Genera: Genus *Nebrius* RÜPPEL, 1837 and Genus *Ginglymostoma* MÜLLER & HENLE, 1837.

## Conclusion

This generic taxon may be suppressed.

## Genus Cantioscyllium WOODWARD, 1889

According to Cappetta 2006 (p.: 284), this extinct Genus is represented by the seven following taxa: *C. lobatum* (REUSS, 1846), *C. decipiens* WOODWARD, 1889, *C. saginatus* MEYER, 1974, *C. meyeri* CASE & CAPPETTA, 1997, *C. alhaulfi* KRIWET, 1999, *C. nessovi* WARD & AVERIANOV, 1999 and *C. hashimiaensis* MUSTAFA, CASE & ZALMOUT, 2002.

Cappetta (2012: p.: 169) reduced this number to five taxa: C. decipiens WOODWARD, 1889, C. meyeri CASE & CAPPETTA, 1997, C. alhaulfi KRIWET, 1999, C. nessovi WARD & AVERIANOV, 1999 and C. nessovi WARD & AVERIANOV, 1999.

#### Odontological characteristics of the Genus Cantioscyllium

#### **Dental root**

The dental root of the teeth of all the species of this extinct taxon is hemiaulacorhyzid and presents a massive medio-intern protuberance flanked by nearly flat and short lateral lobes.

#### **Dental crown**

The dental crown of the teeth of all the species of this extinct taxon is polycuspid, presenting one two three lateral cusplets.

Their apron is large and presents a central retraction giving them an arched morphology. The intern side of the crown is absolutely smooth, but the extern side presents numerous very fine subvertical or undulated costulations.

#### Biological characteristics of the Genus Cantioscyllium

The diverse skeletons examined by the senior-author, as well as others, demonstrate that these sharks were in possession of five pairs of gill slits and two dorsal fins without spines. Eggs were never observed in these skeletons.

#### Conclusion

Cappetta considered the Genus *Cantioscyllium* as a member of the Family Ginglymostomatidae GILL, 1862, the senior-author (See new Systematics proposals) agrees with this systematics conception.

#### Cantioscyllium lobatum (REUSS, 1846) or Squatina lobatum REUSS, 1846

This species is based on isolated teeth discovered in marls of Turonian Age in Bohemia (Czech Republic). This species is considered as a taxon of the Family Squatinidae by Cappetta (2006: p.: 133, but suppressed in Cappetta 2012).

The senior-author considers that this taxon could be attributed to a primitive orectolobid Genus of the Family Orectolobidae *emend*.

For original reference, see: Reuss 1846: p.:101, pl.: 21, fig.: 21.

#### Cantioscyllium decipiens WOODWARD, 1889

This species is based on a skeleton discovered in the Campanian Chalk (Upper Cretaceous) of Kent (England, Great Britain).

For original reference, see: Woodward 1889: p.: 347.

Despite its designation as type species of the Genus *Cantioscyllium*, this taxon was not figured. The teeth of this species were figured by Cappetta in 2012: p.: 169, fig.: 157.

## Cantioscyllium saginatus MEYER, 1974

This species is based on isolated teeth discovered in different Santonian levels (Upper Cretaceous) of Mississipi (U.S.A.), but described in a PhD. Thesis difficult to consult.

According to Cappetta (2006: p.: 202), such an argument is sufficient to refute the validity of a taxon. Cappetta did not modify his opinion in 2012.

The senior-author considers this taxon as a valid taxon of the Family Ginglymostomatidae GILL, 1862.

For original reference, see: Meyer 1974: pp.: 178-179, fig.: 57.

#### Cantioscyllium meyeri CASE & CAPPETTA, 1997

This species is based on isolated teeth discovered in the Kemp Clay Formation (Upper Maastrichtian) in Hunt County (Texas, U.S.A.).

The senior-author considers that this taxon could represent individuals of a tardive population of *Cantioscyllium saginatus* MEYER, 1974 and could be synonymized with this last one.

For original reference, see: Case & Cappetta 1997: p.: 136, pl.: 6, figs.: 5-7.

## Cantioscyllium alhaulfi KRIWET, 1999

This species is based on isolated teeth discovered in the Lower Barremian (lowermost Middle Cretaceous) of the Teruel Province (Spain).

Cappetta (2006: p.: 14 and 2012: p.: 168) considered this taxon as a member of the Family Ginglymostomatidae GILL, 1862. The senior-author agrees completely with his opinion.

For original reference, see: Kriwet 1999: p.: 118, pl.: 1, figs.: 6-8.

#### Cantioscyllium nessovi WARD & AVERIANOV, 1999

This species is based on isolated teeth discovered in a Santonian level of the Kyzylkum Desert in Uzbekistan (Federation of Russia).

Cappetta (2006 and 2012) considered this taxon as a member of the Family Ginglymostomatidae, the seniorauthor considers, more prudently, that this taxon may be considered as a possible ancestor of the Family Ginglymostomatidae GILL, 1862.

> For original reference, see: Ward & Averianov 1999: p.: 90, fig.: 1.

#### Cantioscyllium hashimiaensis MUSTAFA, CASE & ZALMOUT, 2002

This species is based on isolated teeth discovered in an Upper Santonian level of the Karak District (Jordania). Cappetta (2006 and 2012) considered this taxon as a member of the Family Ginglymostomatidae, the senior-author considers, more carefully, that this taxon may be considered as a possible ancestor of the Family Ginglymostomatidae GILL, 1862.

For original reference, see: Mustafa, Case & Zalmout 2002: p.: 483, p.: 487, figs.: 4(1-2) and 4(1-7).

#### Cantioscyllium brachyplicatum (KRIWET, NUNN & KLUG, 2009)

This species is based on isolated teeth discovered in the Lower Cretaceous from Castellote (Leon, Spain).

Without argumentation, such as a simple synonymisation, this taxon is not mentioned in the revised Handbook of Cappetta (2012).

The senior-author, never having had the possibility to examine any specimen of this taxon, cannot give any objective opinion concerning this taxon.

For original reference, see: Kriwet, Nunn & Klug 2009.

#### Genus Brachaelurus OGILBY, 1907

The four following fossil species were also attributed to the Genus Brachaelurus: *B. roklumensis* THIES, 1981 from the Barremian in northern Germany, *B. templeuvensis* MOREAU & MATHIS, 2000 from the Thanetian in northern France, *B. hornestowensis*\* CASE, BORODIN & LEGGETT, 2001 from the New Egypt Formation (Upper Maastrichtian) of the New Jersey (U.S.A.) and *B. alvarezi* BERNARDEZ, 2002 from the Turonian of northern Spain.

\*This taxon is based on a single badly preserved tooth allowing only supposing that is was a brachaelurid tooth.

These fossils allow supposing that this Genus, presently endemic to Australia, had representatives since the Late Cretaceous period deposits in Europe, as well as in Pliocene period deposits in Chile and Peru.

The attribution to the Genus *Brachaelurus* of the first taxon (*B. roklumensis*) and, maybe, the attribution of the Pliocene specimens to this Genus seem plausible, but for the other specimens of Cretaceous to Paleocene Age, diverse paleogeographic and tectonic arguments made this attribution more than dubious.

The senior-author agrees with Cappetta (2006: p.: 283) that they are Orectolobiformes, but is also quite sure that they are not members of the Family Brachaeluridae.

Paleontologists, never having read: L'Odyssée de l'Euregio Meuse-Rhin\* cannot realise which was the geographical position of the Antarctic during the Middle Paleogene.

\*See Bibliography: Bless & Fernandez-Narvaiza 2000.

For references, see: Bernardez, 2002, Cappetta 2006, Case, Borodin & Leggett, 2001, Moreau & Mathis, 2000, Kriwet 2005, Thies 1981 and Williams 1999.

## Genus Crossorhinus WOODWARD, 1918

This Genus is based on a well preserved skeleton of its type species: *Crossorhinus jurrasicus* WOODWARD, 1918, which was discovered in the lithographic stone of Solnhofen (Bayern, Germany).

#### Crossorhinus jurrasicus WOODWARD, 1918

This species is considered (Cappetta 2006 and Cappetta 2012) as a synonym of *Phorcynis catulina* THIOLLIERE, 1852.

## For original reference, see: Woodward 1918: p.: 231, pl.: 1, fig.: 1.

Cappetta (2012: pp.: 181-183) did not precise his opinion concerning the familial position of the Genus *Crossorhinus*.

The senior-author (See new Systematics proposals) considers this Genus as a member of the Family Phorcynidaenov. Fam.

## Genus Corysodon de SAINT-SEINE, 1949

This mono-specific extinct Genus is only represented by its generotype: *Corysodon cirinensis* (de SAINT-SEINE, 1949), presently represented by a lot of skeletons discovered in Cérin (France) and Solnhofen (Germany).

## Main sources of information

Personal observation (1983) on one additional specimen from Cérin (Private Collection) and description and figuration of de Saint-Seine 1949: pp.: 14-17 and Cappetta 2012: pp.: 317-318 and fig.: 302.

## Corysodon cirinensis (de SAINT-SEINE, 1949)

Several skeletons of this species were discovered at Cérin (Charente-Maritime Department, France) and at Solnhofen (Bayern, Germany), all of Upper Jurassic Age.

For original reference, see: de Saint-Seine 1949: p.: 14: fig.: 7, p.: 16: fig.: 8.

#### Odontological characteristics of the Genus Corysodon

#### **Dental root**

The dental root of the teeth of *Corysodon cerinensis* is anaulacorhyzid and presents an arched mass in which the medio-intern protuberance is difficult to distinguish from the lateral lobes.

#### **Dental crown**

The dental crown of the teeth of *Corysodon cerinensis* has a broad, low and rounded mono-cuspid symmetric crown and smooth extern and intern sides.

## Biological characteristics of the Genus Corysodon

The diverse skeletons allow\* supposing that these sharks were in possession of five pairs of gill slits and two dorsal fins without spines.

\*Observed only on one specimen under oblique lighting.

#### Conclusion

The attribution of this taxon to the Order Carcharhiniformes by Cappetta (2006: p.:14 and 2012: p.: 317) seems more than dubious to the senior-author, but its consideration as one of the most primitive representatives of the Order Orectolobiformes (*sensu lato*), such as suggested by de Saint-Seine (1949: p.: 18) reactivates phylogenetic reflections.

In 1949, p.18, Pierre de Saint-Seine wrote: Nous pensons que Corysodon peut être considéré provisoirement comme un Orectolobidé très primitif, peut-être à la souche de plusieurs genres fossiles et actuels tels que Ginglymostoma and Nebrodes\* or: We think that Corysodon may temporarily be considered as a very primitive Orectolobidae, maybe the ancestor of many fossil and living Genera such as Ginglymostoma and Nebrodes\*.

\* Nebrodes GARMAN, 1913 is a junior synonym of Nebrius RÜPPEL, 1837.

## Genus Eostegostoma HERMAN, 1977 in NOLF & TAVERNE, 1977

According to Cappetta (2006: p.: 304 and 2012: p.: 165), this Genus remains only represented by its generotype: *Eostegostoma angustum* HERMAN, 1977 *in* NOLF & TAVERNE, 1977.

Numerous teeth\* of its type-species were discovered in diverse localities and levels of the Middle Eocene of Belgium and northern France and southern England and recently\*\* in a level of Upper Eocene Age of Eastern Flanders Province (Belgium).

\*More than 200, providing no significant information concerning their morphology. \*\*Summer 2013, by two field friends of the senior-author.

The lower jaw of the individuals of *Eostegostoma angustum* possessed one symphyseal tooth row constituted by very narrow and perfectly symmetric teeth.

For original reference, see: Nolf & Taverne 1977: p.: 133, fig.: 4 and pl.: 1, figs.: 3a-3c.

## Odontological characteristics of the Genus Eostegostoma

#### **Dental root**

The dental root of all the teeth of its generotype and single species is hemiaulacorhyzid and possesses a massive and elongated medio-intern protuberance flanked by two short and narrow flat root lobes.

#### **Dental crown**

The dental crown of the teeth of its generotype and single species presents an elongated and relatively narrow cuspid, which may be preceded by a very short cuspid on the lateral tooth of the lower jaw.

Both extern and intern sides of their crown are strongly convex and absolutely smooth. The base of their elongated apron\* is straight (anterior teeth) to rounded and oblique (lateral teeth).

\*All the teeth of the extant Genus *Stegostoma* present an apron with a short median extension giving them a tri-lobed morphology.

#### Conclusion

Some odontological characteristics of the Genus *Eostegostoma* seem to confirm its validity and all its other

odontological characteristics justify its attribution, particularly the strong lateral compression of their teeth, to the Family Stegostomatidae GILL, 1862 and not to the Family Brachaeluridae APPLEGATE, 1974, such as suggested by Cappetta (2012: p.: 165).

This fossil Genus may be considered as the direct ancestor of the Genus Stegostoma MÜLLER & HENLE, 1837.

The strong lateral compression of their teeth is an odontological characteristic they have in common with the teeth of the extinct Genus *Palaeorhincodon* HERMAN, 1974 and the extant Genus *Rhincodon* SMITH, 1829.

Biologically, it is interesting to point out that the two only extant Genera: *Stegostoma* and *Rhincodon*, having strongly laterally compressed teeth, are also in possession of long anterio-posterior dorsal keels.

Such keels exist on the body of the extant Brachaelurus, but they are less pronounced.

For original reference, see:

Herman 1977 in Nolf & Taverne 1977: p.: 133, fig.: 4 and pl.: 1, figs.: 3a-3c.

## Genus Protoginglymostoma HERMAN, 1977

This extinct Genus is based on *Ginglymostoma ypresiensis* CASIER, 1946 discovered in the Upper Ypresian of the Brussels Regio and, later, discovered at Baelegem (Eastern Flanders, Belgium) and also at Egem (Western Flanders, Belgium), in Upper and Lower Ypresian strata.

According to Cappetta (2006: p.: 361), this Genus includes also the two following taxa: *P. bighornensis* CASE, 1987 and *P. estesi* HERMAN, 1977.

For references, see: Casier 1946 p.: 61, pl.: 1, figs.: 2a-2d, Cappetta 2006: p.: 254, Cappetta 2012: p.: 174-175, fig.: 163 and Herman 1977 p.: 134.

## Odontological characteristics of the Genus Protoginglymostoma

## **Dental root characteristics**

The dental root of the teeth of these two fossil taxa: Hemiaulacorhyzid step, medio-intern protuberance highly developed, flanked by very short root lobes.

#### **Dental crown characteristics**

The dental crown of the teeth of these two fossil taxa: The intern side of their low and large crown is absolutely smooth; all the teeth present one or two pairs of low and rounded cusplets. The extern side of their low and large dental crown presents short inclined costulae.

Their apron is very low and large. Its width represents half of the width of the crown and presents a median arched concave form.

## Remark

After the development of the knowledge of the dentition of the extant taxa of the Family Orectolobidae (*sensu lato*), Dr. Edgard Casier completely agreed with the proposal of the Genus *Protoginglymostoma*, based on one of the numerous taxa of which he was the inventor.

The lower jaw of the individuals of *Protoginglymostoma ypresiensis* possessed, apparently, one symphyseal tooth row constituted by narrower and perfectly symmetric teeth.

The senior-author considers the Genus *Protoginglymostoma* as a member of the Family Ginglymostomatidae GILL, 1862 and as a possible link between the extinct Genus *Plicatoscyllium* CASE & CAPETTA, 1997 and the extant Genus *Ginglymostoma* MÜLLER & HENLE, 1837.

## Paleodistribution of the Genus Protoginglymostoma and the Genus Plicatoscyllium

The distribution of the diverse fossil populations of the Genus *Protoginglymostoma* is restricted to the Lower and Upper strata of the Eocene of the central part of Europe and the northern part of Africa.

The distribution of the diverse fossil populations of the Genus *Plicatoscyllium* is far more extended. This one included Campanian and Maastrichtian deposits of North Africa, East Africa, the Middle East, the western Indian Ocean and the Atlantic coasts of North America.

#### Conclusion

The Genus *Protoginglymostoma* may be considered as the ancestor of the Genus *Plicatoscyllium* and as a member of the same Family Ginglymostomatidae GILL, 1862 from which the teeth of its type Genus *Ginglymostoma* differ only by the lack of any ornamentation on the extern side of their dental crown.

The three Genera *Protoginglymostoma*, *Plicatoscyllium* and *Ginglymostoma* are supposed to have formed a phylogenetical lineage marked by the sudden destruction of the part of their genetic code inducing the formation of an ornamentation on the extern side of their dental crown.

Considering the very large geographic distribution of the last representatives of the Genus *Plicatoscyllium*, this genetic event may be an indicator of the very large dispersal and the intensity of this phenomenon, which may correspond to the end of the Cretaceous period.

For original reference and figuration, see: Herman 1977: p.: 134.

## Protoginglymostoma bighornensis (CASE, 1987) or Brachaelurus bighornensis CASE, 1987

This taxon is represented by isolated teeth discovered in the Mesa Verde Formation (Upper Campanian) of the Washakie County (Wyoming, U.S.A).

The senior-author agrees with its attribution to the Genus Protoginglymostoma HERMAN, 1977.

For original reference, see: Case 1987: p.: 20, pl.: 6, figs.: 1 to 6.

#### Protoginglymostoma estesi (HERMAN, 1977) or Mesitea estesi HERMAN, 1977

This taxon is represented by isolated teeth discovered in the Lance Formation (Maastrichtian) in the Wyoming State (U.S.A.). The senior-author agrees with its attribution to the Genus *Protoginglymostoma* HERMAN, 1977.

After having discovered hundreds and hundreds of teeth in its type locality, the senior-author is sure that the lower jaw of the individuals of *Protoginglymostoma estesi* possessed one symphyseal teeth row constituted by lightly narrower and perfectly symmetric teeth.

For original reference, see: Herman 1977: p.: 148 (described as *Mesitea estesi*)

## Genus Cretorectolobus CASE, 1978

According to Cappetta (2012: p.: 160), this Genus regroups the four following extinct species: *C. olseni* CASE, 1978, *C. microcuspidatus* (CASE, 1978), *C. doylei* UNDERWOOD, MITCHELL & VELTCAMP, 2003 and *C. robustus* UNDERWOOD & CUMBAA, 2010.

*Cretorectolobus havreensis* HERMAN, 1977 is not included in this list. Later, this taxon was attributed to the Genus *Cederstroemia* SIVERSON, 1995, which was attributed to the Family Orectolobidae before its present emendation.

The senior-author insists on the fact that *C. havreensis* (HERMAN, 1977) represents a very primitive form of the Family Squatinidae (Order Squatiniformes *sensu* COMPAGNO, 1973).

For references, see: Cappetta 2006: p.: 296, Cappetta 2012: p.: 159-160, Case 1978: p.: 188 and Siverson 1995.

#### **Odontological characteristics of the Genus** *Cretorectolobus*

#### **Dental root characteristics**

All the teeth of the diverse taxa attributed to this Genus present a thick hemiaulacorhyzid dental root with two

short root lobes, a very wide medio-intern protuberance and a short rounded apron.

#### **Dental crown characteristics**

All the teeth of the diverse taxa of this Genus present a monocuspid smooth crown with a short rounded apron and a large medio-intern protuberance.

#### Conclusion

The teeth of the two extinct Genera: Genus *Cerastodermia* SIVERSON, 1995 and Genus *Cretorectolobus* CASE, 1978 present a remarkable morphological continuity with the teeth of the extant Genus *Squatina* DUMERIL, 1806.

This model proposes the progressive transformation of sharks in possession of monocuspid teeth having a dental root with a horizontal base and a low inclined crown followed by sharks in possession of monocuspid teeth having a lightly arched root and a higher straight crown to sharks in possession of monocuspid teeth having a strongly arched root and an elongated straight crown.

The lower jaw of the individuals of the Genus *Cretorectolobus* possessed, apparently, one symphyseal tooth row constituted by narrower and perfectly symmetric teeth.

All the odontological characteristics of the Genus *Cretorectolobus* CASE, 1978 (*sensu stricto*) allow considering this taxon as a primitive member of the Family Squatinidae BONAPARTE, 1838.

## Spatio-temporal distribution of the Genus Cretorectolobus

This Genus is represented by three northern American species: *C. olsoni* CASE, 1978, *C. microcuspidatus* (CASE, 1978) and *C. robustus* UNDERWOOD & CUMBAA, 2010, all of Upper Cretaceous Age.

The taxon *C. gracilis* UNDERWOOD & MITCHELL, 1999, represented by isolated teeth discovered in a level of Lower Albian age in England, seems to need an attribution to another Genus than to the Genus *Cretorectolobus* CASE, 1978 (For explanation: see further).

The odontological characteristics of the species *Cretorectolobus doylei* UNDERWOOD, MITCHELL, VELTCAMP & KEES, 2003 allow supposing that this one could be the oldest known representative of the Genus *Orectolobus* BONAPARTE, 1834.

#### Cretorectolobus olseni CASE, 1978

This species is based on isolated teeth discovered in the Judith River Formation (Campanian, Upper Cretaceous) in Blaine County (Montana, U.S.A.).

For original reference, see: Case 1978: p.: 188, p.: 189: figs.: 9 and 10 and pl.: 3, figs.: 1 and 2.

#### Cretorectolobus microcuspidatus (CASE, 1978) or Eucrossorhinus microcuspidatus CASE, 1978

This species is based on isolated teeth discovered in the Judith River Formation (Campanian) of Blaine County (Montana, U.S.A.).

For original reference, see: Case 1978: p.: 187: fig.: 8 and pl.: 2, figs.: 6 and 7.

#### Cretorectolobus doylei UNDERWOOD, MITCHELL, VELTCAMP & KEES, 2003

This species is based on isolated teeth discovered in the Specton Clay Formation (Hauterivian, Lower Cretaceous) in Yorkshire (England, Great Britain).

It is difficult to admit that these teeth could be fossil representatives of the Genus *Cretorectolobus sensu stricto*, because small benthic coastal Chondrichthyes were unable to cross oceanic trenches, and at this epoch, the North Atlantic Ocean represented a large area marked by eight to ten trenches deeper than thousand metres.

For original reference, see: Underwood, Mitchell, Veltcamp & Kees 2008: 293, pl. 2: figs: 1 and 3, pl.:9, figs.: 9 to 11.

#### Cretorectolobus robustus UNDERWOOD & CUMBAA, 2010

This species is based on isolated teeth discovered in a bone bed of the Cenomanian (Late Cretaceous), in Saskatchewan (Canada).

For original reference, see: Underwood & Cumbaa, 2010.

#### Genus Orectoloboides CAPPETTA, 1979

According to Cappetta 2006 (pp.: 341-342), this Genus regrouped the six following extinct species: *O. parvula* (DALINKEVICIUS, 1935), *O. glashoffi* THIES, 1981, *O. pattersoni* THIES, 1983, *O. multistriatus* WERNER, 1989, *O. reyndersi* ADNET, 2000 and *O. gijseni* HERMAN & VAN DEN EECKHAUT, 2010.

According to Cappetta 2012 (p.: 161), only the two\* following taxa remained representatives of this Genus: *O. parvula* (DALINKEVICIUS, 1935) and *O. multistriatus* WERNER, 1989.

\*Without argumentation and ignoring the two last ones proposed: *O. reyndersi* ADNET, 2000 and *O. gijseni* HERMAN & VAN DEN EECKHAUT, 2010.

## Odontological characteristics of the Genus Orectoloboides

## **Dental root characteristics**

All the teeth of the two taxa of this Genus present a root with an evolved hemiaulacorhyzid structure, very short root lobes and a triangular apron, rounded at its extremity.

#### **Dental crown characteristics**

All the teeth of the two taxa of this Genus have a relatively low crown presenting one principal cuspid flanked by one (anterior teeth) or two (lateral teeth) pairs of cusplets.

The senior-author has observed on teeth discovered in the Albian strata\* of the Aube Department (France) that on commissural teeth one additional cusplet may be observed on their posterior extremity.

\*Thanks to the information concerning the fluctuations of the water level, monthly furnished, by some engineer friends responsible for the Der Water Reserve, the senior-author had the possibility to sieve more than five cubic meters of one precise level of the Albian.

#### Conclusion

All the odontological characteristics of the Genus *Orectoloboides sensu* Cappetta 2012 allow suggesting that this Genus could be regrouped with the four other fossil Genera: Genus *Hologinglymostoma* NOUBHANY & CAPPETTA, 1997, Genus *Eometlaouia* NOUBHANY & CAPPETTA, 2002, Genus *Ornatoscyllium* UNDERWOOD & WARD, 2004 and, as possible oldest representative, Genus *Palaeorectolobus* KRIWET, 2008 and that it constitutes a distinct lineage of the Family Ginglymostomidae GILL, 1862.

The lower jaw of the individuals of the Genus *Orectoloboides* possessed, apparently, one symphyseal tooth row constituted by small, very compressed and more or less dissymmetric teeth.

The lack of examinable material of numerous specific taxa of this proposed lineage obliges the senior-author to give his opinion but does not allow him to propose a Family name distinguishing this orectolobid group.

## Spatio-temporal distribution of the Genus Orectoloboides

This Genus is represented by numerous isolated teeth discovered in different levels of Callovian Age (uppermost part of the Middle Jurassic to Upper Lutetian Age of central Europe.

The teeth discovered in the Middle Cenomanian of Kansas (U.S.A.)\* are not representatives of the Genus *Orectoloboides* because these benthic littoral sharks are unable to cross oceanic trenches.

\*See Bibliography: Bourdon & Everhart 2010.

#### Orectoloboides parvula (DALINKEVICIUS, 1935) or Ginglymostoma parvula DALINKEVICIUS, 1935

This species is based on isolated teeth discovered in Albian strata (Upper Cretaceous) of Lituania. This species is

also a common species of all the Upper Albian strata of northern France and was sporadically encountered in southern England (Great Britain).

For original reference, see: Dalinkevicius 1935: p.: 155, pl.: 12, figs.: 37 to 39.

## Orectoloboides glashoffi THIES, 1981

This species is based on isolated teeth discovered in the Upper Aptian (Lower Cretaceous) of Hannover (Germany).

This species was considered by Cappetta (2006: p.: 342) as a representative of the Genus *Orectoloboides*, but later reconsidered (2012: p.: 161) as a representative of the Genus *Ornatoscyllium* UNDERWOOD & WARD, 2004.

For original reference, see: Thies 1981: p.: 479 and p.: 483: fig.: 7.

## Orectoloboides pattersoni THIES, 1983

This species is based on isolated teeth discovered in the Oxford Clay Formation (Callovian) of southern England (Great Britain) and also from the Callovian of the cliffs of Normandy\* (France).

\*Material collected by the senior-author between 1969 and 1972.

For original reference, see: Thies 1983: p.: 40, pl.: 11, figs.: 1 to 4.

#### Orectoloboides multistriatus WERNER, 1989

This species is based on isolated teeth discovered in the Upper Cenomanian (Upper Cretaceous) of the Djebel District (Egypt).

For original reference, see: Werner 1989: p.: 26: fig.: 9, pl.: 9, figs.: 1 and 2, pl.: 10, figs.: 1 to 3.

#### Orectoloboides reyndersi ADNET, 2000

This species is based on isolated teeth discovered in the Middle Lutetian (Middle Eocene) of the Aquitaine Basin (south western France).

#### Systematics remark

Once again, Cappetta considered (2006: p.: 195) this taxon as a *nomen nudum* because it was described in a PhD Thesis.

The senior-author disagrees with this attitude concerning major University documents which are protected by precise National and European laws. It was possible to obtain a part or the whole copy of such document, after authorisation of the author.

For original reference, see: Adnet 2000: p.: 60, pl.: 16, figs.: 1 to 3.

## Orectoloboides gijseni HERMAN & VAN DEN EECKHAUT, 2010

This species is based on isolated teeth discovered in the Sands of Brussels Formation and the Basal gravel of the Sands of Lede Formation (Middle and Upper Eocene) in the Flemish Brabant Province (Belgium).

For original reference, see: Herman & Van Den Eeckhaut 2010: p.: 45, pls.: 54-55.

#### Systematics remark

The teeth of this taxon are very similar to the teeth of *Orectoloboides reyndersi* ADNET, 2000 and its Upper Eocene population may have constituted the last Nordic survivals of this species.

The fact that Cappetta (2006: p.: 195) considered *O. reyndersi* ADNET, 2000 as a *nomen nudum* and did not mention this taxon in his revised Handbook (2012: p.: 161) confirms the validity of *O. gijseni* HERMAN & VAN DEN EECKHAUT, 2010.

Consequently, O. reyndersi, so perfectly described by Sylvain Adnet, may only represent a possible ancestral population of O. gijseni.

## Genus Squatiscyllium CAPPETTA, 1980

According to Cappetta (2012: pp.: 162-163), this Genus is mono-specific and based on the single species S. *nigeriensis* (WHITE, 1934).

Before 2012, S. casieri (ARAMBOURG, 1952) was considered as a second species of this Genus, but this taxon was selected, in 1997, by Noubhany and Cappetta to be the holotype of an additional new Genus Metlaouia.

They were obliged, five years later, to change it into *Eometlaouia*.

## Odontological characteristics of the Genus Squatiscyllium

## **Dental root characteristics**

Their dental root presents a hemiaulacorhyzid structure, two short root lobes in arched position (anterior teeth), two large root lobes in a virtual horizontal position (lateral teeth) and two elongated root lobes in a horizontal position (posterior and commissural teeth).

Their medio-intern root protuberance is short (anterior teeth) to moderately elongated (posterior and commissural teeth).

## **Dental crown characteristics**

The intern side of their dental crown is absolutely smooth, but their extern side presents a lot of very fine vertical costulae (anterior teeth) decreasing in number and height on the lateral teeth.

The extern side of the crown of their commissural teeth may be completely smooth.

## **Biological characteristics of the Genus** *Squatiscyllium*

Without skeletons it is only the invertebrates remains, discovered in the same levels, which allow supposing that *Squatiscyllium nigeriensis* (WHITE, 1934) was an inhabitant of shallow bottoms in coastal and warm waters.

#### Conclusion

The senior-author considers this generic taxon as a Genus that could be intermediary between the Orecto-lobiformes (*sensu stricto*) \* and the Orectolobiformes (*emend*) \*.

\*For explanations of this distinction: See further.

The presence of an obvious ornamentation on the extern side of the crown of the anterior and lateral teeth of the taxa of the Genus *Squatiscyllium* seems to indicate a narrow phyletic relationship with the primitive members of the Family Ginglymostomatidae GILL, 1862.

## Spatio-temporal distribution of the Genus Squatiscyllium

The two representatives of this fossil Genus: *S nigeriensis* (WHITE, 1934) and *S. casieri* (ARAMBOURG, 1952) are north African taxa known from the Upper Paleocene and the Lower Eocene.

## Squatiscyllium nigeriensis (WHITE, 1934) or Squatina nigeriensis WHITE, 1934

This species is based on isolated teeth discovered in the Thanetian of the Sokoto Basin (Nigeria).

For original reference, see: White 1934: p.: 26, pl.: 2, figs.: 1 to 6.

## Squatiscyllium casieri (ARAMBOURG, 1952) or Squatirhina casieri ARAMBOURG, 1952

This species is based on isolated teeth discovered in the Lower Ypresian of the Ouled Abdoun Basin (Morocco).

For original reference, see: Arambourg 1952: p.: 144, pl.: 22: fig.: 64 and text-fig.: 29.

## Genus Almascyllium CAPPETTA, 1980

According to Cappetta (2006: p.: 275) and (2012: pp.: 155-156), this Genus regroups the two following species: *A. sahelalmae* (PICTET & HUMBERT, 1866) and *A. cheikeliasi* (SIGNEUX, 1949). These two species are based on skeletons.

## Odontological characteristics of the Genus Almascyllium

#### **Dental root characteristics**

All the teeth of the two species attributed to this extinct Genus have a hemiaulacorhyzid root presenting a well developed medio-intern protuberance, flanked by two short root lobes.

## **Dental crown characteristics**

All the dental crowns of the teeth of the two species attributed to this extinct Genus possess a central elongated cuspid flanked by a pair\* of short cusplets and present two to twelve short and delicate enamel folds.

\*On posterior teeth, the posterior cusplet may be partially integrated in the crown.

The apron is very large. Its base is rectilinear (anterior teeth), rounded (lateral teeth) or oblique (posterior teeth).

## Biological characteristics of the Genus Almascyllium

The diverse skeletons examinable of this taxon allow confirming that the individuals of the two taxa of this Genus were in possession of five pairs of gill slits, two dorsal fins without spines and that all their vertebrae present a circular transversal section.

They also possess two short nasal cartilaginous extensions, which may be interpreted as the central support elements of a very short rostrum\* (representing a maximum of one fifteenth of the total length of the individual).

\*Without rostral teeth.

#### Conclusion

Cappetta considered the Genus *Almascyllium* as a member of the Family Hemiscylliidae GILL, 1862. The seniorauthor agrees with this opinion, which makes of this Genus a possible common ancestor of the two extant Genera regrouped in this Family: Genus *Hemiscyllium* MÜLLER & HENLE, 1837 and Genus *Chiloscyllium* MÜLLER & HENLE, 1837.

The fact that the two representatives of this Genus possess also a very short rostrum allows suggesting that the extinct Genus *Almascyllium* was also genetically related to the earlier representatives\* of the saw-sharks: the Order Pristiophoriformes BERG, 1958.

\*Such as the valid Genus Propristiophorus WOODWARD, 1832. See further: Chapter: Fossil Pristiophoriformes.

## Spatio-temporal distribution of the Genus Almascyllium

The two fossil representative species of this Genus were discovered in Lebanon, in levels ranging from the Lower to the Upper Santonian (Upper Cretaceaous of the Near-East).

#### Acanthoscyllium sahelalmae (PICTET & HUMBERT, 1866) or Scyllium sahelalmae PICTET & HUMBERT, 1866

This species is represented by skeletons\*, and isolated teeth\*, discovered in the Upper Santonian (Upper Cretaceous) of Sahel Alma (Lebanon).

\*One other skeleton and about ten isolated teeth in a Private Collection that the senior-author had the possibility to examine at the end of December 1973 at Beyrouth (Lebanon).

## For original reference, see: Pictet & Humbert 1866: p.: 111, pl.: 18, figs.: 2 to 4.

## Almascyllium cheikeliasi (SIGNEUX, 1949) or Chiloscyllium cheikeliasi SIGNEUX, 1949

This species is based on a skeleton discovered in a level marking the transition between the Lower and Middle Santonian (Upper Cretaceous) of northern Lebanon.

## For original reference, see: Signeux 1949: p.: 636, fig.: 2.

#### Remark

It is interesting to note that, despite any fundamental knowledge concerning the dentition of extant generic taxa represented by small animals, François Pictet understood in 1866 the suppleness of these fossil animals, comparing them to the extant cat-sharks (Family Scyliorhinidae) and that in 1952 Jeanne Signeux was able to precise their phylogenetic position (Family Hemiscylliidae).

## Genus Paraginglymostoma HERMAN, 1982

According to Cappetta (2006: p.: 350), this extinct Genus is only based on its type species *Paraginglymostoma bloti* HERMAN, 1982, discovered in the Lower Maastrichtian of northern Germany.

The senior-author considers the Genus *Paraginglymostoma* as a member of the Family Ginglymostomatidae.

## Genus Palaeobrachaelurus THIES, 1983

According to Cappetta (2006: p.: 346), this extinct Genus is based on its type species *Palaeobrachaelurus bed-fordensis* THIES, 1983, discovered in the Callovian in southern England, and also includes the four following extinct taxa: *P. alisonae* THIES, 1983 from the Callovian of southern England, *P. aperizotus* THIES, 1983 from the Upper Aalenian of northern Germany, *P. mitchellli*\* UNDERWOOD, 2004 from the Middle Barremian of southern England and *P. mussetti* UNDERWOOD & WARD, 2004 from the Bathonian of southern England.

\*Considered as a member of the Genus Hemiscyllium of the Family Hemiscylliidae by Thies.

The morphology of the apron and the crown of the teeth of all the taxa of this extinct Genus induce the seniorauthor of this Publication to consider the Genus *Palaeobrachaelurus* as a member of the extinct Family Phorcynidae nov. Family, based on the Genus *Phorcynis* THIOLLIERE, 1854, formerly represented by its single type species *Phorcynis catulina* THIOLLIERE, 1854.

The Genus *Palaeobrachaelurus* is considered as a member of the Family Hemiscylliidae by Thies, but as a member of the Family Brachaeluridae by Cappetta (2006 and 2012).

In addition, the morphology of the apron and the crown of the teeth of all the taxa of this extinct Genus induce the senior-author of this Publication to consider the Genus *Palaeobrachaelurus* as a member of an extinct Order: the Order Phorcyniformes nov. Ord.

This Order Phorcyniformes nov. Ord. will be based on the Family Phorcynidaenov. Fam., based on the Genus *Phorcynis* THIOLLIERE, 1854, formerly represented by its single type species *Phorcynis catulina* THIOLLIERE, 1854.

## Odontological characteristics of the Genus Palaeobrachaelurus

## **Dental root characteristics**

The dental roots of the two species attributed to this Genus are hemiaulacorhyzid and possess a very wide medio -intern protuberance (anterior teeth) to a very narrow medio-intern protuberance (posterior teeth), flanked by one pair of short root lobes forming an arch (anterior teeth) to elongated root lobes horizontally extended (posterior teeth).

The differences observed by the senior-author between the root characteristics of the three taxa attributed to the Genus *Palaeobrachaelurus* accessible for him: *P. alisonae* THIES, 1983, *P. aperizotus* THIES, 1983 and *P. bedfordensis* THIES, 1983 are insignificant.

#### **Dental crown characteristics**

The dental crowns of the different species attributed to this Genus present absolutely smooth extern and intern sides. According to the species or their position in the jaw, they may possess one or two pairs of large lateral cusplets. The commissural teeth sometimes lack\* lateral cusplets.

\*In this case, it is difficult to distinguish these ones from commissural teeth of the Genus *Squatina* or of the Genus *Orectolobus*. Consequently this Genus could be related with the primitive squatinids.

The differences\* observed by the senior-author between the crown characteristics of the three taxa attributed to the Genus *Palaeobrachaelurus* accessible for him: *P. alisonae* THIES, 1983, *P. aperizotus* THIES, 1983 and *P. bedfordensis* THIES, 1983 are sufficiently obvious to allow considering that they represent well diversified populations.

\*Number of pairs of lateral cusplets, variability of the morphology of their apron and variability of the ornamentation of their crown.

## **Biological characteristics of the Genus** *Palaeobrachaelurus*

The invertebrates discovered in the same levels confirm that the environment was this of very shallow and warm marine waters.

#### Conclusion

The senior-author agrees with the proposal of Cappetta (2012: p.: 165) that the diverse species of the Genus *Pa-laeobrachaelurus* are representative taxa of a primitive Genus of the Family Brachaeluridae APPLEGATE, 1974.

## Spatio-temporal distribution of the Genus Palaeobrachaelurus

The remains of the taxa attributed to this extinct Genus were discovered in levels ranging from Bathonian and Callovian Age (Jurassic) to Barremian Age (Lower Cretaceous) from southern England.

## Palaeobrachaelurus alisonae THIES, 1983

This species is represented by numerous isolated teeth discovered in a Callovian level of southern England and, later, by hundreds of perfectly preserved isolated teeth discovered at Aubange (Luxembourg Province, Belgium).

For original reference, see: Thies 1983: p.: 36, pl.: 10, figs.: 1 to 6.

## Palaeobrachaelurus aperizostus THIES, 1983

This species is represented by isolated teeth discovered in Upper Aalenian of Hannover (northern Germany).

For original reference, see: Thies 1983: p.: 33, pl.: 8: figs.: 3 to 5 and pl.: 9: fig.1.

## Palaeobrachaelurus bedfordensis THIES, 1983

This species is represented by isolated teeth discovered in the Callovian of southern England (Great Britain).

For original reference, see: Thies 1983: p.: 35, pl.: 9, figs.: 2 to 6.

## P. mitchellli UNDERWOOD, 2004

This species is represented by isolated teeth discovered in the Middle Barremian of southern England (Great Britain).

For original reference, see Bibliography -Systematics: Underwood 2004: p.: 112, p.: 110: fig.: 3.

#### Palaeobrachaelurus mussetti UNDERWOOD & WARD, 2004

This species is represented by isolated teeth discovered in the Bathonian of southern England (Great Britain).

For original reference, see: Underwood & Ward 2004: p.: 406, pl.5: figs.: 10 to 14.

## Genus Annea THIES, 1983

This Genus regroups the two following extinct species: *Annea carinata* THIES, 1983 and *Annea maubeaugei* DELSATE & THIES, 1995.

This Genus was considered by Cappetta (2006: p.: 114 and 2012: p.: 177) as an Orectolobiformes incertae fam.

#### Odontological characteristics of the Genus Annea

#### **Dental root characteristics**

The dental roots of the two species attributed to this extinct Genus are hemiaulacorhyzid and present a poorly developed medio-intern protuberance.

#### **Dental crown characteristics**

The dental crowns of the two species attributed to this extinct Genus possess a pro-eminent, massive and rounded apron. One high cuspid is flanked by one or two pairs of lateral cusplets, the last ones being very small.

The ornamentation of the crown consists in a single vertical keel on its extern side.

#### Conclusion

The odontological characteristics of the Genus *Annaea* THIES, 1983 allow considering this taxon as a member of the Family Phorcindae nov. Fam.

#### Spatio-temporal distribution of the Genus Annaea

The remains of the taxa attributed to this extinct Genus were discovered in levels ranging from Bathonian Age (Jurassic) to Barremian Age (Lower Cretaceous) of southern England.

#### Annea carinata THIES, 1983

This species is based on isolated teeth discovered in Middle Jurassic strata from the Lower Saxony (Germany).

For original reference, see: Thies 1983: p.: 39, pl.: 10: fig. 7.

## Annea maubeaugei DELSATE & THIES, 1995

This species is based on hundreds, perfectly preserved, isolated teeth discovered in the Middle Toarcian of Aubange (Luxembourg Province, Belgium).

For original reference, see: Delsate & Thies 1995: p.:48 and pl.: figs.: 1 to 8.

## Genus Pseudoginglymostoma DINGERKUS, 1986

The synonymisation of this fossil Genus with the extant Genus *Ginglymostoma* MÜLLER & HENLE, 1837 was proposed by Dingerkus in 1986 and accepted by some paleontologists but, of course, contested by the majority of the biologists and paleontologists.

This contestation is based on the fact that Dingerkus had never examined the teeth of any Orectolobidae, but only their general morphology and particularly their dermal denticles, which are not reliable specific determination tools.

The morphology of the dermal denticles varies largely in function of their position. The functions of these denticles are to protect the body and to enhance the hydraulic performance when swimming.

For original reference, see: Dingerkus 1986: p.: 240.

This Genus is represented by the two following fossil taxa: *P. erguitaense* NOUBHANI & CAPPETTA, 1997 and *P. idiri* NOUBHANI & CAPPETTA, 1997.

For references, see: Cappetta 1987, Cappetta 2006, Cappetta 2012, Dingerkus 1986, Nhoubani & Cappetta 1997.

## Odontological characteristics of the Genus Pseudoginglymostoma

#### **Dental root characteristics**

The dental roots of the teeth of the two fossil taxa of the Genus *Pseudoginglymostoma* are hemiaulacorhyzid, have an arched base and possess a relatively discrete medio-intern protuberance flanked by two short root lobes.

#### **Dental crown characteristics**

The dental crowns of the teeth of the two fossil taxa of the Genus *Pseudoginglymostoma* are constituted by a large, sub-triangular central cuspid flanked by one pair of lateral cusplets.

The large base of their apron is curved, enhancing its similarity with this of juvenile specimens of the extant species *Ginglymostoma brevicaudatum* of the Genus *Ginglymostoma* MÜLLER & HENLE, 1837.

Consequently, for some paleontologists, the extinct taxon *Pseudoginglymostoma* is a synonym of the extant Genus *Ginglymostoma* MÜLLER & HENLE, 1837.

#### **Biological characteristics of these two fossil species**

Without skeletons it is only the invertebrate remains, discovered in the same levels, which allow supposing that the representatives of the Genus *Pseudoginglymostoma* were inhabitants of shallow bottoms in coastal and warm waters.

## Conclusion

These two fossil taxa may be considered as members of the Genus *Pseudoginglymostoma* DINGERKUS, 1986 of the Family Ginglymostomatidae GILL, 1862 and are surely potential ancestors of the extant Genus *Ginglymostoma* MÜLLER & HENLE, 1837

## Spatio-temporal distribution of the Genus Pseudoginglymostoma

Teeth of this Genus were discovered in different levels of Lower to Upper Maastrichtian Age of North Africa.

#### Pseudoginglymostoma erguitaense NOUBHANI & CAPPETTA, 1997

This species is represented by numerous isolated teeth discovered in the Lower Maastrichtian of the Basin of Souss (Morocco). The senior-author never had the possibility to examine any specimen of this species.

For original reference, see:

Noubhani & Cappetta 1997: p.:44, pl.: 17, figs.: 1 to 6.

#### Pseudoginglymostoma idiri NOUBHANI & CAPPETTA, 1997

This species is represented by isolated teeth discovered in the Upper Maastrichtian of the Basin of the Ouled Abdoun (Morocco).

A French friend gave the senior-author 16 teeth of this species, collected in the same locality (Beni Idir).

For original reference, see: Noubhani & Cappetta 1997: p.: 45, pl.:18: figs.: 1 to 8.

#### Genus Cederstroemia SIVERSON, 1995

This extinct Genus regroups the three following taxa: C. havreensis (HERMAN, 1977), C. triangulus SIVERSON, 1995 and C. nilsi SIVERSON, 1995.

## Odontological characteristics of the Genus Cederstroemia

#### **Dental root characteristics**

All the teeth of the diverse taxa of this Genus present a hemiaulacorhyzid root and a wide and massive medio-

intern protuberance flanked by two root lobes. According to their specific attribution and their position in the jaw, the base of their root is more or less arched.

#### **Dental crown characteristics**

All the teeth of the diverse taxa of this Genus present a massive central cuspid\*, sometimes flanked by a pair of large but very low cusplets. Their apron is short and large, with an oval horizontal section.

\*All the teeth of *C. havreensis* (HERMAN, 1977) are strictly monocuspid and have a shorter medio-intern protuberance and an elongated apron with a circular section. These data make the attribution of this taxon to the Genus *Cederstroemia* questionable.

## Biological characteristics of the Genus Cederstroemia

Without skeletons it is only the invertebrate remains, discovered in the same levels, which allow supposing that all\* the representatives of the Genus *Cederstroemia* were inhabitants of shallow bottoms in coastal and warm waters.

\*This remark is also valid for *C. havreensis* (HERMAN, 1977).

## Spatio-temporal Distribution of the Genus Cederstroemia

The oldest fossils attributed to this Genus are of Albian Age (Europe and central Asia) and its more recent representatives are of Upper Campanian Age (Europe: Belgium, France, England and North America).

## Conclusion

All the odontological data of the specific taxa\* attributed to the Genus *Cederstroemia* induce the senior-author to believe that this Genus may be considered as a member of the Family Orectolobidae JORDAN & FOWLER, 1903.

\*Except for *C. havreensis* (HERMAN, 1977) that the senior-author considers as a primitive member of the Family Squatinidae BONAPARTE, 1838.

## Cederstroemia havreensis (HERMAN, 1977) or Squatina havreensis HERMAN, 1977

Numerous other specimens were later collected from the same level, but also in the basis of the Trivières Chalk Formation and five successive thin horizons in the mass of this Formation, which allowed a better understanding of the evolution of this taxon.

For original reference, see: Herman 1977: p.: 126, pl.: 5, figs.: 4a and 4b.

#### Cederstroemia triangulata SIVERSON, 1995

This species is represented by isolated teeth discovered in a Campanian level of the Judith River Formation (Upper Cretaceous) in the Blaine County (Montana, U.S.A.).

For original reference, see: Siverson 1995: p.: 976, fig.: 1.

## Cederstroemia nilsi SIVERSON, 1995

This species is represented by isolated teeth discovered in an Upper Campanian level of the Kristianstad Basin of Scania (Sweden).

For original reference, see: Siverson 1995: p.: 977, fig.: 2.

## Genus Delpitoscylllium NHOUBANI & CAPPETTA, 1997

This extinct Genus is only represented by its generotype Delpitoscylllium africanum (LERICHE, 1927).

## Odontological characteristics of the Genus Delpitoscylllium

## **Dental root characteristics**

The dental root of the single species representing this extinct Genus is hemiaulacorhyzid and possesses a massive elongated medio-intern protuberance.

#### **Dental crown characteristics**

The dental crown of the single species representing this extinct Genus presents a relatively low principal cuspid adjoined by one or two small lateral cusplets. Its intern side is smooth, but its extern side presents a straight keel in its upper part. This central keel may be absent on posterior and commissural teeth.

The morphology of their apron presents a great variability: tongue-shaped to hemi-circular (anterior teeth), arched (lateral teeth) or lobed (posterior teeth).

## Biological characteristics of the Genus Delpitoscylllium

Without skeletons it is only the invertebrate remains, discovered in the same levels, which allow supposing that all the representatives of the Genus *Cederstroemia* were inhabitants of shallow bottoms in coastal and warm waters.

## Conclusion

The senior-author, like Cappetta (2012: p.: 169) considers the Genus *Delpitoscylllium* as a member of the Family Ginglymostomatidae GILL, 1862, but as a co-lateral representative of one of its oldest lineages.

## Spatio-temporal Distribution of the Genus Delpitoscylllium

The fossils attributed to this Genus are of Danian to Thanetian Ages (North Africa, West Africa and the Middle East).

## Genus Ganntouria NHOUBANI & CAPPETTA, 1997

This extinct Genus is only represented by its holotype G. variabilis NOUBHANI & CAPPETTA, 1997.

## Odontological characteristics of the Genus Ganntouria

## **Dental root characteristics**

The dental root of the single species representing this extinct Genus is hemiaulacorhyzid, its medio-intern protuberance varies from very short to elongated and its root lobes present a high morphological variability.

## **Dental crown characteristics**

The dental crown of the single species representing this extinct Genus possesses one main cuspid flanked by one or two pairs of cusplets. One keel is observable on the upper part of the extern side of the crown.

The base of their apron is generally arched.

## Conclusion

The very high variability of dental morphotypes of this taxon justifies its specific assignation *variabilis*, but allows supposing that, in reality, this taxon regroups two or three different species.

The senior-author thinks further research is needed to assure its validity and to make its attribution to one Family of the Order Orectolobiformes *emend*. possible.

Consequently, the senior-author momentarily considers the generic taxon Ganntouria as not valid.

## Ganntouria variabilis NOUBHANI & CAPPETTA, 1997

This species is represented by numerous isolated teeth discovered in the Upper Maastrichtian of the Ganntour Basin (Morocco).

For original reference, see: Noubhani & Cappetta 1997: p.: 28, pl.: 6, figs.: 1 to 7.

## Genus Hologinglymostoma NHOUBANI & CAPPETTA, 1997

This extinct Genus is only represented by its holotype *H. jaegeri* NOUBHANI & CAPPETTA, 1997.

## Odontological characteristics of the Genus Hologinglymostoma

## General morphology

The teeth of this Genus are wide, their height is equal to their width (anterior teeth) or less than a third of their width (lateral to posterior teeth).

#### **Dental root characteristics**

The dental root of the single species representing this extinct Genus is holaulacorhyzid, its medio-intern root protuberance is poorly developed and, according to the position in the jaw, its base is arched to antero-posteriorly elongated and flat.

Seeing the figurations of the teeth (Noubhani & Cappetta, 1997) attributed to this taxon, the senior-author realized that he had discovered some very lateral (or commissural) hemiaulacorhyzid teeth in Lower Thanetian deposits (of the type area). The senior-author supposes they are attributable to this species.

This, apparently, insignificant fact demonstrates once more that commissural teeth may indicate the ancestral origin of a specific or generic taxon.

## **Dental crown characteristics**

The extern and intern sides of the dental crown of the single species representing this extinct Genus present no vertical fold but an extern, more or less pronounced, horizontal basal swelling\*.

\*This basal swelling may be considered as the simplest physical reaction to the unexplained compaction of the crown.

The apron is difficult to distinguish from the extern base of the crown but it is deeply arched. The dental crown of the diverse specimens known of this taxon presents one principal cuspid adjoined by two to five pairs of cusplets.

## Biological characteristics of the Genus Hologinglymostoma

Once more, without a skeleton it is only the invertebrate remains, discovered in the same levels, which allow supposing that all the representatives of the Genus *Hologinglymostoma* were inhabitants of shallow bottoms in coastal and warm waters.

#### Conclusion

The senior-author agrees completely with the systematic proposal of Cappetta (2012: p.: 172) and the integration of the Genus *Hologinglymostoma* in the Family Ginglymostomatidae GILL, 1862, but wants to point out its morphological singularity, its apparition at the end of the Paleocene and its very restricted spatio-temporal distribution.

## Spatio-temporal distribution of the Genus Hologinglymostoma

This generic taxon is only known by isolated teeth from only one level of the Upper Paleocene of Morocco.

## Hologinglymostoma jaegeri NOUBHANI & CAPPETTA, 1997

This species is based on isolated teeth discovered only in one level of the Upper Paleocene of the Ouled Abdoun Basin (Morocco).

## Genus Plicatoscyllium CASE & CAPPETTA, 1997

This extinct Genus is represented by the eight following taxa: *P. minutum* (FORIR, 1887), *P. lehneri* (LERICHE, 1938), *P. rugosum* (DARTEVELLE & CASIER, 1943), *P. globidens* (CAPPETTA & CASE, 1975), *P. antiquum* CASE & CAPPETTA, 1997, *P. derameei* CASE & CAPPETTA, 1997, *P. rugosum* CASE & CAPPETTA, 1997 and *P. youssoufiaensis* NOUBHANI & CAPPETTA, 1997.

## Odontological characteristics of the Genus Plicatoscyllium

## General morphology

Their anterior teeth are as wide as high; the width of their lateral teeth is greater than their height.

#### **Dental root characteristics**

The dental root of all the teeth of all the taxa of this extinct Genus is hemiaulacorhyzid and presents a massive medio-intern protuberance flanked by two lateral root lobes.

The base of their dental crown is short and arched (anterior teeth), lightly arched (lateral teeth) or elongated and nearly flat (posterior teeth to commissural teeth).

## **Dental crown characteristics**

The intern side of the dental crown of the teeth of all the taxa of this extinct Genus is smooth, but their extern side presents a powerful ornamentation constituted by three to more than twenty-two strong sinuous enamel folds. The more lateral the position of the tooth is, the more numerous and elongated they are.

These enamel folds are located on the upper part of the crown (anterior teeth) but progressively occupy, according to their position in the jaw, the whole central part of the crown (lateral to posterior teeth).

The crown presents a large triangular principal cuspid and three\* pairs of large lateral cusplets.

\*Exceptionally four pairs.

The base of their flat and large apron may be regularly curvy-linear, lightly arched to bi-lobed. Its horizontal top section has always an elongated oval form.

#### Biological characteristics of the Genus *Plicatoscyllium*

Such as for all the taxa represented only by isolated teeth, it is only the invertebrate remains, discovered in the same levels, which allow supposing that all the representatives of the Genus *Plicatoscyllium* were inhabitants of shallow bottoms in coastal and warm waters.

#### Spatio-temporal distribution of the Genus Plicatoscyllium

It is interesting to point out that remains of the Genus *Plicatoscyllium* were only discovered in Maastrichtian strata of both sides of the North Atlantic, in Maastrichtian strata of North Africa and in Maastrichtian strata of central Africa.

Considering the fact that the beginning of the division of the North Atlantic Ocean into two plates dates from the Jurassic-Cretaceous Transition, the distance between the North American Plate and the Eurasian Plate at the end of the Cretaceous must represent, at least, some 2.700 kilometres.

For the nectic predators, such a distance has no importance, but for benthic animals unable to colonize deep waters\* it was impossible to cross the North Atlantic Oceans where the bottom ridges were separated by trenches of thousands of metres depth.

\*All the fossil remains of species attributed to this species were discovered in littoral or coastal sediments.

Consequently, the presence of different populations, or species, of the Genus *Plicatoscyllium* on both sides of the North Atlantic Ocean, during the Maastrichtian, the uppermost Stage of the Upper Cretaceous, implies that their Maastrichtian populations had ancestors living separately in these areas far before that period.

If obvious odontological differences between the three North American species\* and the Eurasian and North African species attributed to the Genus *Plicatoscyllium* were demonstrated, this generic name could be preserved for the American species, but the European and North African species could be considered as representatives of another un-named generic taxon, or as last representatives of the Genus *Cantioscyllium* WOODWARD, 1889.

\*P. derameei CASE & CAPPETTA, 1997, P. antiquum CASE & CAPPETTA, 1997 and P. globidens CASE & CAPPETTA, 1997.

The Genus Cantioscyllium WOODWARD, 1889 was also represented on both sides of the North Atlantic Ocean by

diverse species and could be the phyletic origin of the Genus *Plicatoscyllium* CASE & CAPPETTA, 1997. Its oldest taxon *Cantioscyllium alhaulfi* KRIWET, 1999 was discovered in a level of Lower Barremian Age (Lower Cretace-ous).

Moreover, this fact turns this Genus into a very interesting dating and correlation tool. Its teeth are relatively large and easy to collect in the first phases of continental explorations, preliminary to the positioning of the prospection's bore holes.

## Conclusion

The senior-author completely agrees with the proposal of Cappetta (2012: p.: 173) of the integration of the Genus *Plicatoscyllium* into the Family Ginglymostomatidae GILL, 1862.

The senior-author adds that the Genus *Plicatoscyllium* seems to represent the end of a phyletic ginglymostomid lineage marked by the constant increase of the thickness of the folds constituting the ornamentation on the extern side of their dental crown.

## Plicatoscyllium minutum (FORIR, 1887) or Hybodus minutus FORIR, 1887

This species is based on isolated teeth discovered in the Tuffeau de Maastricht Formation (Maastrichtian) in the Dutch Limburg Province (The Netherlands).

> For original reference, see: Forir 1887: p.: 35, pl.: 2, figs.: 2 and 3.

The senior-author and his field friends have discovered teeth of this species in five different horizons of the same Formation in diverse quarries of the Limburg Province and Liège Province (Belgium).

## Plicatoscyllium lehneri (LERICHE, 1938) or Ginglymostoma lehneri LERICHE, 1938

This species is based on isolated teeth discovered in the Vista Bella Formation (Maastrichtian) of La Trinidad.

According to Herman 1977 and Noubhani & Cappetta 1997, this species is considered as a junior synonym of *Plicatoscyllium minutum* (FORIR, 1887).

## For original reference, see: Leriche 1938: p.: 22, pl.: 4, figs.: 1 to 6.

## Plicatoscyllium rugosum (DARTEVELLE & CASIER, 1943) or Ginglymostoma rugosum DARTEVELLE & CASIER, 1943

This species is based on isolated teeth discovered in the Maastrichtian (uppermost Cretaceous) of central D.R. Congo.

For original reference, see: Dartevelle & Casier 1943: p.: 106, pl.: 3, fig.: 9.

## Plicatoscyllium globidens (CAPPETTA & CASE, 1975) or Ginglymostoma globidens CAPPETTA & CASE, 1975

This species is based on isolated teeth discovered in the Lower Maastrichtian (Upper Cretaceous) of the Monmouth County (New Jersey, U.S.A.).

For original reference, see Bibliography-Systematics: Cappetta & Case 1975: p.: 12, p.: 13: figs.: 6A-6G, pl.: 9: figs.: 24-25.

## Plicatoscyllium antiquum CASE & CAPPETTA, 1997

This species is based on isolated teeth discovered in the Kemp Clay Formation (Upper Maastrichtian) in the Hunt County (Texas, U.S.A.).

For original reference, see: Case & Cappetta 1997: p.: 137, pl.: 6, figs.: 1 and 2.

## Plicatoscyllium derameei CASE & CAPPETTA, 1997

This species is based on isolated teeth discovered in the Kemp Clay Formation (Upper Maastrichtian) in the Hunt County (Texas, U.S.A.).

The senior-author is surprised that the same Genus may be represented by two distinct species in the same level of the same locality.

For original reference, see: Case & Cappetta 1997: p.: 137, pl.: 5, figs.: 5 to 7.

## Plicatoscyllium youssoufiaensis NOUBHANI & CAPPETTA, 1997

This species is based on isolated teeth discovered in the Upper Maastrichtian of the Ganntour Basin (Morocco).

For original reference, see: Noubhani & Cappetta: p.: 43, pl.: 16, figs.: 1 to 10.

## Genus Columbusia CASE, SCHWIMMER, BORODIN & LEGGETT, 2001

According to Cappetta (2012: pp.: 372-373), this extinct Genus is represented by two species: its holotype: *C. fragilis* CASE, SCHWIMMER, BORODIN & LEGGETT, 2001 and *C. roessingi* (CASE, 1987).

## Stratigraphical remark

The teeth of these two species were discovered in the same level and in the same locality.

#### Odontological characteristics of *Columbusia roessingi* (CASE, 1987)

#### **General morphology**

All the teeth of this taxon are wider than high and present a very long and protuberant apron.

#### Dental root characteristics *Columbusia roessingi* (CASE, 1987)

Its dental root is holaulacorhyzid. Its medio-intern radicular protuberance is very short. Its lateral lobes are very elongated, slightly arched (anterior teeth) or horizontally expanded (lateral to posterior teeth).

## Dental crown characteristics of *Columbusia roessingi* (CASE, 1987)

Its dental crown is monocuspid (anterior teeth) but presents some indentations similar to very short cusplets (lateral teeth). Its apron is extraordinarily developed and protuberant. Lateral teeth present some vertical folds.

## Biological characteristics of Columbusia roessingi (CASE, 1987)

Without a skeleton, it is only the invertebrate remains, discovered in the same levels, which allow supposing that all the representatives of the Genus *Columbusia* were inhabitants of shallow bottoms in coastal and warm waters. **Conclusions** 

The taxon *C. fragilis*, generotype of the Genus *Columbusia* is incontestably a representative member of this Genus and considered by its inventors, such as by Cappetta (2006: p.: 86) as a member of the Family Orectolobidae JORDAN & FOWLER, 1903. The senior-author agrees with this proposal.

It is the systematic position attributed to the second taxon, *Columbusia roessingi* (CASE, 1987), considered as a member of the Genus *Columbusia* by Cappetta (2012: pp.: 372-373) which induces the supposition that the first populations of this species also passed along the northern coasts of the mass formed by South America and Africa, just before their separation at the Upper Cretaceous.

Cappetta (2012: pp.: 372-373) suggested that *Columbusia roessingi* (CASE, 1987) was a member of the Order Ganopristiformes HERMAN & VAN DEN EECKHAUT, 2010. Absolutely all the taxa of the Ganopristiformes have holaulacorhyzid teeth but *C. roessingi* does not.

Additionally, no rostral teeth were attributed to this taxon discovered in a very fossiliferous level.

## Spatio-temporal distribution of the Genus Columbusia

This Genus is represented by two specific taxa only known from one level marking the transition Lower-Upper Santonian in the State of Georgia (U.S.A.).

## Columbusia fragilis CASE, SCHWIMMER, BORODIN & LEGGETT, 2001

This species is based on isolated teeth discovered in a level marking the transition between the Lower and Upper Santonian (Upper Cretaceous) of the Chattahoochee County (Georgia, U.S.A.).

For original reference, see: Case, Schwimmer, Borodin & Leggett, 2001: p.: 89: fig.: 3, pl.: 2: figs.: 32 to 36.

#### Columbusia roessingi (CASE, 1987) or Squatirhina CASE, 1987

This species is based on isolated teeth discovered in a level marking the transition between the Lower and Upper Santonian (Upper Cretaceous) of the Chattahoochee County (Georgia, U.S.A.).

For original description and illustration, see: Case 1987: p.: 20, pl.: 7, figs.: 1 to 4.

#### Genus Navia BERNARDEZ, 2002

This mono-specific Genus is only represented by its holotype Navia bediae BERNARDEZ, 2002.

Once again, because described and figured in a PhD Thesis\*, Cappetta considered (2006: p.: 338) this taxon as *nomen nudum* and did not mention the existence of the proposal of this Genus in his revised Handbook of 2012.

\*It was specified, by the author himself, in the original document that this document had no nomenclatorial value, but Cappetta did not mention this systematic important precision.

The generic name *Navia* BERNARDEZ, 2002 is a botanical generic name proposed by SCHULT, 1830, regrouping circa 92 species of the Family Bromeliaceae JUSSIEU, 1789\*.

\*Fide: Angiospermae Phylogeny 2010, NCB 2010 and Delta Angiospermae 2010.

Consequently, this generic name must be definitely unvalidated.

#### Odontological characteristics of the orectoloboid taxon Navia bediae

## **General morphology**

The anterior teeth of this species are as wide as high; the posterior teeth are lower than their width. The existence of one symphyseal tooth file is uncertain.

## **Dental root characteristics**

The dental root of all the teeth of this taxon is hemiaulacorhyzid, presents a moderately developed medio-intern protuberance adjoined by a pair of large root lobes.

The base of the root is moderately arched (anterior teeth) to nearly flat (lateral and posterior teeth).

#### **Dental crown characteristics**

The dental crown of all the teeth of this species presents a large principal cuspid flanked by one pair\* of wide, rounded and high lateral cusplets.

\*The presence of one unpaired anterior cusplet on the tooth Pl.: 12: fig.: 1 (Bernardez 2002) is considered as an anomaly by the senior-author.

The lower lateral parts of the dental crown of some teeth\* of 'Navia bediae' present a similar, but less pronounced, swelling than the dental crown of the teeth of the Genus Hologinglymostoma.

This singularity suggests a possible phyletic relation between '*Navia bediae*' and the Genus *Hologinglymostoma* NOUBHANI & CAPPETTA, 1997 from the Thanetian of northern Morocco.

\*See: Bernardez 2002: Plate 13: figs.: 2a and 2d and Plate 14: figs.: 1c and 1d.

The morphology of its commissural teeth as well as its possession of a symphyseal tooth file remain unknown.

The invertebrates discovered in the same level confirm that the environment was this of very shallow and warm marine waters.

#### Spatio-temporal distribution of the taxon Navia bediae

This species is represented by isolated teeth of a single species discovered in Albian levels (Middle Cretaceous) of northern Spain and south-western France\*, before the formation of the Gulf of Gascogne.

\*Discoveries of the senior-author at Maurupt and Pargny (Aube Department, France).

This species is based on well preserved teeth discovered in the Upper Albian from the Asturias (northern Spain). The morphology of its commissural teeth as well as its possession of an upper or lower symphyseal tooth file remain unknown.

The teeth of this species represented 28% of all the teeth collected\* in this level, which is exceptional for dental remains of an orectoloboid taxon and allows supposing that one individual died not far from their discovery place.

\*Personal information from Dr. Enrique Bernardez (December 2013).

The Genus *Navia* must be invalidated, but its single species *bediae* could represent the type species of a small distinct lineage of the Order Hemiscylliformes.

The specific type set of *Navia bediae* being Spanish material, the senior-author could not integrate its revision in a Series devoted to general Systematics and discoveries realized in Belgium.

For original reference and illustration, see: Bernardez 2002: p.: 219, pls.: 12 to 14.

## Genus Eometlaouia NOUBHANI & CAPPETTA, 2002

This extinct Genus is only represented by the two following species: its holotype *E. delpiti* NOUBHANY & CAPPETTA, 2002 and *E. numidica* (ARAMBOURG, 1952).

This last species was considered, in 1952, by Arambourg as a member of the Genus Squatirhina CASIER, 1947.

When Noubhani and Cappetta attributed, in 2002, this species to their new Genus *Eometlaouia*, they did not precise which other taxa of the Genus *Squatirhina*, they also considered as members of their renamed Genus *Eometlaouia* or if they considered their Genus *Eometlaouia* to be mono-specific and based on the sole species *E. delpiti* NOUBHANI & CAPPETTA, 2002.

The morphology of the teeth attributed to the Genus *Squatirhina* by Aramboug in 1952 is, indeed, not compatible with this of the Genus *Squatirhina*.

But the choice of this species as holotype of the 'Genus *Metlaouia*' has for sole result to complicate the reinterpretation\* of the systematic position of the Genus *Squatirhina* CASIER, 1947 and the validation itself of the 'Genus *Metlaouia*' or Genus *Eometlaouia*.

\* See paragraph: Problem of the systematic position of the Genus Squatirhina CASIER, 1947.

## Taxonomic remark

The homonym *Metlaouia* DUMONT, 1928, a Lepidoptera of the Family Noctuidae LATREILLE, 1809 having priority, Noubhani & Cappetta were obliged to modify the generic name *Metlaouia* they had proposed in 1997 into *Eometlaouia* in 2002.

## Odontological characteristics of the restricted Genus Eometlaouia

#### **Dental root characteristics**

The dental root of the single species still representing this extinct Genus is hemiaulacorhyzid, possesses a narrow
medio-intern protuberance adjoined by two short lateral lobes.

#### **Dental crown characteristics**

The dental crown of the single species still representing this extinct Genus is as high as the width of the tooth (anterior teeth) and wider than the width of the tooth (lateral and posterior teeth). Its apron is wide with an angular extremity; its transversal section is oval-shaped.

Its main cuspid is large, presents an extern vertical median keel and one pair of short lateral cusplets.

#### **Biological characteristics of the Genus** *Eometlaouia*

Without a skeleton, it is only the invertebrate remains, discovered in the same levels, which allow supposing that all the representatives of the Genus *Eometlaouia* were inhabitants of shallow bottoms in coastal and warm waters.

#### Spatio-temporal distribution of the Genus Eometlaouia

Eometlaouia delpiti was discovered in only one Thanetian level of the Ouled Abdoun Basin (central Morocco).

#### Eometlaouia numidica (ARAMBOURG, 1952) or Squatirhina numidica ARAMBOURG, 1952

This species is based on isolated teeth discovered in the Ypresian of the Metlaoui Basin (Tunisia). Thanks to his Belgian colleague Dr. Henri Neybergh, the senior-author has received some specimens of this species.

For original description and illustrations, see: Arambourg 1952: p.: 146, fig.: 30 and pl.: 22, fig.: 65.

#### Eometlaouia delpiti (NOUBHANI & CAPPETTA, 2002) or Metlaouia delpiti NOUBHANY & CAPPETTA, 1997

This species is based on isolated teeth discovered in the Thanetian of the Ouled Abdoun Basin (Morocco).

For original description and illustrations, see: Noubhani & Cappetta 1997: p.: 22, pl.: 2, fig.: 9 and pl.: 3, figs.: 1-2.

#### Conclusion

The senior-author considers that the 'Genus *Eometlaouia*', so poorly represented, is a junior synonym of the Genus *Orectoloboides* CAPPETTA, 1977 and a possible ancestor of *Orectoloboides reyndersi* ADNET, 2000, of doubtful status, and that these two taxa, with *Orectoloboides geijseni* HERMAN & VAN DEN EECKHAUT, 2010 constitute a small primitive lineage of the Family Brachaeluridae APPLEGATE, 1974.

#### Genus Microtoxodus DELSATE, 2003

This extinct Genus is mono-specific and only represented by its holotype: *M. gulakmani* DELSATE, 2003 and was considered by Cappetta as a possible synonym\* of the Genus *Folipristrix* KRIWET, 2003.

\*Having seen other specimens of this taxon discovered in the same level and locality, the senior-author agrees with this suggestion.

For descriptions and illustrations, see: Delsate 2003: p.: 28 and Cappetta 2012: pp.: 179-180.

#### Consideration of this taxon

The type set, and the only material known, on which this generic taxon is based, consists of very badly preserved crown fragments discovered in a Toarcian level (uppermost Liassic, Lower Jurassic) of the Luxembourg Province (southern Belgium).

It was a pure non-sense to propose a specific taxon, and surely a generic taxon, when in possession of only such bad material.

The sole data that these fragments added to the knowledge of the fossil orectoloboid Chondrichthyes may be summarized as follows.

Nothing is known about the dental root structure of this hypothetic Genus *Microtoxodus*. Its dental crown remains demonstrate that they were in possession of an apron, but that these teeth did not possess a medio-intern protuberance.

#### Conclusion

The presence of an apron is the unique argument that allows considering these fossils as orectoloboid remains, but the possession of an apron is not the singularity of the sole orectolobid taxa.

The dental crowns of some taxa of the Family Squalidae de BLAINVILLE, 1816, such as all the species of the Genera *Squalus* LINNNAEUS, 1758 and *Megasqualus* HERMAN, 1982 also present an apron.

In 2004 and 2005 the senior-author took additional samples of the same level, without success. He considers that this Genus may be considered as an enigmatic taxon of undeterminable status.

The senior-author thinks that the Genus *Microtodoxus* requires further investigation before being validated.

#### Spatio-temporal distribution of the Genus *Microtoxodus*

This Genus has only one specific taxon discovered in one Toarcian level (Uppermost Lower Jurassic) in southern Belgium.

#### Microtoxodus gulakmani DELSATE, 2003.

This species is based on isolated teeth discovered in the Upper Toarcian (uppermost Liassic, end of the Lower Jurassic) of the Great Dukedom of Luxemburg. See comments in the preceding paragraph.

For original reference, see: Delsate 2003: p.: 23, plate not numbered: figs.: 4 to 6.

## Genus Folipistrix KRIWET, 2003

This extinct Genus is mono-specific and only represented by its holotype: Folipistrix digitulus KRIWET, 2003.

#### Odontological characteristics of the Genus Folipistrix

#### General morphology

All the teeth of this taxon are singularly low and wide.

#### **Dental root characteristics**

The dental root of the single species representing this extinct Genus is hemiaulacorhyzid. Its medio-intern protuberance is short with an extern rectangular aspect and an elongated oval-shaped horizontal section.

#### **Dental crown characteristics**

The dental crown of the single species representing this extinct Genus has a triangular and massive morphology. It is difficult to precise if minute lateral cusplets exist or not.

#### Biological characteristics of the Genus *Folipistrix*

Without a skeleton, no data are available. But the invertebrate fauna of the level in which they were discovered indicate that their environment was this of warm and shallow to coastal waters.

#### Conclusion

The few teeth, presently known, of the Genus *Folipistrix* are so singular that they could represent the generotype of a new Family of the Order Orectolobiformes Ord. emend. for which the senior-author will not propose a name because of the extreme scarcity of its remains.

#### Spatio-temporal distribution of the Genus Folipistrix

This extinct Genus has only one specific representative, based on isolated teeth, discovered in the Middle Jurassic of southern Germany.

#### Folipistrix digitulus KRIWET, 2003

This species is based on isolated teeth discovered in the Lower Aalenian (Middle Jurassic) of Baden-Würtemberg (Germany).

For original reference, see: Kriwet 2003: p.: 586, p.: 587: fig.: 2D, p.: 589: fig.: 1A.

#### Genus Dorsetoscyllium UNDERWOOD & WARD, 2004

This extinct mono-specific Genus is represented only by its holotype: *D. terreafollonicum* UNDERWOOD & WARD, 2004.

#### **General morphology**

All the teeth of this taxon are singularly laterally compressed.

#### Odontological characteristics of the Genus Dorsetoscyllium

#### **Dental root characteristics**

The dental root of the single species representing this extinct Genus is hemiaulacorhyzid, and, according to their position in the jaw, more or less arched in the commissural direction.

Their medio-intern protuberance is massive and flanked by two root lobes. These last ones form a very short arch (anterior teeth) or a nearly straight and flat anterio-posterior surface (posterior teeth).

#### **Dental crown characteristics**

The intern and extern sides of the dental crown of the single species representing this extinct Genus are absolutely smooth. Their apron is broad, with an oval-shaped or tongue-shaped lower extremity.

They have a high cuspid and one quite imperceptible pair of lateral cusplets, so small, that these teeth could be supposed to be monocuspid.

#### Biological characteristics of the Genus Dorsetoscyllium

Without a skeleton, no data are available. But the invertebrate fauna of the level in which they were discovered indicate that their environment was this of warm and shallow to coastal waters.

#### Spatio-temporal distribution of the Genus Dorsetoscyllium

This extinct Genus, based on isolated teeth, discovered in the Middle Jurassic of southern Great Britain, has only one specific representative.

#### Conclusion

The Genus Dorsetoscyllium will be considered as a member of the Family Phorcynidaenov. Fam.

This species is based on isolated teeth discovered in the Frome Clay Formation of Bathonian Age (Middle Jurassic) of southern England (Great Britain).

## Dorsetoscyllium terreafollonicum UNDERWOOD & WARD, 2004

This species is also represented by numerous reworked teeth in the Forest Marble Formation in the same region of England.

For reference, see:

Underwood & Ward 2004: p.: 470, pl.: 7, figs.: 1 to 13.

#### Genus Heterophorcynus UNDERWOOD & WARD, 2004

This extinct Genus is a mono-specific Genus, represented only by its holotype *H. microdon* UNDERWOOD & WARD, 2004.

#### Heterophorcynus microdon UNDERWOOD & WARD, 2004

This species is based on isolated teeth discovered in the Rutland Formation (Bathonian, Middle Jurassic) of southern England (Great Britain).

For reference, see: Underwood & Ward 2004: p.: 467, pl.: 6, figs.: 1 to 11.

#### Odontological characteristics of the Genus Heterophorcynus

#### **General morphology**

All the teeth of this taxon are laterally compressed.

#### **Dental root characteristics**

Their dental root presents a poorly developed\* hemiaulacorhyzid structure and two flat and short root lobes. The medio-intern root protuberance is very short.

\*Their extern median groove is very short.

#### **Dental crown characteristics**

All the teeth present one principal cuspid flanked by one\* or two pairs of very short cusplets. The extern side of their crown is lightly convex, but the intern side of their crown is strongly convex. Both sides of their crown are absolutely smooth.

\*Lateral cusplets may be absent on anterior teeth.

#### Biological characteristics of the Genus Heterophorcynus

Without a skeleton, no data are available. But the invertebrate fauna of the level in which they were discovered indicate that their environment was this of warm and shallow to coastal waters.

#### Conclusion

The Genus Heterophorcynus will be considered as a member of the Family Phorcynidaenov. Fam.

#### Spatio-temporal distribution of the Genus Heterophorcynus

This mono-specific extinct Genus is only known from the Middle Jurassic of southern Great Britain.

## Genus Palaeorectolobus KRIWET, 2008

This extinct Genus is a mono-specific Genus based on the partially preserved skeleton of its holotype and unique specimen *Palaeorectolobus agomphius* KRIWET, 2008, discovered in the Upper Jurassic limestones of the Hinheim-Kelheim Basin (Bayern, southern Germany).

Its head, its dentition, its branchial apparatus and its left pectoral fin are well preserved, which allows an easy comparison with all the other extinct or extant generic taxa of the Orectolobiformes (according to Applegate's conception, 1972).

#### **Odontological characteristics of the Genus** *Palaeorectolobus*

#### General morphology

The height of the teeth of this Genus is more important than their width and their general morphology is very similar to this of the dermal denticles of the most primitive orectoloboids.

## **Dental root characteristics**

The dental root of all the teeth of the single species representing this extinct Genus is hemiaulacorhyzid and presents a very short medio-intern protuberance adjoined by two short lateral lobes.

The base of the anterior teeth is lightly arched; this of the other teeth is nearly flat and heart-shaped.

#### **Dental crown characteristics**

The dental crown of all the teeth of this species is low and massive. The anterior teeth are monocuspid, but the lateral teeth present one pair of very short lateral cusplets. Its ornamentation consists of some strong vertical folds.

#### Biological characteristics of the Genus Palaeorectolobus

Palaeorectolobus agomphius had five pairs of gill slits and possessed short and multi-lobed barbels along the sides of its mouth.

The fossil remains of invertebrates in the Formation in which *P. agomphius* was discovered indicate a shallow and warm marine environment.

#### Conclusion

The senior-author agrees with the inventor of this taxon that its teeth have a primitive orectolobid morphology and suggests that the Genus *Palaeorectolobus* could be considered as the oldest representative of the Order Hemiscylliiformes nov. Ord.

#### Spatio-temporal distribution of the Genus Palaeorectolobus

This mono-specific extinct Genus is only known from the Upper Jurassic of southern Germany.

#### Palaeorectolobus agomphius KRIWET, 2008

This species is based on a partially preserved skeleton discovered in in the Upper Jurassic limestones of the Hinheim-Kelheim Basin (Bayern, southern Germany).

For original reference, see: Kriwet 2008: pp.: 443-45.

#### Genus *Rhincodon* SMITH, 1829 (See Plate 53, Plate 54 and comments)

In February 2014, this extant Genus remains without fossil representatives.

## 10.5. Conclusion and Natural History of the Order Orectolobiformes sensu Cappetta 2012

# **1.** General conclusions of the re-examination of all the data concerning the fossil taxa of the Order Orectolobiformes (*sensu* Applegate 1972)

The odontological and biological\* re-examination of all the extinct generic taxa of this Order allows suggesting their redistribution into eight Families: Family Ginglymostomatidae GILL, 1862, Family Hemiscylliidae GILL, 1862, Family Parascyllidae GILL, 1862, Family Brachaeluridae APPLEGATE, 1974, Family Orectolobidae JORDAN & FOWLER, 1903, Family Rhincodontidae GARMAN, 1913, Family Agaleidae REES, 2000 and Family Phorcynidaenov. Fam.

\*When this taxon is based on a skeleton, or indirectly, by the examination of the invertebrate remains discovered in the same level.

The odontological criteria utilized are: the relation between their crown and their root, the placement of the tooth files, the characteristics of their dental root and the characteristics of their dental crown.

The biological criteria utilized are: the number of their pairs of gill slits and the possible possession of dorsal fin spines.

For the fossil Genera based on skeletons, the senior-author has requested the help of some colleagues\* to try to detect the possible presence of egg cases in these skeletons.

\*Dr. Fritz Pfeil (München, Germany), Dr. Detlev Thies (München, Germany) and Dr. Jürgen Kriwet (Wien, Austria), who are thanked for their assistance.

To try to understand their possible phyletic relations, the spatio-temporal distribution of all the specific taxa of the eleven extant Genera redistributed in these eight Families was also examined.

## 2. Convexity and ornamentation of their dental crown

## **Objective data**

Such as all the extant species of the Order Squatiniformes COMPAGNO, 1973, all the extant species of the Order Orectolobiformes (*sensu* APPLEGATE, 1974) have teeth with a dental crown presenting convex extern and intern sides which are absolutely smooth.

This configuration is the same for all the extinct taxa of the Order Squatiniformes and for all the Cenozoic taxa of the Order Orectolobiformes (*sensu* APPLEGATE, 1974).

But this configuration varies considerably for the diverse generic extinct taxa of the Order Orectolobiformes (*sensu* APPLEGATE, 1974) between the lowermost Jurassic and the uppermost Eocene Periods.

If the dental crown of some generic extinct taxa\* of the Order Squatiniformes presents the same morphology as this of the Oligocene taxa and of the extant ones, the large majority of them have an ornamented extern side.

\*Discovered in levels of Cretaceous to Eocene Ages.

Their extern side changes progressively from a poorly ornamented convex surface, to a flat surface having numerous, more or less, strong sub-vertical folds in the enamel.

#### Interpretation of this evidence

The apparition of crenulations on the cutting edges of the dental crowns has an evident saw-like utility. The apparition of striations on the intern side of the dental crowns has an evident arch-butment-like utility, but it is less easy to find an explanation for the utility of the apparition of folds on the extern side of the dental crowns.

Physically, the formations of these folds may also be explained by the same phenomenon proposed to explain these two other morphological singularities. It consists of a successive decrease of the number of the very narrow canali having their origin in the central nutritive cavity (pulp-cavity).

The function of these canali is to supply some atomic particles indispensable for the formation of the highly complex apatite molecules of the extern enamel layers of the dental crown.

The functional utility of this folded ornamentation remains uncertain but, the acquisition of such extern ornamentation increased the rigidity of the extern face of the crown and improved rasping and grazing activities.

It seems that the disappearance of this ornamentation has seriously decreased the number of their representative taxa because it reduced their competitiveness with other small predators.

#### Geological data of the appearance of this phenomenon and its cessation

Folds or striations affecting the extern side of the dental crown of generic taxa of the Order Orectolobiformes (*sensu* APPLEGATE, 1974) are observable on taxa dating from the Lower Jurassic (*Palaeorectolobus* KRIWET, 2008), to the Eocene Genera *Protoginglymostoma* HERMAN, 1977 and *Orectoloboides* CAPPETTA, 1972, but none of its Oligocene Genus presents this singularity.

It must be admitted that the unknown causes of this phenomenon reached its maximal effect at the end of the Upper Cretaceous Period and ended with the Eocene-Oligocene-Transition.

#### Lineages affected by this phenomenon

Folds or striations affecting the extern side of the dental crown are visible on all the specific taxa of the eleven following Genera\*: *Palaeorectolobus* KRIWET, 2008, *Acanthoscyllium* CAPPETTA, 1980, *Eometlaouia* NOUBHANI & CAPPETTA, 2002, *Squatiscyllium* CAPPETTA, 1980, *Paraginglymostoma* HERMAN, 1982, *Cantio*-*scyllium* WOODWARD, 1889, *Delpitoscyllium* NOUBHANI & CAPPETTA, 1997, *Ornatoscyllium* UNDERWOOD & WARD, 2004, *Hologinglymostoma* NOUBHANI & CAPPETTA, 1997, *Protoginglymostoma* HERMAN, 1977 and *Orectoloboides* CAPPETTA, 1972.

\*This enumeration follows the geological age of these generic taxa.

# **3.** Fossil Genera included in the Order Orectolobiformes before the proposal of its emendation and reconsideration of their Family attribution.

According to Cappetta (2012: pp.: 154 to 182), the Order Orectolobiformes *sensu lato* regrouped the twenty-four following Genera: Genus *Phorcynis* THIOLLIERE, 1854, Genus *Acrodobatis* LEIDY, 1877, Genus *Cantioscyllium* WOODWARD, 1889, Genus *Crossorhinus* WOODWARD, 1918, Genus *Corysodon de* SAINT-SEINE, 1949, Genus *Protoginglymostoma* HERMAN, 1977, Genus *Eostegostoma* HERMAN, 1977, Genus *Protoginglymostoma* HERMAN, 1977, Genus *Cretorectolobus* CASE, 1978, Genus *Acanthoscyllium* CAPPETTA, 1980, Genus *Paraginglymostoma* HERMAN, 1982, Genus *Annea* THIES, 1983, Genus *Palaeobrachaelurus* THIES, 1983, Genus *Pseudoginglymostoma* DINGERKUS, 1986, Genus *Delpitoscylllium* NHOUBANI & CAPPETTA, 1997, Genus *Ganntouria* NHOUBANI & CAPPETTA, 1997, Genus *Policatoscyllium* CASE & CAPPETTA, 1997, Genus *Eometlaouia* NOUBHANY & CAPPETTA, 2002, Genus *Folipistrix* KRIWET, 2003, Genus *Dorsetoscyllium* UNDERWOOD & WARD, 2004, Genus *Heterophorcynus* UNDERWOOD & WARD, 2004 and Genus *Paraorectolobus* KRIWET, 2008.

## 4. Reconsideration of their attribution and proposal of one new Family

#### 1. General conclusion

One Genus, the Genus *Cretorectolobus* CASE, 1978, of this list is considered as a member of the Family Squatinidae BONAPARTE, 1838\*. The Family Pseudoginglymostomatidae DINGERKUS, 1986 is considered to be valid and one new Family is proposed: Family Phorcynidaenov. Fam.

#### 2. Detailed review

## Family Agaleidae REES, 2000

This Family still includes only its generotype: Genus Agaleus DUFFIN & WARD, 1983.

## Family Phorcynidae nov. Fam.

The senior-author proposes the Genus *Phorcynis* as generotype of the Family Phorcynidaenov. Fam. and suggests to include the five following Genera in this Family: Genus *Annaea* THIES, 1983, Genus *Palaeobrachaelurus* THIES, 1983, Genus *Heterophorcynus* UNDERWOOD & WARD, 2004, Genus *Dorsetoscyllium* UNDERWOOD & WARD, 2004 and Genus *Garrigascyllium* GUINOT, CAPPETTA & ADNET, 2014.

## Family Orectolobidae JORDAN & FOWLER, 1903

#### **Systematics**

In 2006, Cappetta (pp.: 398-399), regrouped in this Family the extant Genus *Orectolobus* BONAPARTE, 1834 and the seven following extinct Genera: Genus *Orectoloboides* CAPPETTA, 1977, Genus *Cretorectolobus* CASE, 1978, Genus *Squatiscyllium* CAPPETTA, 1980, Genus *Cederstroemia* SIVERSON, 1995, Genus *Columbusia* CASE, SCHWIMMER, BORODIN & LEGGETT, 2001, Genus *Columbusia* CASE, SCHWIMMER, BORODIN & LEGGETT, 2001, and Genus *Eometlaouia* NOUBHANI & CAPPETTA, 2002.

In 2012, Cappetta 2012 (pp.: 158-163), modified his systematics' conception of this Family and regrouped the extant Genus *Orectolobus* BONAPARTE, 1834 and the six extinct Genera: Genus *Orectoloboides* CAPPETTA, 1977, Genus *Cretorectolobus* CASE, 1978, Genus *Squatiscyllium* CAPPETTA, 1980, Genus *Squatiscyllium* CAPPETTA, 1980, Genus *Cederstroemia* SIVERSON, 1995 and Genus *Eometlaouia* NOUBHANI & CAPPETTA, 2002 in this Family.

Despite the lack of discovery of rostral teeth attributable to the extinct Genus *Columbusia* CASE, SCHWIMMER, BORODIN & LEGGETT, 2001 and the presence of an elongate and subvertical apron on its dental crowns, this Genus was considered as a member of the Family Sclerorhynchidae CAPPETTA, 1980.

## Family Orectolobidae emend.

The senior-author regroups in this Family, he largely emends, its three extant Genera: Genus *Orectolobus* BONA-PARTE, 1834, Genus *Sutorectus* WHITLEY, 1939 and Genus *Eucrossorhinus* REGAN, 1906 and the two extinct Genera: Genus *Cederstroemia* SIVERSON, 1995 and Genus *Columbusia* CASE, SCHWIMMER, BORODIN & LEGGETT, 2001.

#### Remarks

The specific taxon *Cederstroemia ziaensis*\* BOURDON, WRIGHT, LUCAS. SPIELMANN & PENCE, 2011, based on isolated teeth discovered in a level of upper Santonian Age (Upper Cretaceous) of central Mexico is of doubtful attribution.

\*See Bibliography-Systematics: Bourdon, Wright, Lucas, Spielmann & Pence 2011.

It is the systematic position of the second taxon, *Columbusia roessingi* (CASE, 1987), considered as a member of the Genus *Columbusia* by Cappetta (2012: pp.: 372-373) which induces the supposition that the first populations of this species also passed along the northern coasts of the mass formed by South America and Africa, just before their separation at the Upper Cretaceous.

## Family Brachaeluridae APPLEGATE, 1974

This Family regroups the two extant Genera: Genus *Brachaelurus* OGILBY, 1907 and Genus *Heteroscyllium* REGAN, 1908 and the two extinct Genera: Genus *Orectoloboides* CAPPETTA, 1977 and Genus *Palaeobrachaelurus* THIES, 1983.

## Family Ginglymostomatidae GILL, 1862

#### **Systematics**

This Family, represented by the two extant Genera: Genus *Ginglymostoma* MÜLLER & HENLE, 1837 and Genus *Nebrius* RÜPPEL, 1837, may include the eleven following extinct Genera: Genus *Cantioscyllium* WOODWARD, 1889, Genus *Orectoloboides*\* CAPPETTA, 1977, Genus *Protoginglymostoma* HERMAN, 1977, Genus *Squatiscyllium*\* CAPPETTA, 1980, Genus *Paraginglymostoma*\* HERMAN, 1982, Genus *Plicatoscyllium* CASE & CAPETTA, 1997, Genus *Delpitoscyllium* NOUBHANY & CAPPETTA, 1997, Genus *Delpitoscyllium* NOUBHANY & CAPPETTA, 1997, Genus *Eometlaouia* NOUBHANY & CAPPETTA, 2002, Genus *Ornatoscyllium* UNDERWOOD & WARD, 2004 and Genus *Palaeorectolobus* KRIWET, 2008.

\*Cappetta (2006: pp.: 398-399) considered the Genus *Orectoloboides* and the Genus *Squatiscyllium* as members of the Family Orectolobidae *sensu* Applegate 1972 and the Genus *Paraginglymostoma* as a member of the Family Brachaeluridae.

According to Cappetta 2006 (p.: 398), the eight extinct Genera represent ancestral populations of the Family Ginglymostomatidae: Genus Acrodobatis LEIDY, 1877, Genus Cantioscyllium WOODWARD, 1889, Genus Delpitoscyllium NHOUBANI & CAPPETTA, 1997, Genus Ganntouria NHOUBANI & CAPPETTA, 1997, Genus Hologinglymostoma NHOUBANI & CAPPETTA, 1997, Genus Plicatoscyllium CASE & CAPPETTA, 1997, Genus Protoginglymostoma HERMAN, 1977 and Genus Pseudoginglymostoma DINGERKUS, 1986.

In 2012, Cappetta (p.: 162) rejecting without any explanation the fundamental revision, proposed in 1972 by Applegate, of the systematics of this Family, modified his opinion and considered that the two extinct Genera *Orectoloboides* and *Squatiscyllium* were members of the Family *Orectolobidae sensu* JORDAN & FOWLER, 1903 and that the Genus *Paraginglymostoma* remains (p.: 166) a member of the Family Brachaeluridae APPLEGATE, 1974.

The senior-author adds that the Genus *Plicatoscyllium* CASE & CAPPETTA, 1997 seems to represent the end of a phyletic ginglymostomid lineage marked by the constant increase of the thickness of the folds constituting the ornamentation on the extern side of their dental crown.

The senior-author, like Cappetta (2012: p.: 169), considers the Genus *Delpitoscylllium* NOUBHANI & CAPPETTA, 1997, as a member of the Family Ginglymostomatidae GILL, 1862, but as a co-lateral representative of one of its oldest lineages.

## Reproduction

The majority of the generic taxa of the Family Ginglymostomatidae are ovoviviparous.

## Genus Ginglymostoma Müller & Henle, 1837

#### 1. Fossil representatives of this Genus

According to Cappetta (2006: 308-309), sixteen fossil taxa represent ancient populations of this Genus: G.

angolensis DARTEVELLE & CASIER, 1943, G. botmaense NOUBHANI & CAPPETTA, 1997, G. chenanei NOUBHANI & CAPPETTA, 1997, G. cristata (PROBST, 1878), G. cuspidata CASE, BORODIN & LEGGETT, 2001, G. dartevellei CASIER, 1946, G. delfortrei DAIMERIES, 1889, G. erramii NOUBHANI & CAPPETTA, 1997, G. khouribgaense NOUBHANI & CAPPETTA, 1997, G. maghrebianum CASIER, 1947, G. malembeense DARTEVELLE & CASIER, 1943, G. maroccanum NOUBHANI & CAPPETTA, 1997, G. pectinatum NOUBHANI & CAPPETTA, 1997, G. serra (LEIDY, 1877), G. sokotense WHITE, 1934 and G. subafricanum ARAMBOURG, 1952.

#### 2. Material examined

G. angolensis DARTEVELLE & CASIER, 1943, numerous perfectly preserved teeth from the Lutetian of Cabinda, Atlantic coast of Africa (Collections M.R.A.C., Tervueren, Belgium), G. botmaense NOUBHANI & CAPPETTA, 1997, numerous perfectly preserved teeth from the Maastrichtian of the Ouled Abdoun Basin, Morocco (I.R.S.N.B. Collections and Private Belgian and French Collections), G. chenanei NOUBHANI & CAPPETTA, 1997, numerous perfectly preserved teeth from the Thanetian of the Ganntour Basin, Morocco (Collections I.R.S.N.B., Belgium and Private French Collections), G. cristata (PROBST, 1878), twelve reworked teeth from the Lower Miocene of the Bade-Würtemberg, Germany (Private Collections), G. cuspidata CASE, BORODIN & LEGGETT, 2001, six perfectly preserved teeth from the Upper Maastrichtian of New Jersey, U.S.A., (Private Collections), G. dartevellei CASIER, 1946, types and other teeth (Collections M.R.A.C., Tervueren, Belgium), from the Danian of Cabinda, G. delfortrei DAIMERIES, 1889, teeth never seen by the senior-author, from the Miocene of the Aquitanian Basin, France, G. erramii NOUBHANI & CAPPETTA, 1997, six teeth from the Upper Maastrichtian of the Ganntour Basin, Morocco, (Collections I.R.S.N.B., Belgium Private French Collection), G. khouribgaense NOUBHANI & CAPPETTA, 1997, twelve teeth from the Upper Maastrichtian of the Ouled Abdoun Basin, Morocco, (Private French Collection), G. maghrebianum CASIER, 1947, types in repository in the I.R.S.N.B. Collections, but not retrieved, from the Lower Eocene of Tunisia, G. malembeense DARTEVELLE & CASIER, 1943, types and other teeth (Collections M.R.A.C., Tervueren, Belgium), from Cabinda, G. maroccanum NOUBHANI & CAPPETTA, 1997, forty teeth (Private Collection) from the Thanetian and sixty teeth (Private Collection) from the Ypresian of the Ouled Abdoun Basin, Morocco, G. pectinatum NOUBHANI & CAPPETTA, 1997, eight teeth (Private Collection) from the Upper Maastrichtian of the Meskala Basin, Morocco, G. serra (LEIDY, 1877), six teeth from the Miocene\*, but reworked from the Upper Eocene of South Carolina, U.S.A., G. sokotoense WHITE, 1934, figuration, from the Thanetian of the Sokoto Basin, Nigeria, and G. subafricanum ARAMBOURG, 1952, four teeth (L. Dubertret Collection) from the Danian of the Ganntour Basin, Morocco.

\*Reconsideration of the age of the discovery level by American colleagues.

#### 3. Conclusions

#### 1. Paleogeographical and stratigraphical distribution of the Genus Ginglymostoma

Maastrichtian to uppermost Eocene from diverse eastern and western Atlantic geological Formations.

#### 2. Paleoecological distribution of the Genus Ginglymostoma

Considering the other vertebrate and invertebrate remains associated to these fossil teeth in all the diverse type localities, it seems obvious that the extinct populations of this Genus inhabited similar ecological niches as their extant representatives.

#### 4. Natural History of the Genus Ginglymostoma

#### **1.** Distribution of its extant representatives

#### **Objective data**

The single representative species of this extant Genus, *Ginglymostoma cirratum* (BONNATERRE, 1788), is represented by four main groups of more or less dense populations occupying shallow bottoms of the eastern Atlantic Ocean\*, one inhabiting nearly all the eastern coasts of the American Continent, from the boundary between Canada and U.S.A. to the southern coasts of Brazil and a fourth group of populations inhabiting nearly\*\* all the eastern coasts of the American Continent from the Sea of Cortez to the southern boundary of Peru.

\*One small group scattered along the northern coasts of Spain and one huge group occupying all the western coasts of Africa, from North Morocco to North Angola.

\*\*The Genus *Ginglymostoma* is absent from the eastern coast of the Yucatan Peninsula (Mexico) to the Dutch Guyana coast.

#### Source: <u>www.fr.academic.ru</u>

#### 2. Distribution of its extinct representatives

As far as known, the Eocene paleogeographical distribution of its extinct representatives covered the British-French-Belgian Basin, the northern African Basin, the Angola Basin and the central part of the North American Continent.

Such a large Cenozoic paleodistribution could explain the actual distribution of the Genus *Ginglymostoma*, but gives no explanation for the problem represented by its crossing of the North Atlantic trenches.

Genetic investigations of these diverse extant populations will surely demonstrate that their affinities require reconsiderations.

For the Eocene European, North African and western African representatives of this Genus, the Jurassic Genera *Phorcynis* THIOLLIERE, 1852, the Cretaceous Genus *Paraginglymostoma* HERMAN, 1982, the Paleocene Genus *Hologinglymostoma* NOUBHANY & CAPPETTA, 1997 and the Eocene Genus *Protoginglymostoma* HERMAN, 1977 seem to be possible ancestors.

#### 3. Conclusion

The oldest representatives surely attributable to this Genus are: *G. africanum* LERICHE, 1927, from the Thanetian of Cabinda and Morocco, *G. angolense* DARTEVELLE & CASIER, 1943 from the Ypresian (Cabinda) and the Lutetian (Morocco, Guinea Bissao and Togo).

For references, see: Cappetta 2012, Dartevelle & Casier 1943 and Leriche 1927.

#### Genus Nebrius RÜPPEL, 1837 (See Plate 38 and comments)

#### 1. Fossil representatives of this Genus

According to Cappetta 2006 (p.: 338), four or five extinct species represent ancestral populations of this Genus: *N. thielensi* (WINKLER, 1873) present and abundant in the Lower, Middle, Upper and Uppermost Eocene of the Anglo-Belgian-French Basin, *N. obliquus* (LEIDY, 1877) present and abundant from the Eocene of New Jersey, U.S.A., *N. bequaerti* (LERICHE, 1920) from the Danian of Landana, Cabinda, *N. blanckenhorni* (STROMER, 1905) from the Bartonian\* of Wadi Ramlich, Egypt and *N. priemi*\*\* GEMMELLARO, 1912 from the Lutetian of Sicilia, Italy.

\*Its precise geological age is not sure. \*\*Of dubious validity because based on only one badly preserved tooth.

#### 2. Geological range

Early Paleocene to Recent Times.

#### 3. Natural History of the Genus *Nebrius*

#### **Distribution of its extant representatives**

The geographical distribution of the extant populations of its single representative may be summarized as follows: It includes all the coasts of the Red Sea, of the eastern side of Africa, the southern Arabian Peninsula, of the Persian Gulf, of India and Ceylan, and of the western coasts of the Pacific Ocean from northern Australia to southern Japan. For more details, consult the source below.

#### Source: www.en.academic.ru

#### **Distribution of its extinct representatives**

The paleogeographical distribution of all the extinct European and African representatives of the Genus *Nebrius* explains perfectly its present distribution and depth range.

#### Conclusion

Such as for many fossil taxa attributed to the Genus *Ginglymostoma* MÜLLER & HENLE, 1837 a careful odontological re-examination of all the North American taxa attributed to the extant Genus *Nebrius* could be interesting for a better understanding of their dispersion.

These Chondrichthyes being benthic inhabitants of shallow waters had no possibilities to cross the Atlantic Ocean after the Upper Jurassic Period and surely not at the Upper Cretaceous Period.

Their single possibility to colonize northern American territories was to progress along the continental mass that formed Africa and South America. But its extant populations have a large and understandable distribution.

The most representative fossil taxon of this Genus is *Nebrius thielensi* (WINKLER, 1874) from which isolated teeth are some of the most common fossils collectable in all the Lower to the Uppermost Eocene levels of the English-French-Belgian Basin.

For references, see: Bourdon 2007, Compagno 1984, Herman, Hovestadt-Euler & Hovestadt 1993, Herman, Hovestadt-Euler & Hovestadt 1997 and Seposky 2002.

## Family Stegostomatidae GILL, 1862

Some odontological characteristics of the Genus *Eostegostoma*, particularly the strong lateral compression of their teeth, seem to confirm its validity and justify its attribution to the Family Stegostomatidae GILL, 1862 and not to the Family Brachaeluridae APPLEGATE, 1974, such as suggested by Cappetta (2012: p.: 165).

## Family Pseudoginglymostomatidae DINGERKUS, 1986

The representatives of the Genus *Pseudoginglymostoma* DINGERKUS, 1986 of the Family Pseudoginglymostomatidae DINGERKUS, 1986 are surely potential ancestors of the extant Genus *Ginglymostoma* MÜLLER & HENLE, 1837.

## Family Hemiscylliidae GILL, 1862

Cappetta considered the Genus *Almascyllium* as a member of the Family Hemiscylliidae GILL, 1862. The seniorauthor agrees with this opinion, which makes of this Genus a possible common ancestor of the two extant Genera regrouped in this Family: Genus *Hemiscyllium* MÜLLER & HENLE, 1837 and Genus *Chiloscyllium* MÜLLER & HENLE, 1837.

The fact that the two representatives of the Genus *Almascyllium* also possess very short enforced cartilaginous nasal appendages allows suggesting that the extinct Genus *Almascyllium* could be genetically related to the earlier representatives of the saw-sharks: the Order Pristiophoriformes BERG, 1958.

The senior-author agrees with the inventor of this taxon that its teeth have a primitive orectolobid morphology and suggests that the Genus *Palaeorectolobus* could be considered as the oldest representative of the Family Hemiscylliidae of the Order Hemiscylliiformes nov. Ord.

#### Family Parascylliidae GILL, 1862

This Family regroups the extant Genus *Parascyllium* GILL, 1862 and the extinct Genus *Pararhincodon* HERMAN *in* CAPPETTA, 1976.

## Family Rhincodontidae GARMAN, 1913

This Family regroups the extant Genus *Rhincodon* GARMAN, 1913 and the extinct Genus *Palaeorhincodon* HERMAN, 1974. This proposal seems to have been accepted by Cappetta (2006: p.: 399).

The Genus *Palaeorhincodon* is represented by numerous isolated teeth attributed to three species of Lower to Upper Eocene Age, living in a zone including North Africa, central Europe and central Asia.

The extant Genus *Rhincodon* is represented by numerous populations and has a world-wide distribution, but no fossil representatives.

## Genus Rhincodon SMITH, 1829

#### **Systematics**

This extant Genus is only represented by its world-wide distributed species and generotype *Rhincodon typus* SMITH, 1829.

#### Odontological characteristics of the Genus Rhincodon

#### Placement of the teeth in the jaws

Their extremely laterally compressed and very small monocuspid teeth are arranged in independent parallel rows.

### **Dental root characteristics**

The dental roots of all the teeth of this Genus are holaulacorhyzid (anterior teeth) or hemiaulacorhyzid (lateral to posterior teeth).

#### **Dental crown characteristics**

Their very short apron is poorly prominent and presents a subcircular section (anterior teeth) to an oval-shaped section (lateral to posterior teeth).

For figuration, see Bibliography-Systematics:

Cappetta 2012: p.: 177 and fig.: 165 (drawing) and Herman, Hovestadt-Euler & Hovestadt 1992: pl.: 27.

## Biological characteristics of the Genus Rhincodon

These huge nectic Chondrichthyes have two dorsal fins without fin-spines, five pairs of branchial girdles transformed into filtering-feeding organs and, such as *Stegostoma fasciatum* (HERMANN, 1783), prominent ridges on the sides of their bodies.

#### Rhincodon typus SMITH, 1829

This species is represented by numerous populations\* of a very variable number of individuals inhabiting the major part of the Atlantic, Indian and Pacific Oceans.

\*Numbers never specified.

#### **Atlantic Ocean**

On the western side of the Atlantic Ocean, it may be encountered between the latitude of  $40^{\circ}$  North (Norfolk, U.S.A.) to *circa* 35° South (off Rio de Janeiro, Brazil) and on the eastern side of the Atlantic Ocean, off the American coasts and between the latitude of  $20^{\circ}$  North (Mauritania) to the latitude of  $35^{\circ}$  South (Cape of Good Hope, South Africa).

#### **Indo-Pacific Oceans**

On the western side of the Indo-Pacific Oceans, its populations are dispersed between the latitude of  $25^{\circ}$  North (northern extremity of the Red Sea) and the latitude of  $35^{\circ}$  South (Cape of Good Hope, South Africa), and on the eastern side of these Oceans, its populations are dispersed between the latitude of  $35^{\circ}$  North (southern California, U.S.A.) and the latitude of  $25^{\circ}$  South (northern Chile).

Only the temperature of the upper part of the marine waters seems to restrict their distribution.

See its distribution map on: www.nl.wikipedia.org

#### Genus Pararhincodon HERMAN, 1976 in CAPPETTA, 1976

#### **Systematics**

The extinct Genus *Pararhincodon* HERMAN *in* CAPPETTA, 1976 was represented by six taxa: *P. crochardi* HERMAN, 1977, from the Campanian of the Mons Basin, Belgium, and the Turonian of northern France, *P. ypresiensis* CAPPETTA, 1976, from the Lower Ypresian in southern England and all the Ypresian strata from

Belgium, *P. lehmanni* CAPPETTA, 1980, from the Cenomanian of northern Lebanon, *P. groessensi* HERMAN, 1982, from the Maastrichtian of northern Germany, *P. germaini* ADNET, 2000, from the Middle Lutetian of south-western France and *P. susanae* BERNARDEZ, 2002, from the Upper Campanian of the Asturias, Spain.

#### **Odontological characteristics of the Genus** *Pararhincodon*

For description and illustrations: Cappetta 1976: p.: 571, Cappetta 2002: pp.: 156-157 and fig.: 150 and Herman *in* Cappetta 1977: p.: 561.

#### Remark

This extinct Genus had a very large spatio-temporal range and distribution. It was represented by diverse taxa from the Cenomanian to the Middle Lutetian, and as far as known, from northern Germany to northern Spain and Lebanon.

The Genus *Pararhincodon* seems to be one of the numerous victims of the Eocene-Oligocene Transition, and *Parirhincodon lehmanni* CAPPETTA, 1980, living in the Upper Cretaceous is maybe the ancestor of the extant Indo-Pacific species.

For references, see: Adnet 2008, Bernardez 2002, Cappetta 1976, Cappetta 1980, Cappetta 2006, Cappetta 2012, Herman 1977 and Herman 1982.

# 10.6. Systematic problems: the Orectolobiformes incertae Family sensu CAPPETTA, 2012

## 1. List of the taxa

The following eight extinct generic taxa were considered valid but of *incertae* Family: Genus *Phorcynis* THIOLLIERE, 1852, Genus *Squatirhina*\* CASIER, 1947, Genus *Annaea* THIES, 1983, Genus *Cretascyllium* MÜLLER & DIEDRICH, 1991, Genus *Folipistrix* KRIWET, 2003, Genus *Dorsetoscyllium* UNDERWOOD & WARD, 2004, Genus *Heterophorcynus* UNDERWOOD & WARD, 2004 and Genus *Ornatoscyllium* UNDERWOOD & WARD, 2004.

\*Among the fossil taxa attributed erroneously to the Genus *Squatirhina*, *Squatirhina americana* ESTES, 1964 is considered as a *Rhinobatoidei incert. Fam.* (Cappetta 2006: p.: 382).

#### 2. Partial Solution

In his Revised Handbook (End July 2012), Cappetta remained careful concerning the systematic position to the seven following extinct Genera\* and persists to consider all these taxa as *Orectolobiformes incertae sedis*.

\*Genus *Phorcynis* THIOLLIERE, 1852, Genus *Annaea* THIES, 1983, Genus *Cretascyllium* MÜLLER & DIEDRICH, 1991, Genus *Folipistrix* KRIWET, 2003, Genus *Dorsetoscyllium* UNDERWOOD & WARD, 2004, Genus *Heterophorcynus* UNDERWOOD & WARD, 2004, and Genus *Ornatoscyllium* UNDERWOOD & WARD, 2004.

#### 3. Morphological observations

The flat and elongated morphology of the crown tooth, and particularly the tongue-like apron of the three extinct Genera\*: *Phorcynis* THIOLLIERE, 1852, *Heterophorcynus* UNDERWOOD & WARD, 2004 and *Dorsetoscyllium* UNDERWOOD & WARD, 2004 allow suggesting that a strong phylogenetic relation between them is more than probable.

\*Enumerated according to their geological Age.

The same morphological considerations allow suggesting that there is a possible phylogenetic relation between the two extinct Genera\*: *Dorsetoscyllium* UNDERWOOD & WARD, 2004 and *Ornatoscyllium* UNDERWOOD & WARD, 2004.

But the relatively strong ornamentation of the extern side of the dental crowns of the diverse species of the Genus *Ornatoscyllium* indicates that they must be considered as members of the Family Ginglymostamidae GILL, 1862.

The Genus Orectoloboides CAPPETTA, 1977 may have been the last representative of this second lineage.

# 11. Problem of the systematic position of the Genus *Squatirhina* CASIER, 1947

## 11.1. Ancient data concerning the Genus Squatirhina

#### Genus Squatirhina CASIER, 1947

#### **Systematics**

According to Cappetta (2012: p.: 356), this extinct Genus regroups the four following species: *Squatirhina lonzeensis* CASIER, 1947, *Squatirhina kannensis* HERMAN, 1977, *Squatirhina thiesi* BIDDLE, 1993 and *Squatirhina westfalica* MÜLLER & DIEDRICH, 1991.

#### **Odontological characteristics of the Genus** *Squatirhina*

#### Generalities

The tri-lateral overlapping of the dental crown of all their teeth and the absence of lateral notches on the dental root guarantee that their teeth were not interlinked.

#### **Dental root characteristics**

All the dental roots of the teeth of the four taxa attributed to this Genus are holaulacorhyzid. Their median central groove is wide and deep.

Their dental crown is monocuspid\* and, except for some extern short basilar costulae, absolutely smooth.

\*This data is also valid for their supposed juvenile teeth.

The lateral radicular lobes of their anterior teeth are perfectly symmetric, as well as these of their lateral teeth, and they may seem to be too symmetric for orectoloboid teeth.

#### **Dental crown characteristics**

The dental crowns of the teeth of the four taxa attributed to this Genus are monocuspid and the base of their dental crown overlaps generously the top of their holaulacorhyzid dental root.

#### **Biological characteristics of the Genus** *Squatirhina*

In absence of any skeleton, its anatomical characteristics remain unknown, but the general morphology of its teeth allows supposing that the representatives of the four species attributed to this Genus were active middle-sized predators. It is difficult to estimate how flattened their body was.

#### Spatio-temporal distribution of the Genus Squatirhina

This Genus is represented by isolated teeth discovered in Aptian\* levels of Great Britain, in Albian levels of western Europe and central Asia\*\*, in Turonian levels of northern France, in the Coniacian-Santonian boundary in Belgium, in the Lower and Upper Campanian from northern France\*\*\* and in the Lower and Upper Maastrichtian of Belgium and the Netherlands.

\*See Bibliography-Systematics: Underwood & Ward 2004

\*\*see Bibliography-Systematics: Cappetta 2012: p.: 356.

\*\*\*Prospections of the senior-author at Hardivillers and Hem (Somme Department, France).

The Genus *Squatirhina* seems to have disappeared at the end of the Cretaceous Period, but some teeth remarkably preserved, were discovered\* in a level, constituted principally by the accumulation of bryozoan fragments, of the Tuffeau of Ciply Formation of Danian Age at Ciply (Hainaut Province, Belgium).

\*Prospections of the senior-author between 1974 and 1981. The vertebrates remains discovered during these prospections were included in the *Crochard Collection* in possession of the Department of Vertebrate Paleontology of the I.R.S.N.B. (Brussels, Belgium).

#### Squatirhina lonzeensis CASIER, 1947

The perfectly preserved teeth of the type species of this Genus were discovered in a level of the Glauconite of Lonzee Formation of Santonian Age (Upper Cretaceous) at Lonzée, near Gembloux (Namur Province, Belgium).

For references and illustrations, see: see Casier 1947: p.: 13, p.: 12 fig.: 4b and pl.: 5: fig.: 2. and Herman 1977: pl.: 9: figs.: 9a and 9b.

#### Squatirhina kannensis HERMAN, 1977

Perfectly preserved teeth, representing the type-set of this species were discovered in the *coprolithes level* of the Tuffeau of the Maastricht Formation of Maastrichtian Age (uppermost Cretaceous) at Kanne (Limburg Province, Belgium), but also in four other levels of the same Formation in diverse quarries of the Liège and Limburg Provinces in the same area.

Many other well preserved teeth were discovered in the basal conglomerate of the Chalk of Obourg Formation (Upper Campanian) at Obourg, and some in the five phosphatic levels of the Trivières Chalk Formation (Lower Campanian), at Trivières, in the Hainaut Province (Belgium).

This species is also a common species of diverse phosphatic Maastrichtian levels in the Limburg Province of the Netherlands.

The senior-author has also discovered two teeth of this species in prospective borings for chalk exploitations in the Liège Province (Belgium) in the uppermost Campanian.

For references, see: Herman 1977: p.: 157. For illustrations, see: Herman 1977: pl.: 6, figs.: 10a to10j.

#### Squatirhina thiesi BIDDLE, 1993

This species, based on numerous perfectly preserved isolated teeth discovered in the Middle Albian at Pargny, Maurupt and some other neighbouring localities in the Aube Department (France), where they seem to be relatively common.

The senior-author has also discovered some teeth attributable to this species in the Albian of the Cap-Blanc-Nez in the Pas-de-Calais Department (France).

For references, see: Biddle 1993: p.: 216, pl.: 6, figs.: 9-11.

## Squatirhina westfalica Müller & Diedrich, 1991

This species is based on isolated teeth discovered in a Lower or Middle Cenomanian level in northern East Germany.

For references, see: Müller & Diedrich 1991: p.: 47: fig.: 6, pl.:19, fig.: 5

#### **11.2.** Additional reflections

The senior-author adds one argument to the fundamental argumentation of their holaulacorhyzid radicular structure. The fact that marginal friction marks are visible on the edges of the base of the dental crown of numerous teeth\* allows supposing that their teeth were not arranged in parallel rows but in imbricated rows.

\*Supposed to have been functional teeth.

Additionally, the senior-author points out the fact that the oldest fossil teeth attributed to this Genus are of Aptian Age (earlier Upper Cretaceous) and that, at this period, no true rajiform Batoidei had been discovered.

## 11.3. Systematic readjustment and Conclusion

The fact that all the teeth of all its fossil representatives were in possession of a large and prominent apron was considered by the majority of the paleochondrichthyologists as a sufficient criterion to consider the Genus

*Squatirhina* as a possible fossil link between the Family Squatinidae BONAPARTE, 1836 and the Family Orectolobidae APPLEGATE, 1974.

In 2012, Cappetta (2012: pp.: 355-356) proposed a very interesting different attribution. As all the representatives of the Genus *Squatirhina* have a holaulacorhyzid\* dental root, this Genus could be a Batoidei and not a Selachii.

\*All the teeth of all the extant or extinct representatives of the Order Squatiniformes and the Order Orectolobiformes *sensu lato* are hemiaulacorhyzid.

The large majority of the paleochondrichthyologists opted for its attribution to the Family Orectolobidae *sensu* APPLEGATE, 1974. For the two additional data, previously mentioned, the senior-author opts for the same proposal.

# 12. Order Pristiophoriformes BERG, 1958

## **12.1.** Living representatives of the Order Pristiophoriformes

## **Systematics**

This Order regroups all the extant and extinct representatives of the extant Families: Family Pristiophoridae BLEEKER, 1859.

## Family Pristiophoridae BLEEKER, 1859

The Family Pristiophoridae regroups the three\* following Genera: The two extant Genera: Genus *Pristiophorus* MÜLLER & HENLE, 1837 and Genus *Pliotrema* REGAN, 1909 and the extinct Genus *Propristiophorus* WOODWARD, 1932.

\*The validity of the Genus *Ikamauius* KEYES, 1879, based only on one broken rostral tooth seems more than dubious. It was suggested that it could be the extremity of a siluroid spine (Pisces -Teleostei). See Herman & Van Waes 2012: *Géominpal Belgica*. **2**. p.: 65.

# Genus Pristiophorus Müller & Henle, 1837

(See Plates 58 to 62 and comments)

## **Systematics**

According to Compagno 1984, and FishBase 2011, this Genus is represented by the seven\* following extant species: *P. cirratus* (LATHAM, 1794), *P. japonicus* GÜNTHER, 1870, *P. nudipinnis* GÜNTHER, 1870, *P. schroederi* SPRINGER & BULLIS, 1960, *P. delicatus* LAST & WHITE, 2008, *Pristiophorus peroniensis* YEARSLEY, LAST & WHITE, 2008 and *P. nancyae* EBERT & CAILLIET, 2011.

\*But only six if *Pristiophorus peroniensis* YEARSLEY, LAST & WHITE, 2008 may be synonymised with *P. delicatus* LAST & WHITE, 2008. Delicate problem for the co-authors of these two specific taxa.

Exception made for *P. schroederi* SPRINGER & BULLIS, 1960, living off the coasts of the Bahamas Islands (Florida, U.S.A.) and caught at depths of eighty to thousand metres, all the *Pristiophorus* taxa are inhabitants of shallow waters of the Indo-Pacific Ocean.

For references, see:

Herman, Hovestadt-Euler & Hovestadt 1992 and Kiraly, Moore & Jasinsky 2003.

#### **Biological characteristics of the Genus** *Pristiophorus*

The six extant species of this Genus possess a, more or less, elongated rostrum with marginal rostral teeth, five pairs of gill slits and two dorsal fins without fin-spines. They possess one pair of rostral *cirri* helping them to detect their preys.

They have an elongated spindle-shaped body. All the representatives, of the species sufficiently known, are ovoviparous.

All their individuals are predators of small invertebrates and very small teleostean fishes living on, or embedded

in, the sea bottom.

#### **Odontological characteristics of the Genus** *Pristiophorus*

#### Placement in the jaws

Their oral teeth are arranged in independent parallel rows.

#### **Dental root**

All the extant taxa examined\* of the Genus *Pristiophorus* have an irregularly shaped\*\* holaulacorhyzid root with two elongated central foramina, an extremely short bi-lobed medio-intern protuberance and two root lobes horizontally extended.

\*Five species.

\*\*Suggesting that their teeth, as well as their body, had been laterally compressed.

#### **Dental crown**

All the extant and extinct taxa examined of the Genus *Pristiophorus* have a monocuspid crown. Their unique cuspid is narrow and acuminate, and the intern side is absolutely smooth. The extern side presents some small basal costulae.

#### **Rostral teeth**

All the extant and extinct taxa examined of the Genus *Pristiophorus* are in possession of a long, narrow and acuminate rostrum presenting numerous straight to lightly curved rostral teeth, alternating in size.

These rostral teeth are constituted by a calcium-phosphate peduncle and a capuchin, such as the crown of the oral teeth, made of apatite.

#### Mode of reproduction

All\* the extant taxa of the Genus *Pristiophorus* are ovoviviparous. For the species of which the gestation was observed, this period requests twelve months or a little more.

\*The mode of reproduction of *P. nancyae* EBERT & CAILLIET, 2011 remains uncertain.

#### Pristiophorus cirratus (LATHAM, 1794)

#### Distribution

The diverse scattered populations of *Pristiophorus cirratus* (LATHAM, 1794), distinguishable only by some very light morphological details such as the proportions of the length and the width of their rostrum, inhabit principally\*, the sandy bottoms off the south-western and southern coasts of Australia and off the coasts of Tasmania and all the islands of the Bass Strait.

\*Divers and fishermen friends of the senior-author said that this species may be encountered in some estuaries, which allows supposing that some of their populations support brackish environments.

#### Source: www.en.wikipedia.org

#### **Depth record**

The same sources of information seem to be coherent and confirm that this species frequents sea bottoms comprised between 30 metres to 180 metres, but that some specimens were caught at a maximum of 350 metres depth.

#### **Reproduction mode**

#### Ovoviviparity.

#### Pristiophorus japonicus GÜNTHER, 1870

#### Distribution

The diverse populations of Pristiophorus japonicus GÜNTHER, 1870 occupy a very large marine area covering all

the coasts of the China Sea, the Japan Sea and all the coasts of Taiwan and the eastern coasts of Japan.

#### **Depth record**

According to FishBase, the individuals of this species live from littoral waters to a depth of 500 metres.

#### **Reproduction mode**

Ovoviviparity

For references, see: Compagno 1984, Günther 1870 and Last & Stevens 1994.

#### Pristiophorus nudipinnis GÜNTHER, 1870

#### Distribution

The diverse populations of *Pristiophorus nudipinnis* GÜNTHER, 1870 are dispersed along the southwestern coasts and the southern coasts of Australia. They are also present along all the coasts of Tasmania and along the coasts of all the islands of the Bass Strait.

Source: www.en.wikipedia.org

#### **Depth record**

Divers and fishermen friends of the senior-author agree that this species may be encountered from 30 to 180 metres depth (personal communication).

#### Mode of reproduction

Ovoviviparity

For references, see: Compagno 1984, Günther 1870 and Last & Stevens 1994.

# Pristiophorus schroederi SPRINGER & BULLIS, 1960

#### Distribution

The diverse, but not numerous, populations of *Pristiophorus schroederi* are scattered off some parts of the coasts of Florida State (U.S.A.), the Bahamas Islands (U.S.A.) and off northern Cuba.

Source: www.nl.wikipedia.org

#### **Depth record**

According to diverse fishermen friends' personal information, living individuals of *Pristiophorus schroederi* inhabit sea bottoms of a depth comprised between 360 and 1050 metres.

#### Mode of reproduction

Ovoviviparity

#### Singularity

Rostral teeth of the Belgian Pliocene were attributed to this species, but, at this period, the depth of the Kattendijck Sands Formation deposits in the Antwerp Basin represented sea bottoms of a maximum of 40 metres depth.

For references, see: Compagno 1984, Herman 1974 and Springer & Bullis 1960.

#### Pristiophorus delicatus YEARSLEY, LAST & WHITE, 2008

#### Distribution

The poorly known populations of Pristiophorus delicatus are dispersed off the south western coasts of Australia.

Source: www.en.wikipedia.org

#### **Depth record**

According to diverse fishermen friends' personal information, living individuals of *Pristiophorus delicatus* live on sea bottoms of a depth comprised between 220 and 380 metres. Records of 405 metres depth.

#### Mode of reproduction

Ovoviviparity

For references, see: Yearsley, Last & White 2008.

#### Pristiophorus peroniensis YEARSLEY, LAST & WHITE, 2008

#### Distribution

If the populations attributed to this species represent effectively a distinct species and are not a synonym of *P. delicatus* YEARSLEY, LAST & WHITE, 2008, they are reported as inhabitants of the southern East part of Australia.

#### Source: www.en.wikipedia.org

This depth range partially covers the depth range attributed to *P. delicatus* YEARSLEY, LAST & WHITE, 2008 and nearly the same geographical distribution. Analysis of its mitochondrial DNA may resolve this problem.

The fact whether *P. peroniensis* is a synonym of *P. delicatus* or not, changes nothing to the Natural History of the Genus *Pristiophorus*.

#### **Depth record**

The individuals attributed to *Pristiophorus peroniensis* inhabit bottoms having a depth comprised between 100 and 630 metres.

## Mode of reproduction

Ovoviviparity

For references, see: Yearsley, Last & White 2008.

#### Pristiophorus nancyae EBERT & CAILLIET, 2011

#### Distribution

The three groups of small populations attributed to *Pristiophorus nancyae* occupy three distribution areas without any relation: The first one, including its holotype, is located off the Mozambique coast.

The second group of populations attributed to this species was discovered off the Socotra Island, at *circa* 8.300 kilometres in the northern direction, and the third group of populations attributed to this species was discovered off the Katiawar coasts (India), at more than 11.500 kilometres in the North-North-East direction.

The fact that these three groups of populations, separated by such huge distances, could represent a single species is more than dubious and requires further investigations. Analysis of their mitochondrial DNA should resolve this problem.

But a thorough anatomical investigation of some individuals of these three populations could also resolve this problem and its cost would be far less expensive than a genetic approach.

#### Source: <u>www.de.wikipedia.org</u>

The holotype of this species was caught, in 2010, off the coast of Mozambique at a depth of circa 500 metres.

#### Mode of reproduction

#### Supposed ovoviviparity

For references, see: Ebert & Cailliet 2011.

# Genus Pliotrema REGAN, 1906

(See Plates 63 to 65 and comments)

#### **Systematics**

This extant Genus is based on its holotype and unique representative Pliotrema warreni REGAN, 1906.

#### **Odontological characteristics of the Genus** *Pliotrema*

#### Placement of the teeth in the jaws

Their oral teeth are placed in independent parallel rows.

#### **General morphology**

They are relatively narrow.

#### Dental root characteristics of the Genus *Pliotrema*

All the teeth of all the extant individuals of the single species of the Genus *Pliotrema* have a hemiaulacorhyzid root.

#### Dental crown characteristics of the Genus Pliotrema

All their teeth present a narrow monocuspid crown presenting a large arched apron separated from the basal extremities of the crown by two deep notches.

Their medio-intern protuberance is long but narrow and adjoined by one pair of lightly arched root lobes, enhancing their appearance of laterally compressed teeth.

The extern side of their crown presents a short keel on its upper extremity. This keel is more marked on the crown of the anterior teeth and its volume decreases progressively in the commissural direction. The intern side of their dental crown is absolutely smooth.

Just above their medio-intern radicular protuberance, their crown presents an elongated sub-vertical extension (uvula).

Contrarily to the rounded extremity of the *uvula* of the dental crown of the different species of the Genus *Pristiophorus*, the *uvula* of the dental crown of *Pliotrema* has a pronounced bifid or trifid extremity.

#### **Rostral teeth characteristics**

The main characteristics of the growth process of the rostral teeth of the Genus *Pliotrema* are identic to the growth process of the rostral teeth of the Genus *Pristiophorus*, but, on its median part, the rear side of the enameloid capuchin of all the mature rostral teeth of *Pliotrema warreni* is strongly serrated and presents massive oblique folds between this serration.

This singular ornamentation does not exist on the rostral teeth of embryos or new born individuals, but it develops very quickly.

The capuchin of the rostral teeth of new born individuals is soft and twice shorter than their height. The capuchin solidifies in the days following their hatching and begins to grow. One week later, the height of the capuchin is equal to the height of the peduncle and the serration appears.

The base of the peduncles of the new born looks like a camel's saddle, with two very long vertical lateral extensions to assure its anchorage on the side of the rostrum.

One week later the peduncle has its definitive horse's saddle morphology, with shorter lateral extensions. Its base is lightly curved.

#### Biological characteristics of the Genus Pliotrema

The unique species of this Genus possesses a, more or less, elongated rostrum with marginal rostral teeth, six pairs of gill slits and two dorsal fins without fin-spines. The individuals possess one pair of rostral *cirri* helping them to detect and localise their preys. They have an elongated spindle-shaped body and are ovoviparous.

All their individuals are predators of small invertebrates and very small teleostean fishes living on, or embedded in, the sea bottom.

#### **Systematics**

The extant Genus *Pliotrema* is represented only by its holotype: *P. warreni* REGAN, 1906. The individuals of this species possess six gill slits and rostral teeth presenting transverse ridges. The longest rostral teeth have a posterior crenulation.

#### **Biological remark**

The possession of a sixth pair of gill slits is supposed to have the same genetic-traumatic origin as the one having affected the Super Order Echinorhinomorphii, which passed, suddenly and successively, from five to six and later to seven pairs of gill slits and the Rajiformes of the Family Hexatrygonidae, which also passed suddenly from five to six pairs of gill slits.

#### **Geological range**

Some fossil remains were reported\* from Thanetian strata of California and Middle Miocene strata of South Africa.

\*According to Keyes 1982.

#### Pliotrema warreni REGAN, 1906

#### Distribution

The diverse populations of this species have a very restricted distribution area, located on four principal zones off the South African coasts and one off the more southern part of Madagascar.

#### See their distribution map on the site: www.en.wikipedia.org

They are generally encountered in depths comprised between 40 to 60 metres, but some individuals were caught deeper than 450 metres\*.

\*Information from Madagascar fishermen.

#### Particularity of their rostral teeth

The teeth of the saw of the *Pliotrema warreni* individuals alternate, such as those of all the extant and extinct taxa\* of the Genus *Pristiophorus*, presenting successively, on both sides of their saw, a long and a short rostral tooth.

\*Known by skeletons.

#### **Behaviour**

The individuals of *Pliotrema warreni* detect their invertebrate preys, embedded in muddy or sandy bottoms of their personal territory, using their cirri and their very highly sensible sensorial cells.

#### Feeding

The individuals of the five populations known feed principally on annelids, crustaceans, squids and small fishes.

For references, see: Compagno 1984, Herman, Hovestadt-Euler & Hovestadt 1992, Keyes 1982 and Regan 1906.

# 12.2. Odontological characteristics of the Order Pristiophoriformes

The extern side of the dental crown of the oral teeth of all the extant and extinct species attributed to this Order overlaps the top of their hemiaulacorhyzid root.

The dental crown of the oral teeth of all the extant and extinct species attributed to this Order presents an arched apron and a long intern expansion covering the main part of the surface of the medio-intern protuberance of their dental root.

The intern side of the dental crown of the oral teeth of all the extant and extinct species attributed to this Order is absolutely smooth.

## **12.3.** Biological characteristics of the Order Pristiophoriformes

All the extant species of Pristiophoriformes demonstrate that they are ovoviviparous Chondrichthyes possessing five or six pairs of gill slits, two dorsal fins without spines, two cirri, cylindrical vertebrae and a rostrum with rostral teeth.

The embryos of all the extant taxa of the two Genera *Pristiophorus* MÜLLER & HENLE, 1837 and *Pliotrema* REGAN, 1906, regrouped in this Order, do not have rostral teeth yet. They appear and grow very quickly after their birth.

## 12.4. Biological data detectable on fossil skeletons of the Order Pristiophoriformes

The skeletons of Pristiophoriformes discovered in the Upper Cretaceous of Lebanon demonstrate that their oldest representatives were Chondrichthyes possessing five pairs of gill slits, two dorsal fins without spines, two cirri, cylindrical vertebrae and a rostrum with rostral teeth.

## 12.5. Fossil representatives of the Order Pristiophoriformes

## Remark

The best and the most complete source of illustrations of the teeth of all the extinct taxa of the Order Pristiophoriformes is the revised Handbook of Palaeoichthylogy – Vol. 3E. 2012. 512 p., 438 figs. Author: Henri Cappetta. Editor: Dr. Fritz Pfeil Verlag. München.

Illustrations concerning pristiophorid taxa, see: figs.: 130 and 131.

## Family Pristiophoridae BLEEKER, 1859

The senior-author considers that the Family Pristiophoridae regroups the three following Genera: The extinct Genus *Propristiophorus* WOODWARD, 1932 and the two extant Genera: Genus *Pristiophorus* MÜLLER & HENLE, 1837 and Genus *Pliotrema* REGAN, 1906.

#### Genus Pristiophorus Müller & Henle, 1837

Cappetta admitted (2006: p.: 399) that the seven following fossil taxa\* were attributed to the Genus *Pristiophorus: P. lanceolatus* DAVIS, 1888, based on a rostral tooth, from the Oligocene of New Zealand, *P. suevicus* JAEKEL, 1890 from the Middle Miocene of the Baden-Würtemberg, southern Germany, *P. napierensis* CHAPMAN, 1918, rostral teeth from the Pliocene of New Zealand, *P. lineatus* APPLEGATE & UYENO, 1968 from the Upper Oligocene of Hokkaido, Japan, *P. palaeocenicus* (HERMAN, 1973) from the Thanetian of the Ouled Abdoun Basin, Morocco, *P. rupeliensis* STEURBAUT & HERMAN, 1978 from the Middle Oligocene of Belgium, *P. lacipidinensis* ADNET, 2002 from the Middle Eocene of southwestern France.

\*Except for the oral teeth of *P. lanceolatus* DAVIS, 1888 and *P. napierensis* CHAPMAN, 1918, the senior-author had the possibility to examine these of the five other taxa and to collect himself hundreds of rostral and oral teeth of *P. rupeliensis* STEURBAUT & HERMAN, 1978.

#### Genus Propristiophorus WOODWARD, 1932 (See Plate 66 and comments)

The Genus *Propristiophorus* WOODWARD, 1932 is based on its single specific representative *Propristiophorus tumidens* WOODWARD, 1932 represented by one remarkably preserved skeleton discovered at Sahel Alma in a level of the Cenomanian (Upper Cretaceous) of northern Lebanon.

Its holotype lies on its back and is still preserved in the Collections of the American University of Beyrouth (Lebanon).

## Criteria that allow suggesting its revalidation

The arguments proposed to suggest the revalidation of the Genus *Propristiophorus* WOODWARD, 1932 are of diverse types: odontological criteria, anatomical criteria and paleogeographical considerations.

The Department of Vertebrate Paleontology of the M.N.H.N. received, between 1948 and 1972, numerous specimens\* from the Upper Cretaceous of northern Lebanon.

\*Donations of Ir. Louis Dubertret.

These donations included a second very well preserved specimen of *Propristiophorus tumidens* WOODWARD, 1932. This last one also lies on its back and a very large part of its dentition is examinable.

## Anatomical criteria

An examination of this very well preserved second specimen allows enumerating numerous osteological and odontological data.

#### Rostrum

Its rostrum is narrow and elongated. Its length represents, approximately, one eighth of its width. It is characterized by the absence of enlarged denticles along the lateral margins of its rostrum.

On this specimen, no rostral teeth are observable, but some places where they could have been located are.

These rostral teeth are perfectly preserved on the second specimen given, in 1960, to the M.N.H.N. (Paris, France). These last ones differ also from the rostral teeth of all the other taxa attributed to the extant Genus Pristiophorus (See further).

#### Pectoral girdle

Its radial cartilages are relatively shorter and more slender than these of the pectoral girdle of the extant taxa of the Genus *Pristiophorus*.

### Vertebral centrae

The vertebral centrae of the anterior part of their vertebral column seem to have been less calcified than the vertebral centrae of the extant taxa of the Genus *Pristiophorus*.

If confirmed by the examination of the specimen of the M.N.H.N., these data could allow supposing that *Propristiophorus* was unable to dress its head as high as all the living representatives of the Genus *Pristiophorus* do.

## **Odontological criteria**

The teeth of its holotype, lying on its ventral face, have never been described, but the second specimen, discovered in 1960, lying on its back made the examination of its oral teeth possible.

A rapid examination of the dentition of this specimen immediately demonstrates the evident odontological characteristics that allow differentiating the extinct Genus *Propristiophorus* WOODWARD, 1932 from the extant Genus *Pristiophorus* MÜLLER & HENLE, 1837.

All the oral teeth of the two specimens known of *Propristiophorus tumidens* WOODWARD, 1932 have a dental crown of which the base presents an ornamentation constituted by numerous subvertical folds, which are absent on all the dental crowns of all the representatives of the Genus *Pristiophorus* MÜLLER & HENLE, 1837.

The structure of their pectoral girdles and the basal ornamentation of their rostral teeth, details observed by Woodward himself, enforce the idea that two different Genera are concerned.

The Genus Propristiophorus will probably be revised by Dr. Fritz Pfeil (München, Germany).

## **Rostral teeth particularities** Ornamentation of their capuchin

The capuchin of the rostral teeth of *Propristiophorus tumidens* presents numerous very long and fine enamel folds which extend from the base of the capuchin to the end of this one.

These of the extinct and extant taxa attributed to the Genus Pristiophorus present only very short basal costulae.

#### Structure of their peduncle

The median anterio-posterior basal groove of their peduncle is not as deep as this of the Genus *Pristiophorus* and its lateral protective lobes are not so developed.

## **Paleogeographical arguments**

The opening of the North Atlantic Ocean, during the Upper Jurassic Period, progressively separated the continental mass of North America from the Eurasian continental mass.

This major geophysical event had for effect the formation of parallel trenches of thousands of metres and the dislocation and submersion of a central pacific micro-continent and, or, a continuous chain of central pacific Archipelagos.

The achievement of the formation of the Cordilleras de los Andes definitely stopped all marine faunal access to the Atlantic Ocean.

In its central part, subsisted\* some narrow straits connecting the Pacific Ocean and Atlantic Ocean.

\*To the Lower or Middle Pliocene.

## 12.6. Conclusion and Natural History of the Order Pristiophoriformes

### Conclusion

This extant Order is only represented by one Family, the Family Pristiophoridae including only two extant Genera: Genus *Pristiophorus* and Genus *Pliotrema*.

The Genus *Pliotrema* is endemic to Australia, but the Genus *Pristiophorus* (*sensu* MÜLLER & HENLE, 1837) has a much wider distribution, including diverse parts of the Indian Ocean, the Pacific Ocean and the western side of the North Atlantic Ocean.

The Genus *Pristiophorus* having no extant representatives in the Mediterranean Sea, its ancestor could be the extinct Genus *Propristiophorus* living in the Near-East during the Upper Cretaceous Period.

## Natural History of the Order Pristiophoriformes

## 1. The Natural History of the Genus *Pristiophorus*

The opening of the North Atlantic Ocean produced numerous parallel trenches of thousands of metres that no pristiophorid taxon was able to cross.

Their diverse coastal to upper slopes populations had only two possibilities: colonise northern coasts or oriental coasts.

The dislocation and the deep submersion of a central pacific micro-continent and, or, a continuous chain of central pacific archipelagos fixed the majority of them on the western side of the Great Pacific Barrier and definitely stopped all further attempts of any more oriental colonisation.

Only the ancestors of the extant populations of *Pristiophorus schroederi*, the sole extant species of the Genus crossed this huge mountain chain in its central part, where some narrow straits subsisted to the Neogene Period, connecting the Pacific Ocean and the Atlantic Ocean.

## 2. The Natural History of the Genus Pliotrema

The extant Genus *Pliotrema* REGAN, 1906, seems to be endemic to Australia. By its possession of a sixth pair of gill slits and the ornamentation of its rostral teeth, this Genus may be considered as the more evolved taxon of the Family Pristiophoridae BLEEKER, 1859.

It is logical to consider this Genus, and its single representative *P. warreni* REGAN, 1906 as a local population of the Genus *Pristiophorus* of which the genetic code was significantly modified.

As far as known, the Genus *Pliotrema* has no fossil representative and *Pristiophorus lanceolatus* DAVIS, 1888, based on one rostral tooth discovered in an Oligocene level in New Zealand, is the last fossil representative of the Genus *Pristiophorus* in this part of the world.

The sudden apparition of the Genus *Pliotrema* in this area allows supposing that the modification of the genetic code of one population of the Genus *Pristiophorus* is of post Oligocene Age and results from a brutal but local perturbation of the environment.

## **12.7. Similarities and differences existing between the members of the Order Ganopristiformes and the members of the Order Pristiophoriformes**

## **1.** General morphology of their body

All the extinct taxa, known by skeletons and the extant specific taxa of the Order Pristiophoriformes present a laterally compressed body.

Even at their embryo stage, this fact is valid for all the extant taxa of the Order Pristiophoriformes.

All the extinct taxa, known by skeletons and the extant specific taxa of the Order Pristiophoriformes are in possession of a narrow and elongated rostrum.

## 2. Constitution of their rostral teeth

All the taxa of the two Orders Pristiophoriformes and Ganopristiformes possess numerous holaulacorhyzid rostral teeth constituted by a capuchin in apatite and a phosphate-carbonate peduncle.

# 3. Mode of implantation of the rostral teeth

This mode of implantation is identic for all the taxa of the two Orders Pristiophoriformes and Ganopristiformes. On both extern sides of the rostrum they are arranged as follows: one long rostral tooth alternating with one to three shorter rostral teeth.

This implantation mode is different from this of the Family Pristidae (Batoidei) which consists in a, more or less, deep insertion in the mass of the rostrum.

## 4. Oral teeth

The base of the monocuspid dental crown of all the representatives of the Order Pristiophoriformes and all the representatives of the Order Ganopristiformes overlaps the top of their holaulacorhyzid root.

All the extant and extinct specific taxa of the Order Pristiophoriformes present a smooth dental crown, but all the oral teeth of the specific taxa of the Order Ganopristiformes are ornamented.

The dental crown of all the representatives of the Order Pristiophoriformes and all the representatives of this Order Ganopristiformes are in possession of an apron, the most typical characteristic of all the extinct and extant representatives of the Super Order Orectolobomorphii.

## 5. Vertebral column

The vertebral column of all the extant specific taxa of the Order Pristiophoriformes and the extinct Order Ganopristiformes, known by skeletons, possess only cylindrical vertebrae.

## 6. Mode of reproduction

All the extant taxa of the Order Pristiophoriformes are ovoviviparous

and have a gestation period of circa twelve months.

The mode of reproduction of all the taxa of the extinct Order Ganopristiformes is of course unknown, but the morphology of their pelvic girdle allows supposing that they were also ovoviviparous.

## 7. Zone of apparition and Epoch

These two Orders appeared, approximately, in the same area and at the same Period: the lower part of the Upper Cretaceous in the Near-East (Lebanon-Syria).

#### 8. Odontological conclusion

The Ganopristiformes and the Pristiophoriphormes have for ancestors Families of two distinct lineages of the Super Order Orectolobomorphii. The Pristiophoriformes have for ancestor a Family of the Order Hemiscylliformes and the Ganopristiformes have for ancestor a Family of the Order Orectolobiformes rev.

The senior-author considers the members of the Order Ganopristiformes as evolved representatives of Selachii and not as representatives of Batomorphii.

# 9. Differences presented by the specific taxa of the Order Ganopristiformes and the Order Pristiophoriformes

## **Oral teeth**

All the dental crowns or the oral teeth of the Pristiophoriformes are smooth, but all the dental crowns or the oral teeth of the Ganopristiformes present various types of ornamentation.

## **Geological range**

Remains of Ganopristiformes were discovered in diverse strata ranging from the Lower Cretaceous of the Middle East, central Europe, North Africa, North America and central Asia to strata of uppermost Cretaceous ages in the same area.

Remains of Pristiophoriformes were discovered in diverse strata ranging from the Lower Cretaceous of the Middle East to the uppermost Pliocene strata. The rare survivals of this Order are presently represented in some areas of the Pacific Ocean.

Only one species, *Pristiophorus schroederi* SPRINGER & BULLIS, 1960 lives in the central western part of the Atlantic Ocean (off the coasts of the Bahamas Islands).

# **13.** New Parasystematic proposals

All the preceding anatomical, odontological and ancient or actual distribution data seem to allow the proposal of the three new Super Orders: Super Order Chlamydoselachomorphii, Super Order Squatinomorphii, and Super Order Pristiomorphii.

## 13.1. Super Order Chlamydoselachomorphii nov. Sup. Order

This new Super Order regroups the two following Orders: the Order Phoebodontiformes and the Order Chlamydoselachiformes.

#### Odontological characteristics of the Chlamydoselachomorphii

### **Dental root characteristics**

Because being so different of all the other extinct or extant types, a new term is proposed for their dental root-type: Chlamydoselaschorhyzid.

### **Dental crown characteristics**

The diverse elements constituting their dental crown are posed on the top of their dental root. Their dental crowns present one principal cuspid adjoined by one pair of high cusplets separated by diastema. Their crowns sometimes present one pair of small intermediary cusplets. Cuspids and cusplets are elongated and acuminated.

## Biological characteristics of the Chlamydoselachomorphii

The two extant representatives of this Super Order are in possession of six pairs of gill slits, the anterior one being fused. All their vertebrae have a cylindrical form and a circular transversal section. They possess two dorsal fins without fin-spines and are ovoviviparous.

# 13.2. Super Order Orectolobomorphii HERMAN & VAN WAES, 2012

According to their odontological characteristics, it seems logical to regroup the three Orders: Order Squatiniformes de BUEN, 1926, Order Orectolobiformes Ord. rev. and Order Hemiscylliiformes nov. Ord. in one Super Order: the Orectolobomorphii.

## Systematics

#### This Super Order regroups the three following Orders

The two extant ones: the Order Squatiniformes and the Order Orectolobiformes *sensu* GILL, 1896 and a new Order: the Order Hemiscylliformes which regroups two extinct Families: the Family Phorcynidae nov. Fam. and the Family Agaleidae REES, 2000 and the six extant Families: Family Brachaeluridae APPLEGATE, 1974, Family Ginglymostomatidae GILL, 1862, Family Stegostomatidae nov. Fam., Family Hemiscylliidae GILL, 1862, Family Rhincodontidae GARMAN, 1913, all represented by extant and fossil taxa.

# **Odontological characteristics of this Super Order**

All the teeth of the extinct or extant taxa included in this Super Order are placed in parallel rows, have a dental crown overlapping the top of their dental root, possess a crown presenting smooth anterio-posterior cutting edges, a hemiaulacorhyzid root and an apron.

The monocuspidy or the polycuspidy of their crown of highly variable morphology, allow the identification of their diverse Families.

# **Biological characteristics of this Super Order**

The extant taxa of this Super Order have five pairs of gill slits, two dorsal fins, without fin spines, oval-shaped *cervical* vertebrae and are oviparous or ovoviviparous.

The three first characteristics have been observed on many fossil skeletons, the oldest being of Lower Jurassic Age.

The mode of reproduction of the fossil taxa remains, of course, unknown.

The Phorcynidae nov. Fam. are characterized by teeth with a crown presenting a flat, rounded and more or less elongated apron.

The Squatiniformes are characterized by teeth with a crown presenting a cylindrical apron.

# 13.3. Super Order Pristiophoromorphii nov.

## **Order Pristiophoriformes**

This new Super Order is based on the single Order Pristiophoriformes, itself based on the single Family Pristiophoridae regrouping the extinct and extant generic taxa characterized by holaulacorhyzid oral teeth and the possession of a rostrum presenting rostral teeth.

## 13.4. Order Hemiscylliiformes nov.

This new Order, based on the extant Family Hemiscylliidae GILL, 1862, includes also the two extinct Families: Family Agaleidae REES, 2000 and Family Phorcynidae nov. Fam.

## Odontological characteristics of the Order Hemiscylliiformes

Their low dental crown presenting a central cuspid flanked by one pair of short rounded lateral cusplets overlapping the top of their hemiaulacorhyzid root, the possession of a short concave to convex apron, the possession of two short arched root lobes and a crown with intern and extern smooth faces are the principal odontological characteristics of this Order.

## **Biological characteristics of the Order Hemiscylliiformes**

All the extant and extinct representatives of this Order are in possession of five pairs of lateral gill slits, two dorsal fins without spine, two powerful pectoral and two strong pelvic fins able to move independently, the lack of an anal fin and their oviparous mode of reproduction are the principal biological characteristics of this Order.

## Spatio-temporal distribution of the Order Hemiscylliiformes

This Order regroups the six Families: Family Porcynidae, Family Agaleidae, Family Hemiscylliidae, Family Brachaeluridae, Family Parascylliidae and Family Ginglymostomatidae.

The two other orectolobid-like Families: The Family Stegostomatidae GILL, 1862 and the Family Rhincodontidae are regrouped in the Order Stegostomatiformes nov.

## Family Phorcynidae nov.

This new Family is proposed for regrouping the seven extinct Genera: Genus *Phorcynis* THIOLLIERE, 1854, Genus *Mesitea* GORJANOVIC-KRAMBERGER, 1885, Genus *Doratodus* SCHMID, 1861, Genus *Annaea* THIES, 1983, Genus *Dorsetoscyllium* UNDERWOOD & WARD, 2004, Genus *Heterophorcynis* UNDERWOOD & WARD, 2004 and Genus *Garrigascylium* GUINOT, ADNET & CAPPETTA, 2014.

## **Odontological characteristics of the Family Phorcynidae**

## General morphology

The base of the dental crown of all the teeth of all the taxa attributed to this extinct Family overlaps the top of their narrow and elongated dental crown on the extern side.

#### **Dental root**

Their dental roots are characterized by their hemiaulacorhyzid structure, their short root lobes and their arched form.

#### Dental crown

Their dental crowns are characterized by their flat and tongue-like protruding apron, their extern and intern smooth sides and the spiny form of their cusplets when present.

## **Biological characteristics of the Family Phorcynidae**

The fossil skeletal remains of some taxa attributed to this Family allow certifying that the representatives of these taxa were in possession of only five pairs of gill slits, a vertebral column constituted exclusively by vertebrae presenting a cylindrical centrum, two dorsal fins without fin-spine, one anal fin and teeth disposed in parallel rows.

The poor development of the anterior apertures of their neurocranium allows excluding the possibility that they could be the direct ancestors of Chondrichthyes disposing of a rostrum. Barbels\* surrounding the lower face of their mouth were never mentioned.

\*Which represent a distinctive characteristic of all the representatives of the Order Oretolobiformes *sensu* Gill 1896.

## Spatio-temporal distribution of each of its Genera

The Genus *Phorcynis* is based on *P. catulina* THIOLLIERE, 1852 represented by one skeleton discovered in a Kimmerigian level (Upper Jurassic) of Cérin (Ain Department, France).

The mono-specific Genus *Mesiteia* GORJANOVIC-KRAMBERGER, 1855 is based on skeletal remains of *Mesiteia emiliae* GORJANOVIC-KRAMBERGER, 1885 discovered in one level of Campanian Age (Upper Cretaceous) in Lebanon.

Other specimens were in possession of private merchants. Their examination, in 1973, confirmed the general morphology of their dentition. The lower jaw of one of these specimens allowed guaranteeing the presence of one symphyseal tooth-row.

The senior-author had the possibility to examine, in 1973, another skeleton in a Lebanese private Collection. This very well preserved specimen showed its two dorsal fins, without spine, its two pectoral fins, its two pelvic fins and its five pairs of gill slits. The dental crown of its lower lateral teeth presented a second pair of very short lateral cusplets.

The Genus Annaea THIES, 1983 is based on isolated teeth of its type-species Annaea carinata THIES, 1983 discovered in a level of upper Aalenian Age in northern Germany. It includes a second species: Annaea maubeugei DELSATE & THIES, 1995 based on isolated teeth of Toarcian Age in southern Belgium.

The mono-specific Genus *Doratodus* SCHMID, 1861 is based on isolated teeth of its type-species *Doratodus tricuspidatus* SCHMID, 1861 discovered in a level of Triassis Age in Germany.

The mono-specific Genus *Heterophorcynis* UNDERWOOD & WARD, 2004 is based on isolated teeth of its typespecies *Heterophorcynis microdon* discovered in a level of Bathonian Age (Middle Jurassic) in southern England.

The mono-specific Genus *Dorsetoscyllium* is based on *Dorsetoscyllium terraefullonicum* UNDERWOOD & WARD, 2004, represented by numerous isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England.

The mono-specific Genus *Garrigascyllium* is based on *Garrigascyllium aganticensis* GUINOT, CAPPETTA & AD-NET, 2014 represented by numerous isolated teeth discovered in a level of Valanginian Age (Lower Cretaceous) in south-western France.

### Conclusion

This Family had specific representatives ranging from Triassic Age in northern Germany to Valanginian Age (Lower Cretaceous) in south-western France.

As far as known, the members of the Family Phorcynidae inhabited shelf and coastal waters or waters covering a zone comprised between western Europe to the Near East.

#### Remark

The Genus *Protospinax* WOODWARD, 1918 presents all the odontological characteristics of the representatives of the Order Hemiscylliiformes, but its type species *P. annectans* WOODWARD, 1918 based on skeletal remains discovered in a level of Tithonian Age (uppermost Jurassic) presents one short vestigial dorsal fin spine.

This Genus may be considered as a parallel lineage of the ancestors of the Family Phorcynidae.

This extinct Genus is said to include also six other species: *P. lochensteinensis* THIES, 1983 based on isolated teeth discovered in a level of upper Oxfordian Age (Middle Jurassic) in western Swabian (Germany), *P. muftius* THIES, 1983 based on isolated teeth discovered in a level of Callovian Age (Middle Jurassic) in southern England, *P. bilobatus* UNDERWOOD & WARD, 2004 based on isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England, *P. carvvalhoi* UNDERWOOD & WARD, 2004 based on isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England, *P. carvvalhoi* UNDERWOOD & WARD, 2004 based on isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England, *P. planus* UNDERWOOD & WARD, 2004 based on isolated teeth discovered in a level of Kimmeridgian Age (Middle Jurassic) in southern England and *P. magnus* UNDERWOOD & WARD, 2004 based on isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England and *P. magnus* UNDERWOOD & WARD, 2004 based on isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England and *P. magnus* UNDERWOOD & WARD, 2004 based on isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England.

The validity of the four last taxa based on isolated teeth discovered in levels separated by very short time intervals and in geographical localities of close vicinity of the discovery of *P. muftius* THIES, 1983 require re-examination.

For descriptions and illustrations, see: Cappetta 2012: pp.: 147 to 149 and figs.:135 and 136. Thies 1983, Underwood & Ward 2004 and Woodward 1918.

## Family Agaleidae DUFFIN & WARD, 1983

The mono-generic Family Agaleidae includes only its mono-specific Genus *Agaleus* DUFFIN & WARD, 1983 represented only by its type species *A. dorsetensis* DUFFIN & WARD, 1983 based on isolated teeth discovered in a level of lower Sinemurian Age (Lower Jurassic) in southern England.

The fossil invertebrates discovered in the same level demonstrate that its paleoenvironment was representative of shallow water.

## Family Hemiscylliidae GILL, 1862

This Family regroups the two extant Genera: Genus *Hemiscyllium* MÜLLER & HENLE, 1837 and Genus *Chiloscyllium* MÜLLER & HENLE, 1837 and two extinct Genera: Genus *Acanthoscyllium* CAPPPETTA, 1980 and Genus *Almascyllium* CAPPPETTA, 1980.

The Genus *Hemiscyllium*, based on *Hemiscyllium ocelllatum* (BONNATERRE, 1788), regroups all the populations of the diverse extant species scattered along the coasts of the Indo-Pacific Ocean, Indonesia, Papua and Australia.

This Genus includes also two extinct taxa: *Hemiscyllium bruxelliensis* HERMAN, 1977, based on hundreds of isolated teeth discovered in levels of Middle and Upper Eocene Ages in Belgium and *Hemiscyllium hermani* MÜLLER, 1989, based on numerous isolated teeth discovered in one level of upper Campanian Age in Westfalia (Germany).

The Genus *Chiloscyllium* MÜLLER & HENLE, 1837 based on *Chiloscyllium plagiosum* (BENNETT, 1830) regroups all the populations of the diverse extant species scattered along the coasts of the Indo-Pacific Ocean, Indonesia, Papua and Australia.

This Genus includes also nine extinct taxa: *Chiloscyllium humboldti* (REUSS, 1845), based on some isolated teeth of Turonian Age discovered in the Czech Republic, *Chiloscyllium broennimani* CASIER, 1958, based on some isolated teeth of Maastrichtian Age (Upper Cretaceous) from Trinidad Island, *Chiloscyllium daimeriesi* (HERMAN, 1973), based on hundreds of isolated teeth of Selandian Age (Middle Paleocene discovered in Belgium, *Chiloscyllium greeni* (CAPPETTA, 1973), based on some isolated teeth of Turonian Age discovered in Dakota (U.S.A.), *Chiloscyllium missouriense* CASE, 1979, based on some isolated teeth of Campanian Age discovered in Montana (U.S.A.), *Chiloscyllium gaemersi* MÜLLER, 1989, based on some isolated teeth of upper Campanian Age discovered in Westfalia (southern Germany), *Chiloscyllium mereretiae* WERNER, 1989, based on isolated teeth of upper Canpanian Age in Egypt, *Chiloscyllium meraense* NOUBHANI & CAPPETTA, 1997, based on numerous isolated teeth of upper Ypresian Age in central Morocco.

The two American taxa require re-examination, because members of a Genus regrouping only small benthic sharks could not cross the North Atlantic after the Upper Cretaceous Period.

The Genus *Acanthoscyllium* CAPPETTA, 1980, based on *Acanthoscyllium sahelalmae* (PICTET & HUMBERT, 1866), is represented by numerous skeletons and skeletal remains discovered in levels of upper Santonian Age in Lebanon.

The Genus *Almascyllium* CAPPETTA, 1980, based on *Almascyllium cheikeliasi* (SIGNEUX, 1952), is represented by numerous skeletons and skeletal remains discovered in levels of upper Santonian Age in Lebanon.

#### Conclusion

This Family had specific extinct representatives ranging from upper Cenomanian Age (in Egypt, northern Africa) to the Middle and Upper Eocene Ages (in Belgium, Europe) and extant representatives scattered along the coasts of of the Indo-Pacific Ocean, Indonesia, Papua and Australia.

Fossil or extant representatives were never encountered more eastern than the Great Pacific Barrier.

## Family Brachaeluridae APPLEGATE, 1974

The Family Brachaeluridae regroups the two extant Genera: Genus *Brachaelurus* OGILBY, 1908 and *Heteros-cyllium* REGAN, 1908 and the two extinct Genera: Genus *Paraginglymostoma* HERMAN, 1982 and Genus *Palaeobrachaelurus* THIES, 1983.

The mono-specific extant Genus *Brachaelurus* is represented by its generotype *Brachaelurus waddi* (BLOCH & SCHNEIDER, 1801) inhabiting some north-eastern coasts of Australia. It had as plausible ancestor: *Brachaelurus templeuvensis* MOREAU & MATHIS, 2000, based on numerous teeth discovered in levels of Thanetian Age (Upper Paleocene) in northern France.

The mono-specific extant Genus *Heteroscyllium* is represented by its generotype *Heteroscyllium colcloughi* (OGILBY, 1908), inhabiting some northern and eastern coasts of Australia.

The mono-specific Genus *Paraginglymostoma* HERMAN, 1982 is based on *Paraginglymostoma bloti* HERMAN, 1982, represented by some teeth discovered in only one level of Maastrichtian Age in Nieder-Elbe (northern Germany).

The mono-specific Genus *Palaeobrachaelurus* THIES, 1983 is based on *Palaeobrachaelurus bedfordensis* THIES, 1983, represented by some teeth discovered in one level of Callovian Age (Middle Jurassic) in southern England.

#### Conclusion

This Family has extinct representatives ranging from Callovian Age (Middle Jurassic) in southern England to Maastrichtian Age (uppermost Cretaceous) in northern Germany, to Thanethian Age in northern France and has extant representatives endemic to Australia.

As a paleontologist, the senior-author insists to point out this inexplicable spatio-temporal discontinuity of distribution. All the fossil taxa attributed to the extant Genus *Brachaelurus* require revision.

## Family Ginglymostomatidae GILL, 1862

This Family regroups the two extant Genera: Genus *Ginglymostoma* MÜLLER & HENLE, 1837 based on its holotype and sole extant representative *G. cirratum* (BONNATERRE, 1788) and Genus *Nebrius* RÜPPEL, 1837 based on its holotype and sole extant representative *N. ferrugineus* (LESSON, 1831).

This Family includes also the seven following extinct Genera: Genus *Cantioscyllium* WOODWARD, 1889, Genus *Protoginglymostoma* HERMAN, 1977, Genus *Plicatoscyllium* CASE & CAPPETTA, 1977, Genus *Pseudoginglymostoma* DINGERKUS, 1986, Genus *Delpitoscyllium* NOUBHANI & CAPPETTA, 1997, Genus *Ganntouria* NOUBHANI & CAPPETTA, 1997 and Genus *Hologinglymostoma* NOUBHANI & CAPPETTA, 1997. Their odontological and biological characteristics were described in part **9.5**.

The type species of the Genus *Ginglymostoma* is the extant species *Ginglymostoma cirratum* (BONNATERRE, 1788). This extant Genus regroups also diverse extinct species.

The type species of the Genus *Nebrius* is the extant species *Nebrius concolor* RÜPPEL, 1837. This extant Genus regroups also diverse extinct species.

The type species of the extinct Genus *Cantioscyllium* is *Cantioscyllium decipiens* WOODWARD, 1889, based on one skeleton and isolated teeth discovered in a level of Cenomanian Age in southern England.

This Genus includes the six other species: *Cantioscyllium lobatum* (REUSS, 1846), based on isolated teeth discovered in a level of Turonian Age in Czech Republic, *Cantioscyllium saginatus* MEYER, 1974, based on isolated teeth discovered in a level of Santonian Age in Mississipi (U.S.A.), *Cantioscyllium meyeri* CASE & CAPPETTA, 1997, based on isolated teeth discovered in a level of upper Maastrichtian Age in Texas (U.S.A.), *Cantioscyllium nessovi* WARD & AVERIANOV, 1999, based on isolated teeth discovered in a level of Coniacian-Santonian Age in Uzbekistan, central Asia, *Cantioscyllium alhaulfi* KRIWET, 1999. based on isolated teeth discovered in a level of lower Barremian Age (Lower Cretaceous) in Teruel Province (Spain) and *Cantioscyllium hashimiaensis* MUSTAFA, CASE & ZALMOUT, 2002, based on isolated teeth discovered in a level of upper Santonian Age (Lower Cretaceous) in central Jordan (Near East).

The type species of the mono-specific extinct Genus *Protoginglymostoma* is *Protoginglymostoma ypresiensis* (CASIER, 1946). The senior author agrees with Cappetta (2012: p.: 175) who considered this Genus as an Eocene taxon of Ypresian Age (Lower Eocene) and Lutetian Age (Middle Eocene) present in southern England, northern France and Belgium.

The type species of the Genus *Pseudoginglymostoma* is the extant species *Pseudoginglymostoma brevicaudatum* GÜNTHER *in* PLAYFAIR & GÜNTHER, 1866, represented by diverse dense populations inhabiting the coasts of Tanzania and all the coasts of Madagascar.

This Genus includes two extinct specific taxa: *Pseudoginglymostom erguitaense* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of lower Maastrichtian Age (Upper Cretaceous) in the Souss Basin (Morocco) and *Pseudoginglymostoma idiri* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of upper Maastrichtian Age in the Ouled Abdoun Basin (Morocco).

The senior-author had the possibility to examine numerous teeth of these two taxa and concluded that the odontological characteristics of these two taxa are so similar that *P. erguitaense* could represent one ancestral population of *P. idiri*.

The type species of the extinct mono-specific Genus *Ganntouria* is *Ganntouria variabilis* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in one level of upper Maastrichtian Age (uppermost Cretaceous) of the Ganntour Basin (Morocco).

The type species of the extinct mono-specific Genus *Delpitoscyllium* is *Delpitoscyllium africanum* (LERICHE, 1927), based on isolated teeth discovered in only one level of Thanetian Age (Middle Paleocene) in Cabinda (western Africa).

The type species of the extinct mono-specific Genus *Hologinglymostoma* is *Hologinglymostoma jaegeri* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in one level of Thanetian Age (Middle Paleocene) in the Ouled Abdoun Basin (Morocco).

The type species of the extinct Genus *Plicatoscyllium* is *Plicatoscyllium derameii* CAPPETTA & CASE, 1997. This Genus includes also (Cappetta 2012: pp.: 173-174), the six other fossil taxa: *Plicatoscyllium derameii* CAPPETTA & CASE, 1997, based on isolated teeth discovered in a level of upper Maastrichtian Age in Texas (U.S.A.), *Plicatoscyllium minutum* (FORIR, 1887), based on isolated teeth discovered in diverse levels of Maastrichtian Age in north-eastern Belgium and in the Netherlands, *Plicatoscyllium globidens*\* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of lower Maastrichtian Age in the Ouled Abdoun Basin (Morocco) and *Plicatoscyllium gharbii*\* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of lower Maastrichtian Age (Upper Cretaceous) in the Ganntour Basin (Morocco), *Plicatoscyllium gharbii* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of upper Maastrichtian Age (Upper Cretaceous) in the Ganntour Basin (Morocco), *Plicatoscyllium gharbii* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of upper Cretaceous) in the Ganntour Basin (Morocco), *Plicatoscyllium gharbii* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of upper Cretaceous) in the Ganntour Basin (Morocco), *Plicatoscyllium gharbii* NOUBHANI & CAPPETTA, 1997, based on isolated teeth discovered in a level of upper Cretaceous) in the Ganntour Basin (Morocco) and *Plicatoscyllium antiquum* CAPPETTA & CASE, 1997, based on isolated teeth discovered in a level of upper Cretaceous) in Texas (U.S.A.).

The senior-author had the possibility to examine numerous teeth of *P. gharbii* and *P. globidens* and concluded that the odontological characteristics of these two taxa are so similar that *P. gharbii* could represent one ancestral population of *P. globidens*.

#### Conclusion

The oldest representatives of this Family were discovered in sediments of lower Barremian Age (Lower Cretaceous) in central Spain.

Since this period, the Family Ginglymostomatidae was represented by numerous upper cretaceous populations scattered around the coasts of Europe, North and South America, western Africa, northern Africa.

Its last fossil representatives are some taxa of the Anglo-French-Belgian uppermost Eocene, such as *Nebrius thielensi* (WINLER, 1874).

## Final conclusions concerning spatio-temporal distribution of the Order Hemiscylliiformes

This Order had specific representatives ranging from the lower Valanginian Age to the Present Times. As far as known, none of its representatives was ever encountered more eastern than Madagascar.

As a paleontologist, the senior-author points out the complete lack of data concerning their evolution during the upper Valanginian Age to the lower Cenomanian Age, which represents a time interval of circa thirty-two million Years.

## Remarks

The diverse extinct and extant species included in the Order Hemiscylliiformes were, during the Middle Jurassic to the Upper Cretaceous, inhabitants of lagoonal, coastal and continental shelf zones of western Europe. Some of their representatives moved, during the Upper Cretaceous, to the Near East.

As small benthic predators, they migrated progressively more northern, more southern and more eastern along the European, African, Asian coasts and colonized progressively all the coasts of former Indochina, China, Japan, Indonesia and Australia, but they never crossed the Great Pacific Barrier.

# 13.5. Order Stegostomatiformes nov.

This new Order is proposed for regrouping the three Families: Family Stegostomatidae GILL, 1862, the Family Parascyllidae GILL, 1862 and the Family Rhincodontidae GARMAN, 1913.

## Spatio-temporal distribution of the Order Stegostomatiformes

This Order has representatives in levels of Cenomanian Age (Upper Cretaceous) in central Europe, in levels of Ypresian to Bartonian Age (Lower to Upper Eocene) in central Europe and central Asia and is still represented by one large mono-specific benthic Genus\* and by one huge filter-feeding Genus\*\*.

\*Genus Stegostoma. \*\*Genus Rhincodon.

## Family Stegostomatidae GILL, 1862

This Family is proposed to regroup the extant Genus *Stegostoma* MÜLLER & HENLE, 1837 and the extinct Genus *Eostegostoma* HERMAN *in* NOLF & TAVERNE 1977.

The three extant Families: Family Parascylliidae GILL,1862, Family Stegostomatidae GILL, 1862 and Family Rhincodontidae GARMAN, 1913 seem to constitute a phylogenetic lineage extending from the Upper Cretaceous to the Recent times.

## Odontological characteristics and their progressive modifications

Their teeth are characterized by a lateral compression and by the fact that the base of their dental crown overlaps the top of their dental root. These data are valid for all their fossil and extant representatives.

All their teeth possess an apron, quite imperceptible (Family Parascylliidae), obvious but poorly developed (Family Stegostomatidae) or obvious but laterally compressed (Family Rhincodontidae).

The dental roots of the extinct or extant taxa attributed to these three Families are hemiaulacorhyzid, but the anterior teeth of the single extant taxon representing the Family Rhincodontidae are holaulacorhyzid.

All the teeth of all the extinct or extant taxa attributed to the Families Parascylliidae and Stegostomotatidae are in possession of one pair of lateral cusplets. These lateral cusplets lack on the anterior and lateral teeth of the single extant representative of the Family Rhincodontidae, *Rhincodon typus*, but they are present on the commissural teeth of the juvenile individuals.

The extern and intern sides of the dental crown of the extinct and extant representatives of this Family are smooth.

## **Biological characteristics of the Family Stegostomatidae**

All the extant taxa attributed to this Family are in possession of five pairs of gill slits and two dorsal fins without a fin-spine.

The extant representatives of the Families Stegostomatidae GILL, 1862 and Rhincodontidae GILL, 1862 are in possession of prominent lateral ridges on their body.

All the individuals of the huge nectic *Rhincodon typus*, having a world-wide distribution, have a filter-feeding nutritional mode.

In absence of a fossil skeleton, it is impossible to know if the representatives of the extinct European Eocene Genus *Eostegostoma* HERMAN, 1977 were in possession of lateral ridges or not.

# Family Parascylliidae GILL, 1862

This Family regroups the three extant Genera: Genus Parascyllium GILL, 1862, Genus Cirrhoscyllium SMITH &

RADCLIFFE, 1913, Genus *Heteroscyllium* REGAN, 1908 and the extinct Genus *Pararhincodon* HERMAN *in* CAPPETTA, 1976.

The type species of the Genus *Parascyllium* is the extant species *Parascyllium variolatum* DUMERIL, 1806. This extant Genus regroups five species represented by, more or less, dense populations which inhabit the coasts of the southern half of the sub-continent Australia.

The type species of the Genus *Cirrhoscyllium* is the extant species *Cirrhoscyllium expolitum* SMITH & RADCLIFFE, 1913. This extant Genus regroups three species. The populations of each of its species remind its progressive colonisation of the coasts of the Persian Gulf to the more southern point of India, the coasts of Taiwan and the coasts of the China Sea.

The type species of the mono-specific Genus *Heteroscyllium* is the extant species *Heteroscyllium colcloughi* (OGILBY, 1908). This extant species is endemic to eastern Australia.

## **Odontological characteristics of the Family Parascylliidae**

The millimetric-sized, laterally compressed, teeth of the five extant species attributed to this Genus have holaulacorhyzid\* (exceptional cases) to hemiaulacorhyzid (general rule) dental roots.

\*Observed on the dentition of some individuals of *Parascyllium collare* and *Parascyllium variolatum*.

Their dental crowns present one principal elongated and relatively narrow cuspid flanked by one pair of short rounded and divergent lateral cusplets. This pair of lateral cusplets is present on all their teeth (commissural teeth included). Their intern and extern sides lack any ornamentation.

The apron, principal odontological characteristic of all the members of the Order Squatiniformes and the Order Hemiscylliformes, is virtually absent.

This fact allows suggesting that this Family could be a member of the Order Scylliorhinomorphii and not of the Super Order Squatinomorphii.

## **Biological characteristics of the Family Parascylliidae**

All the extant members of this Family are in possession of five pairs of gill slits, two pectoral and two pelvic fins one anal fin and two dorsal fins without spine. Their gill slits are located on both sides of their body. They are oviparous\* to aplacental viviparous\*\*. Such a disparity requires a long time of evolution and demonstrates their very long existence.

#### \*Genus Parascyllium. \*\* Genus Heteroscyllium.

In the Family Parascylliidae, some extant species of the Genus *Parascyllium* GILL, 1862, such as *P. collare* RAMSAY & OGILBY, 1908 and *P. ferrugineum* McCULLOCH, 1911 present some discrete lateral ridges, which may be considered as the beginning of the formation of the strong anterio-posterior lateral ridges of the extant representatives of the two Genera *Stegostoma* and *Rhincodon*.

See images on: <u>www.superstock.com</u> and <u>www.commons.wikimedia.org</u> The most evolved representatives of this lineage originated during the Upper Cretaceous Period.

# Family Rhincodontidae GARMAN, 1913

The Family Rhincodontidae GARMAN, 1913 regroups the mono-specific extant Genus *Rhincodon* SMITH, 1829 and the extinct Genus *Pararhincodon* HERMAN, 1974.

The type species of the mono-specific Genus *Rhincodon* is *Rhincodon typus* SMITH, 1829, which is represented by diverse populations presenting a world-wide distribution. In fact its diverse populations encountered occupy scattered zones of all the oceans.

The type species of the extinct Genus *Pararhincodon* is *Pararhincodon crochardi* HERMAN *in* CAPPETTA, 1976. This extinct Genus includes four other species: *Pararhincodon crochardi* HERMAN *in* CAPPETTA, 1976, *Pararhincodon ypresiensis* CAPPETTA, 1976, *Pararhincodon lehmani* CAPPETTA, 1980 and *Pararhincodon germani* ADNET, 2006.

Pararhincodon crochardi HERMAN in CAPPETTA, 1976 is based on numerous\* teeth discovered in three levels of

upper Cenomanian to middle Turonian Age (Lower Cretaceous) in northern France, four levels of lower Campanian Age (Lower Cretaceous) in the Mons Basin (Belgium) and two levels of lower Campanian Age (Lower Cretaceous) in the Somme Department (France) \*\*.

\*More than thousand teeth were discovered at Bettrechies (France) between 1974 and 2010. \*\*Prospections of the senior-author and his wife.

*Pararhincodon ypresiensis* CAPPETTA, 1976 is based on numerous\* teeth discovered in the Anderlecht Clay Formation and the Sands of Forest Formation (Upper Ypresian, Lower Eocene), in three levels of Lower to uppermost Ypresian Age at Egem (Western Flanders, Belgium).

\*More than thousand teeth were discovered, between 1974 and 2003, in its type locality: Forest (Brussels Regio, Belgium).

*Pararhincodon lehmani* CAPPETTA, 1980 is based on one partially preserved skeleton discovered in one level of Cenomanian Age (Lower Cretaceous) in Lebanon.

*Pararhincodon germani* ADNET, 2006 is based on numerous isolated teeth discovered in one level of middle Lutetian Age (Middle Eocene) in the Aquitaine Basin (south-western France).

### Conclusion

The Family Rhincodontidae was represented by diverse taxa ranging from Cenomanian Age (Upper Cretaceous) in Lebanon and northern France to uppermost Ypresian Age (Lower Eocene) in Belgium and, presently, survive as huge nectic filter-feeding Neoselachii in all the Oceans of the world.

#### **Remark concerning its evolution**

The sudden transformation of small benthic extinct predators regrouped in the Genus *Pararhincodon* into large extinct benthic predators, represented by the mono-specific Eocene Genus *Eostegostoma* indicates that they have been affected by a significant genetic modification of their DNA at the end of the Eocene Period.

A continuous increase of size is sufficient to explain the evolution from eostegostomid-Neoselachi to stegostomid-Neoselachi, represented by the extinct and extant species of the Genus *Stegostoma*.

But a second sudden genetic modification of their DNA is necessary to explain the transformation of these large benthic predators into the huge filter-feeding nectic populations of the extant Genus *Rhincodon*.

The Genus *Eostegostoma* HERMAN, 1977 and the Genus *Stegostoma* GILL, 1862 being members of the Family Stegostomatidae MÜLLER & HENLE, 1837, these reflections imply that the phyletic origin of the Family Rhinco-dontidae could be the Order Stegostomatiformes.

Such sudden modifications of the genetic code of various and numerous living animal or vegetal forms could be due to inversions of the magnetic field of the earth, occurring at a regular rhythm, since the formation of the Earth's crust, by repetitive *krons*\* and *excursions*\*.

\*Reminder: A Kron means that the whole biosphere is affected and an Excursion means that only a part of the biosphere is affected.

Krons and Excursions do not seem to be directly related with climatic changes from glacial Periods to warm Periods.

### **Odontological characteristics of the Family Rhincodontidae**

The very small teeth of the single extant representative of this Genus have dental roots presenting a holaulacorhyzid root (anterior to latero-posterior teeth) or a hemiaulacorhyzid root (last posterior to commissural teeth).

Their dental crowns are monocuspid or in possession of one pair of minute lateral cusplets (commissural teeth of neonate individuals).

Their dental crowns present a very short, massive and rounded apron. Their intern and extern sides lack any ornamentation.

### **Biological characteristics of the Family Rhincodontidae**

All the extant individuals of this Family are in possession of five pairs of gill slits, two pectoral and two pelvic

fins, one anal fin and two dorsal fins without spine. Their gill slits are located on both sides of their body. They have a filter-feeding mode. They are ovoviparous.

# 14. The Hemiscylliidae as possible ancestors of the Order Pristiophoriformes

# 14.1. Principles of the modus operandi utilised for searching a possible ancestor of one taxon

The senior-author has used biological arguments, anatomical criteria, data furnished by Odontology, data furnished by Ontogeny, data furnished by Taphonomy and distribution particularities of their extant and extinct representatives for argumentation.

## 1. Biological arguments

These arguments combine anatomical criteria, odontological criteria and criteria concerning the data of the distribution of the extant and extinct representatives of the Rank examined.

The Natural History of the lineage constituted by the two extant Orders, the Order Squatiniformes and the Order Orectolobiformes *emend*. is a very good example to demonstrate the importance of this combination.

One single isolated tooth also furnishes plenty of information concerning the morphology, the mobility and, consequently, of the systematic position of its owner.

#### 2. Anatomical criteria

The position of their first pectoral fins\* is the simplest anatomical criterion that allows distinguishing the extant representatives of the two Genera: *Orectolobus* BONAPARTE, 1834, *Sutorectus* WHITLEY, 1939 and *Eucrossorhinus* REGAN, 1908.

\*See Compagno 1984: p.: 178.

The possession of dermal lobes, surrounding the head or only present on the sides of the head are anatomical criteria\* that allow identifying representatives of the two extant Genera: *Orectolobus* and *Eucrossorhinus* REGAN, 1908.

\*See Compagno 1984: p.: 178.

These three Genera regroup ambush predators remaining permanently on the sea bottom. This fact is deductible from their obvious flattened morphology, but also from the size of their anterior teeth.

## 3. Odontological data furnished by one isolated tooth of the Genus Squatina

The general morphology of one fossil individual is deductible from the morphology of its teeth. The dignathic homodonty of the teeth of the extant representatives of the Genus *Squatina* DUMERIL, 1806 suggests that, despite their flattened appearance, they are still able to swim above the sea bottom to catch their prey.

Their teeth are narrow, elongated and straight. Their function is to ensure that, once caught, their preys have no chance to escape. These animals may remain permanent resting ambush predators and do not need to swim to pursue their preys such as the extant representatives of the Genus *Squatina* are obliged to do.

# 4. Odontological data furnished by other isolated teeth

(Results of diverse observations of the senior-author realized between 1977 and 2013)

An isolated tooth furnishes plenty of other data utilizable when searching the possible ancestors of its taxon, such as the presence of an anterior radicular notch, the presence of lateral cusplets on its dental crown, the presence of diverse types of ornamentation.

#### Presence of a radicular notch

Such singular deformation of the anterior part of the dental root of all the teeth of all the extant and extinct taxa attributed to the Genera *Notorynchus* AYRES, 1855, *Hexanchus* RAFINESQUE, 1810, *Heptranchias* RAFINESQUE, 1810 and also present on the lower teeth of all the extant and extinct taxa attributed to numerous members of the
Super Order Squalomorphii HERMAN & VAN WAES, 2012 are discernable on the teeth of their embryos.

#### Presence of lateral cusplets

The dental crown of all the extinct and extant taxa attributed to the Families: Bracheluridae APPLEGATE, 1974, Ginglymostomatidae GILL, 1862, Pseudoginglymostomatidae DINGERKUS, 1986, Hemiscylliidae GILL, 1862 and Parascylliidae GILL, 1862 present, at least, one pair but often two or more, pairs of lateral cusplets.

The apparition and the development of the first pair of cusplets, such as the formation and the progressive development of the additional pairs are also observable on the teeth of their embryos and their juveniles.

#### Presence of an ornamentation

This presence is also observable on the teeth of their embryos as well as its progressive modification.

#### Presence of ancestral teeth without function

Jaws of some extant specific taxa present seven to eleven rows of minute commissural teeth: these of the Genus *Notorynchus* AYRES, 1855, these of the Genus *Hexanchus* RAFINESQUE, 1810 and these of the Genus *Heptranchias* RAFINESQUE, 1810.

All these minute commissural teeth have a specific morphology\*, demonstrating the narrow phyletic relationship existing between these three Genera and their common hybodontoid ancestor.

\*See Bibliography-Systematics: Herman, Hovestadt-Euler and Hovestadt 1987, plates 1 to 9.

## 5. Data furnished by Ontogeny

The examination of the different steps of growth of the embryos to the juvenile hatched individual and to the mature individual of one taxon furnishes precious indications that allow specifying the possible ancestor of a Genus.

#### Distribution particularities of their extant and extinct representatives

The geographical distribution and the depth range of the extant representatives of a Genus furnish indications that allow restricting the area where their direct ancestors logically lived.

The geographical distribution and the depth range of the extinct representatives of a Genus furnish indications concerning their possible phylogenetic relations and help to understand their progressive expansion.

# 6. Data furnished by Taphonomy

### **Objective data**

All the extant or extinct taxa of Pisces\* present one of the three following morphologies: Laterally compressed, dorso-ventrally compressed or elongated with an oval to circular section.

\*Cartilaginous fishes or bony-fishes.

A laterally compressed dead fish will fossilize on one of its sides. A dorso-ventrally compressed fish will also fossilize on one of its sides. A fusiform dead fish will also fossilize on one of its sides, but if it was in possession of a rostrum, the mass of its rostrum induces a horizontal position of fossilisation.

If putrefied before stranded, the fish always fossilise on their backs and are more or less distorted. The sedimentary compression significantly increases the width\* of fossilised fusiform fish.

\*With a maximum of 1.57, half of the number Pi.

#### Deduction

The width of the fossils of Propristiophoriformes, Pristioforiformes and Ganopristiformes is always enlarged.

The Laws of Geometry imply that the maximum of their enlargement approximately equals half of their original circumference. Consequently, all the representatives of the Order Propristiophoriformes, the Order Pristio-phoriformes and the Order Ganopristiformes were selachian-like fusiform fishes because the observed pheno-

menon of compression of their bodies implies that their gill slits were on the sides of their bodies and not on the ventral side.

# 7. Distribution of their extant and extinct representatives

One extant species is represented by diverse extant populations, each one inhabiting a, more or less, extended territory.

All these populations must have an original distribution area which covered all these areas, a more extended but continuous area or a more restrictive area. This last supposition is the more probable.

Searching in older and older geological levels, it is possible to discover this ancestral distribution zone and to define its environmental conditions.

More primitive populations must normally live in similar conditions, differing from the more recent ones by some particularities, such as a smaller size\*, a less compressed morphology and more primitive odontological characteristics than those of the more evolved forms.

\*Increase of the size of the teeth is the most common sign of continuous evolution and a sudden decrease of size and morphology of the teeth indicated a significant genetic perturbation.

This could mean: a lower number of lateral cusplets, the absence of an ornamentation, a more primitive dental root structure or the absence of a characteristic of their dental crown.

Changes in the direction of oceanic currents and apparition of new oceanic currents must also be kept in mind, as well as the Plate Tectonics which erect ecological barriers or suppress existing archipelagos and subcontinents.

# 14.2. Geophysical arguments

The movements of the diverse Tectonic Plates inducing the formation of abyssal trenches and the isolation of some Basins were important features that affected the possibility of the dispersal of all the benthic communities.

Benthic Chondrichthyes did not escape their effects.

If stopped in their progression by oceanic currents, all the benthic populations inhabiting the vicinity of new trenches had, of course, more chance to be the first ones to colonize these new areas.

# **14.3.** Astrophysical arguments

# **1.** Solar loss of highly ionized particles

It is important to remind the fact that the solar winds frequently expulse huge quantities of the constitutive elements of the Sun and that this plasma is ejected from the Sun at a supersonical speed.

The continuous loss of its constitutive elements has progressively decreased its mass and its initial gravitational power. It induced a constant increase of the distance separating the Sun from its satellites and a constant increase of the duration of their elliptical revolution around it.

# 2. Influence of the solar winds on the terrestrial biosphere

None, as long as the Van Allen Rings continue to protect the biosphere against their penetration.

### 3. Inversions of the Earth's magnetic poles and their possible influence on the Evolution.

As a field-geologist, the senior-author had many times observed that the radioactivity was always obviously higher in sedimentary levels separating two lithostratigraphic Units. It is supposed to be contemporaneous of an inversion of the Earth's magnetic poles\*.

\*Phenomenon confirmed by the analysis realized by diverse specialized Institutions.

It is this sudden increase of radioactivity which could be the cause of numerous mutations of the genetic code of all living forms confronted with this extern aggression.

# **15.** Reflection concerning the eggs of the Chondrichthyes

Even if it is not demonstrated that the morphology of one egg of an oviparous Chondrichthyes allows a categorical determination of its specific owner, it is sure that it allows its generic determination.

## 15.1. Eggs of Holocephali

During his marine explorations in the North Atlantic, the senior-author had the possibility to collect numerous eggs of: *Chimaera monstrosa* LINNAEUS, 1758 (Family Chimaeridae BONAPARTE, 1831) and of *Rhinochimaera atlantica* HOLT & BYRNE, 1909 (Family Rhinochimaeridae GARMAN, 1901).

#### Other taxa of the Genus Chimaera

Later he had the possibility to examine eggs of the following taxa: *Chimaera cubana* HOWELL-RIVEIRO, 1936, *Chimaera jordani* TANAKA, 1905 and of *Chimaera owstoni* TANAKA, 1905.

#### **15.2. Eggs of Neoselachii** (See Plates 3 to 8 and comments)

In fact, all the egg-capsules of all the Genera of the Super Order Heterodontomorphii HERMAN & VAN WAES, 2012 and all the egg-capsules of all the Genera of the Super Order Scyliorhinomorphii HERMAN & VAN WAES, 2012 and all the egg-capsules of the Hemiscylliomorphii nov. Sup. Ord. were produced to try to ensure a maximal protection to their embryos.

The two most interesting cases are represented by the egg-capsules of the different species of the Genus *Heterodontus* de BLAINVILLE, 1816 and egg-capsules of the different species attributed to the Genus *Cephaloscyllium* GILL, 1862.

#### Eggs of the different species of the Genus *Heterodontus* (See Plate 3, Plate 4 and comments)

Their characteristic spiraled forms with large surrounding flat and thin surfaces have for principal function an increase of a maximal extraction of oxygen from sea waters. The cases of each species have also a specific morphology.

Each extant species of the Genus *Heterodontus* protects a precise surface of the sea bottom and does not hesitate to eat egg-capsules of other species trying to invade its own territory.

#### Eggs attributed to the Genus *Cephaloscyllium* (See Plate 4: fig.: 3 and comments)

The morphology of the egg-capsules of the different specific taxa attributed to this 'Genus' allows an obvious distinction between two groups: One group has egg-capsules similar to these of *C. umbratile* JORDAN & FOWLER, 1903 and the second group these has egg-capsules similar to these of *C. ventriosum* (GARMAN, 1880).

# **15.3. Eggs of Batoidei**

Only the species of the thirty extant Genera of the Family Rajidae BONAPARTE, 1831 are oviparous. This biological characteristic separates this Family from all the other Families of the Batoidei.

### Remarks

The morphology of the egg-capsules of all the generic taxa of the Family Rajidae BONAPARTE, 1831 is distinguishable.

# 16. Proposals for a global Parasystematics of the Selachii (2010-2014): A critical Synthesis

# Reminder

The senior-author is the sole responsible for the following considerations.

The last generic taxa included in this critical synthesis are some published before 15 January 2014.

This partial Synthesis concerns only the super-Orders, Orders and Families having extant generic representatives.

After obtaining his PhD,

except for official requests of National Institutions, the senior-author has never published taxa discovered in other Countries by colleagues, even if he was in possession of plenty of specimens.

The generic taxa of which the senior-author did not have the possibility to examine some teeth are not concerned by this Synthesis.

# 16.1. Respect of the bi-nominal Nomenclature of Linné and Artedi

Even if the senior-author has a complex notion of what one species represents, his basic intention was, and remains, to follow the principle of the bi-nominal nomenclature.

# 1. Origin of the bi-nominal Nomenclature of all the living forms

At the beginning of the 18<sup>th</sup> century, when the notion of Evolution was still completely ignored, the conception of a bi-nominal nomenclature applicable to all the living, vegetal or animal forms of life was itself a revolutionary proposal.

Contemporary biologists and paleontologists of all the countries of the world are indebted to Pierre Artedi (1705-1735) and Karl von Linné (1707-1778), two Swedish naturalist pioneers, for this realisation.

According to the I.C.Z.N., when mentioning the name of one species it is not an obligation to include subgeneric names.

#### 2. The intentions of Pierre Artedi and Karl von Linné

#### **Basic Data**

Some letters exchanged between these two eminent naturalists of the 18<sup>th</sup> century reveal the progressive achievement of their works.

All their diagnoses were proposed in a Late Middle Age Latin, using the common Latin name of the animals and plants, many of them having, since the Antiquity, a vernacular Latin or Greek name, such as such as canis, lupus, vulpes or orchis.

The final suffix allowed to recognize its origin, such as *-pteris* (Latin) or *-pteryx* (Greek), because the 'y' did not exist in the Latin alphabet.

After diverse consultations, principally with Willughby and Seba, their common intention was, since 1728, to propose an international bi-nominal nomenclatural Systematics System. Each of them, in function of his own main centres of interest\*, will be responsible for a part of this huge work.

\*The premature and surprising death of Artedi in 1735, far more interested in Ichthyology than von Linné, explains the relative simplicity of the classification of the Pisces in the *Systema naturae* in which von Linné regrouped plenty of sharks in its Genus *Squalus* and plenty of rays in its Genus *Raja*.

Having understood, far before Darwin, that diverse species may be grouped in one Genus, they always opted for the better known name for one Genus. That is the origin of the Genus *Canis*, regrouping *Canis canis*, *Canis lupus* and *Canis vulpes*, three species of which crossed individuals are not sterile.

The other fundamental principle of their common Systematics proposal was that a generic name of one Regnum may never be used for a Genus of the other Regnum.

Therefore, a different terminal designation was proposed to allow distinguishing immediately a vegetal Family or Order (-eae and -ales) from an animal Family or Order (-idae and -iformes).

After having noted the numerous cases of synonymy of Genera of Plantae\* with Genera of Animals, it was the members responsible for the I.C.Z.N., who later decided to admit that an animal Genus and a vegetal Genus may have the same name. \*Always having priority by anteriority.

#### 3. Remark

Despite the hope of Artedi and von Linné that their proposal for using the same bi-nomal designation for all living vegetal or animal taxa would help to establish a world-wide connection between all the scientists, force is to observe that plenty of zoologists and paleontologists continue to ignore the works of botanists.

It is also a pity to observe that plenty of biologists never efficiently illustrate the hard parts of the new taxa they describe, suppressing so any chance for a paleontologist to identify their possible ancestors.

#### 4. The tri-nominal nomenclature

The first scientists to have used a tri-nominal nomenclature seem to be Carl Friedrich Bruch, a German ornithologist. (*circa* 1850) and Herman Schlegel, another German ornithologist.

The third one was also an ornithologist: John Cassin, of American nationality. Zoologists of other disciplines than Ornithology have respected the wish of Artedi for a longer time.

Before 1930, the use of this nomenclatural form was very rarely used and completely rejected by many anthropologists wishing to avoid any form of human racism that this practice could induce.

# 16.2. Criteria used by the senior-author of *Géominpal Belgica*

The principal originality of the Parasystematics of the Chondrichthyes proposed in the Series *Géominpal Belgica* consists in the fact that it mixes the principal anatomical criteria, the odontological ones and the spatio-temporal distribution data\* concerning both extant and extinct taxa.

\*Which partially result from the Plate Tectonics.

Whereas the odontological criteria are observable on their extant and extinct representatives, their anatomical criteria are, of course, only observable on their living representatives and on their relatively rare skeletal remains discovered.

After many years of research on living and fossil materials, the senior-author of these new Parasystematics proposals has concluded that one isolated tooth allows deducing the nutrition type, the approximate mass and the generic position of its owner.

The senior-author adds that he has discovered, at least, fifty-six odontological criteria and twenty biological criteria. All these proposed criteria are easily observable with naked eyes without sophisticated instrumentation.

The senior-author has also tried to use only the first designations utilized by von Linné: Phyllum, Class, Order, Family, Genus and species but never a sub-taxon.

He suggested regrouping different Orders, in logically structured Super Orders covering all the extant specific taxa and a maximum of extinct specific taxa of the Elasmobranchii.

He pointed out that an extant or extinct species must be considered as a complex assemblage of, more or less numerous and dense populations, each having its own spatio-temporal distribution.

A new species must be represented by one holotype, or better, by a type-set. But a paleontologist must be conscious that a holotype, or a type-set, never integrates the complete morphological variability of the diverse populations constituting one species.

# 1. Odontological Criteria

The principal odontological criteria selected are the sixty-five following ones.

#### Remark

In the proposed examples: A Name\* represents an extinct Genus.

\*Non exhaustive lists.

#### The relation between the dental crown and the dental root

Five possibilities: Crown posed on the top of the root<sup>1</sup>, crown in the same plane as this of the root<sup>2</sup>, crown overlapping the complete periphery of the root<sup>3</sup>, crown overlapping only the extern side of the top of the root<sup>4</sup> or intern face of the root presenting a massive central intern protuberance<sup>5</sup>.

#### Examples

1: Chlamydoselachus, Hybodus\*, Polyacrodus\*, Synechodus\*. 2: Echinorhinus, Hexanchus, Heptranchias, lower teeth of Isistius. 3: Ptychodus\*. 4: Squatina, Nebrius. 5: Odontaspis, Isurus.

#### The vascularisation and the innervation of the dental root

To be better adapted to the reality, the original list of vascularisation and innervation types proposed needed to be extended from five to eight. The following type-list is proposed: Chlamydoselachorhizyd<sup>1</sup>, Echinorhizyd<sup>2</sup>, Pseudopolyaulacorhizyd<sup>3</sup>, Primary Anaulacorhizyd<sup>4</sup>, Hemiaulacorhizyd<sup>5</sup>, Holaulacorhizyd<sup>6</sup>, Secondary Anaulacorhizyd<sup>7</sup> and Polyaulacorhizyd<sup>8</sup>.

#### Examples

Chlamydoselachus, Proteothrinax\*. 2: Echinorhinus, Hexanchus, Heptranchias, Notorynchus.
3: Synechodus\*, Orthacodus\*. 4: Hybodus\*, Polyacrodus\*, Acrodus\*.
5: Squatina, Orectolobus, Ginglymostoma, Nebrius, Hemiscyllium.
6: Scyliorhinus, Raja, Dasyatis, Rhinobatos.
7: Odontaspis, Carcharodon. 8: Myliobatis, Rhinoptera.

The Notidanorhyzid type, presently added, regroups all the extant and extinct Elasmobranchii in possession of a very high and flat dental root presenting a variable number of vertical furrows.

This one is the vascularisation type of the all the species of the four extant Genera: *Echinorhinus* de BLAINVILLE, 1816, *Notorynchus* AYRES, 1855 and *Hexanchus* RAFINESQUE, 1810, *Heptranchias* RAFINESQUE, 1810 and the five extinct Genera: *Notidanoides* MAISEY, 1986, *Notidanodon* CAPPETTA, 1975, *Weltonia* WARD, 1979, *Pachy-heptranchias* CAPPETTA, 1980 and *Paraheptranchias* PFEIL, 1981.

The Genus *Weltonia* is based on *Notidanus (Heptranchias) ancistrodon* ARAMBOURG, 1952 from the upper strata of the Montian and the lower Thanethian of the Ouled Abdoun Basin (Morocco) and includes a second taxon: *Weltonia burnhamensis* WARD, 1979 from the Thanethian of the London Basin (England).

The senior-author remembers a remark formulated by Georges Wouters, one of his field-friend, corresponding to his own observation, concerning the similarity existing between the number of teeth attributable to *Weltonia ancistrodon* and the number of teeth attributable to the Genus *Hexanchus* discovered in these strata.

Cappetta (2012: p.: 97) pointed out the strong morphological similarity between the dental root of the Genus *Weltonia* and the dental root of the Genus *Hexanchus*.

Consequently, it is conceivable that the taxon *Weltonia* regroups only the upper teeth of a Heptranchiformes\*, such as suggested by Arambourg when he proposed *Notidanus (Heptranchias) ancistrodon.* 

\*In 1952, Arambourg was really surprised that for the zoologists as well as for many paleontologists, the number of pairs of gill slits of a Chondrichthyes seemed to have no systematics or evolutionary signification. He signalized his surprise to his friend Louis Dubertet who transmitted this remark to the senior-author in 1973.

#### The consistence of the root

Two possibilities: The root is compact<sup>1</sup> or presents a spongy aspect<sup>2</sup>

#### Examples

1: General situation 2: *Lonchidion*\* and some *Polyacrodus*\*

#### The cuspids of the crown and their morphology

The dental crown is monocuspid<sup>1</sup> or polycuspid. Their lateral cusplets may be short and massive<sup>2-1</sup>, elongated and pointed<sup>2-2</sup> or flat and rounded<sup>2-3</sup>, which together represents four possibilities.

#### Examples

1: Isurus, Carcharodon. 2-1: Otodus\*, Procarcharocles\*. 2-2: Odontaspis, Mitsukurhina. 2-3: Galeocerdo.

#### The presence of diastema

The presence<sup>1</sup>, or the absence<sup>2</sup>, of diastema between the cuspid and the lateral cusplets on the dental crown adds two other significant possibilities.

#### Examples

1: Chlamydoselachus, Lethenia\*, Lamna. 2: Odontaspis, Scyliorhinus, Triakis, Ginglymostoma

#### **Relation between the tooth rows**

Three possibilities: The teeth are disposed in parallel rows<sup>1</sup>, the teeth are placed in imbricated rows<sup>2</sup>, or in quicunx<sup>3</sup>.

#### Examples

1: Upper and lower teeth of *Squatina, Hemiscyllium, Pristiophorus, Etmopterus.* 2: The lower teeth of *Isistius, Somniosus, Scymnodon.* 3: *Rhinobatos, Ptychotrygon\*, Rhina, Dasyatis.* 

#### Homodonty or Heterodonty

Three possibilities: Homodonty<sup>1</sup>, monognathic Heterodonty<sup>2</sup> or dignathic Heterodonty<sup>3</sup>.

#### Examples

1: The largest majority of the Genera of the Selachii and the Batoidei. 2: *Heterodontus*. 3: *Isistius, Scymodon, Dalatias*.

#### The extension of the root lobes

Three possibilities: Short to moderate<sup>1</sup>, extremely elongated<sup>2</sup> or short, flat and rounded<sup>3</sup>.

#### Examples

1: Hemiscyllium, Lamna, Carcharodon, 2: Scapanorhynchus, Odontaspis. 3: Pseudocorax\*, Anacorax\*, Galeocerdo.

#### Labio-lingual symmetry of the tooth

Three possibilities exist: More or less symmetric teeth<sup>1</sup> (General rule), sigmoidal teeth<sup>2</sup> or completely dissymmetric teeth<sup>3</sup>.

Examples

1: Squatina, Hemiscyllium, Scyliorhinus, Raja, Rhinobatos. 2: Anterior teeth of Xenodolamia\*. 3: Hexanchus, Heptranchias, Galeus.

#### The ornamentation of the crown

Ten possibilities: Vertical<sup>1</sup>, transversal<sup>2</sup>, network-like<sup>3</sup>, granulose<sup>4</sup>, intern<sup>5</sup>, extern and intern<sup>6</sup>, basal extern<sup>7</sup>, double basal extern<sup>8</sup>, serrulation present<sup>9</sup> or serrulation absent<sup>10</sup>.

#### Examples

1: Striatolamia\*, 2: Rhina. 3: Aculeola. 4: Ptychodus\*, Leidybatis\*, Rhina. 5: Striatolamia\*, 6: Synechodus\*. 7: Palaeohypotodus\*. 8: Cetorhinus maximus. 9: Carcharodon, Galeocerdo. 10: Isurus, Lamna.

#### The morphology of a possible apron, or extern protuberance of the base of the dental crown

Eight possibilities: The presence<sup>1</sup> or the absence<sup>2</sup> of an apron. This apron<sup>1</sup> may be prominent and massive,

cylindrical and elongated<sup>1-1</sup> or cylindrical and short<sup>1-2</sup>, bi-lobed<sup>1-3</sup> or not<sup>1-4</sup>, or rounded and flat<sup>1-5</sup>, or discrete and nearly imperceptible<sup>1-6</sup>.

#### Examples

1: All the Orectolobiformes: Representatives of 1<sup>1</sup>: Squatina, Orectolobus, Eucrossorhinus, Sutorectus. 1<sup>2</sup>: Hemiscyllium, Chiloscyllium, 1<sup>3</sup>: Parascyllium. 1<sup>4</sup>: Eostegostoma\*, 1<sup>5</sup>: Phorcynis\*, Ginglymostoma, Nebrius and 1<sup>6</sup>: Rhincodon. 2: All the extant non-Orectolobiformes taxa.

#### The morphology of a possible lingula, or intern vertical formation of the base of the crown

Two possibilities: This lingula is  $present^1$  or  $absent^2$ .

Examples

1: Rhinobatos, Pristis, Anoxypristis. 2: Dasyatis, Raja.

#### The general morphology of the dental crown

Four principal possibilities: The occlusal form of a dental crown may be inserted in a circle<sup>1</sup>, in a rhombus<sup>2</sup>, in a rectangle<sup>3</sup> or in a hexagon<sup>4</sup>.

#### Examples

1: Rhinobatos, Pristis. 2: Ptychotrygon\*, Rhina. 3: Ptychodus\*. 4: Rhombodus\*, Myliobatis.

#### Presence of numerous parallel cristae on the dental crown

Two possibilities: The occlusal face of a dental crown possesses only one cutting line<sup>1</sup> or many<sup>2</sup> parallel cristae.

Examples

1: Hexanchus, Squatina, Phorcynis\*, Hemiscyllium. 2: Ptychodus\*, Ptychotrygon\*, Rhina.

#### The general morphology of a dental root

This one may be qualified as: Flat and arched<sup>1</sup>, flat and horizontally extended<sup>2</sup>, flat and vertically extended<sup>3</sup> or tri-podial<sup>4</sup>, which represents four additional possibilities.

#### Examples

Palaeospinax\*, Squatina, Orectolobus, Hemiscyllium. 2: Synechodus\*, Orthacodus\*.
3: Echinorhinus, Hexanchus, Heptranchias, Notorynchus, Galeocerdo, Carcharodon.
4: Isurus, Odontaspis, Alopias.

#### The inclination of a dental crown

This last one may be qualified as: Straight<sup>1</sup> or curved<sup>2</sup>, which represents two additional possibilities.

#### Examples

1: Galeocerdo, Carcharodon. 2: Isurus, Lamna, Odontaspis, Alopias.

## 2. Biological Criteria

The principal biological criteria selected are the twenty-six following ones.

#### General morphology of the body

Two possibilities: more or less cylindrical<sup>1</sup>, or dorso-ventrally compressed<sup>2</sup>

#### Examples

1: All the Neoselachhii, including the Pristiophoromorphii and the Ganopristomorphii\*. 2: All the Batomorphii. **Remarks** 

For the Teleostei, a third possibility exists: laterally compressed

The Ptychodontomorphii are considered as dorso-ventrally compressed Euselachii.

#### Position of the gill slits

Two possibilities: on the sides<sup>1</sup> or ventral<sup>2</sup>

#### Examples

1: All the Neoselachhii, including the Pristiophoromorphii and the Ganopristomorphii\*. 2: All the Batomorphii.

#### **Taphonomical remark**

The partial embedding of their body and the compaction of the sediments give the illusion that all the fossilised Pristiophoromorphii and Ganopristomorphii were in possession of ventral gill slits.

But, in fact, their gill slits were located on the lower part of the sides of their body.

#### Possession of a protrusible jaw

Two possibilities: faculty existing<sup>1</sup> or not<sup>2</sup>.

#### Examples:

1: Mitsukurina. 2: Chlamydoselachus, Orectolobus, Hemiscyllium, Stegostoma.

#### The number of pairs of gill slits

Three possibilities: An Elasmobranchii may be in possession of five<sup>1</sup>, six<sup>2</sup> or seven<sup>3</sup> pairs of gill slits.

#### Examples

1: Orectolobus, Hemiscyllium, Pristiophorus. 2: Hexanchus, Rhina. 3: Heptranchias, Notorynchus.

#### The possession of dorsal fin spines

Two possibilities: The two dorsal fins of an Elasmobranchii possess<sup>1</sup> a dorsal fin spine or not<sup>2</sup>.

#### Examples

1: Heterodontus, Squalus. 2: Chlamydoselachus, Echinorhinus, Orectolobus, Scyliorhinus, Pristiophorus.

#### The possession of an anal fin

Two possibilities: this fin exists<sup>1</sup> or not<sup>2</sup>.

#### Examples

1: Chlamydoselachus, Orectolobus. 2: Echinorhinus and all the Squalomorphii.

#### The degree of calcification of the elements of the pectoral girdle

Two extreme possibilities: These elements are purely cartilaginous<sup>1</sup> or significantly calcified<sup>2</sup>.

Examples

1: Chlamydoselachus, Echinorhinus, Orectolobus. 2: Hemiscyllium, Chiloscyllium, Pristiophorus.

#### The morphology of the first vertebrae

Two possibilities: Their anterior vertebrae present a more or less oval-shaped<sup>1</sup> vertical section or a circular<sup>2</sup> vertical section.

#### Examples

1: Squatina, Orectolobus, Sutorectus. 2: Chlamydoselachus, Ginglymostoma, Hemiscyllium, Pristiophorus.

#### The presence of a lower symphyseal tooth row

Two possibilities: Present<sup>1</sup> or Absent<sup>2</sup>.

#### Examples

1: Hexanchus, Heptranchias, Ginglymostoma, Isistius. 2: Echinorhinus, Lamna, Odontaspis, Carcharodon.

#### The presence of commissural tooth rows

Two possibilities: Present<sup>1</sup> or Absent<sup>2</sup>.

#### Examples

1: Hexanchus, Heptranchias, Notorynchus. 2: Echinorhinus, Squalus, Lamna, Odontaspis, Carcharodon.

#### The possession of a rostrum

Two possibilities: The specimen examined is in possession<sup>1</sup> of a rostrum or not<sup>2</sup>.

#### Examples

1: Anoxypristis, Pristis, Propristiophorus\*, Pristiophorus, Pliotrema. 2: All the other extant Genera.

#### The mode of reproduction

Three possibilities: Oviparity<sup>1</sup>, ovoviviparity<sup>2</sup> or aplacental viviparity<sup>3</sup>.

#### Examples

1: Apristurus, Scyliorhinus, Galeus, Raja. 2: Chlamydoselachus, Hexanchus, Notorynchus, Ginglymostoma. 3: Squatina, Orectolobus, Sutorectus.

## **3.** Surprising results

The possession of five of these eighty-five criteria allows identifying one super-Order, four of these characterizing one of its Orders, three of these characterizing one of its Families, two of these characterizing one of its Genera and one detail\* of the ornamentation will allow distinguishing two species of one Genus.

\*Such as the presence of a serrulation or a granulation.

# 4. Other sources of information

The growth of the teeth as well as the development of the neurological system of the Elasmobranchii have also furnished interesting data, which certainly require further investigation.

The growth of the teeth of the Elasmobranchii furnishes information concerning their ancestors and the development of their neurological system allows a better understanding of some of their morphological changes, such as the formation of a rostrum and other sensorial adaptations, such as their capacity to detect preys and to orientate themselves according to the Earth's Magnetic Field.

# 4.1. The growth of the teeth of Selachii and Batoidei

#### Generalities

Contrarily to the other Vertebrata, the teeth of the Selachii and the Batoidei are indurated dermal productions. Their dental crown is the first to grow, their dental root grows later.

## Growth of the dental crown

During the first stages of growth the dental crowns remain flexible and supple because their apatite molecules are only partially connected.

It is the fragment of RNA, called cytochrome b, which carries, via the central pulp cavity and its radial vessels, the oxygen extracted from water, first, to the cutting edges of the dental crown and later to its central part.

The Selachii and the Batoidei have a continuous process of replacement of their functional teeth throughout their lives. The crowns of the replacement teeth may easily be deformed or sectioned during predatory acts.

#### Growth of the dental root

During the first stage of growth the dental crowns, the dental roots are inexistent. They only appear after the complete formation and the beginning of the induration of the dental crowns.

Like the bones of the upper vertebrates they are principally constituted by phosphate carbonates.

The hormone responsible for the growth of the bones of all the vertebrates is somatropine, which is secreted by the cells of the anterior part of the hypophysis\*.

\*The hypophysis is: A small structure attached to the base of the brain, constituting the master endocrine gland affecting all hormonal functions of the body.

A temporary dysfunction of this gland is sufficient to induce diverse malformations of an individual or of its sole dentition.

The embryos of the Chondrichthyes find this hormone in the yolk enclosed in their egg (oviparous species), in the yolk bag fixed to them (ovoviviparous species), or they extract it from the walls of the maternal uterus (aplacental viviparous species). A deficit of secretion of this hormone induces nanism, an excessive secretion induces gigantism.

### Examples of growth of fossil selachian teeth

The two most demonstrative examples, the senior-author has observed are: The growth phases of the teeth of a Middle Eocene representative of the Genus *Isistius* GILL, 1865 and the growth of the teeth of a Triassic Age (not specified) representative of the Genus *Polyacrodus* JAEKEL, 1889.

The principal originality of the Parasystematics of the Chondrichthyes proposed in the Series *Géominpal Belgica* consists in the fact that it mixes the principal anatomical criteria, the odontological ones and the spatio-temporal distribution data\* concerning both extant and extinct taxa.

\*Which partially result from the Plate Tectonics.

Whereas the odontological criteria are observable on their extant and extinct representatives, their anatomical criteria are, of course, only observable on their living representatives and on their relatively rare skeletal remains discovered.

After many years of research on living and fossil materials, the senior-author of these new Parasystematics proposals has concluded that one isolated tooth allows deducing the nutrition type, the approximate mass and the generic position of its owner.

### 1. Teeth of *Isistius trituratus* (WINKLER, 1873)

At Meldert (Flemish Brabant Province, Belgium), in the upper part of the Sands of Lede Formation, all the growth stages of the teeth of a population of *Isistius trituratus* (WINKLER, 1873) were discovered\*.

\* By the senior-author, between 1994 and 2003, in the sifting residues of circa five hundred cubic metres of one level.

Complete teeth of two to six millimetres height from adult and juvenile specimens were associated with teeth at all stages of growth: simple lambda-form apatite structures\*, unachieved triangles, complete triangles, serrated triangles, triangles with thin elongated radicular fibers and solid achieved serrated teeth. \*Not yet serrated.

### 2. Teeth of Polyacrodus sp.

From a Triassic level of unknown precise Age, the senior-author received some blackish sediments plenty of teeth of *Polyacrodus* sp. from a member of one of the French expeditions (between 1969 and 1974) in the Svalbard Island (Spitzberg Islands).

Complete teeth of three to four centimetres length from adult and juvenile specimens were associated with teeth at all stages of growth: isolated thin apatite rounded conulae with thin radial costulae; some others fused and aligned rounded conulae of similar morphology; similar ones with a partial filling of phosphate carbonates to completely formed and functional teeth.

# 4.2. Evolution of the neurological system of the Elasmobranchii

The neurological system of a vertebrate is responsible for the mobility and the perception of the complexity of the environment where it lives.

This was also true for all the extinct representatives attributed to this Order, and particularly for the development of their singular ability to move.

Diverse modifications of the ramifications of the neurological system of the extant members of this group are deductible from the frequent augmentations of the number of secondary apertures of their neurocranium.

Further investigations of the fossil neurocrania observable on some skeletons of the Jurassic and the Upper Cretaceous Periods will surely lead to a better interpretation of their evolution.

The development of a complex neurological system of the primitive nasal cartilages of some hemiscylliid taxa was an indispensable step to develop a sensitive rostrum so quickly.

# Remarks

# **Classical modes of storage of the extant specimens and consequences**

In a Museum localized in a region of low seismic activity, the living forms are stored in recipients filled with alcohol, after a more or less prolonged\* immersion in a formaldehyde solution. In other regions, of higher seismic activity, they are immediately stored in recipients filled with a formaldehyde solution.

\*In function of their mass.

Even if the two methods allow preserving their bodies and protecting their intern organs against putrefaction, the consequence is the same: the DNA molecules are damaged.

# **Recent solution**

The most efficient method tested is to collect numerous individuals in the type zone of various species, of different rank, but estimated valid by diverse taxonomists and to compare the DNA of these individuals.

This method has confirmed the validity of many ancient taxa and demonstrated the existence of numerous unknown species.

The most successful results were the analyses based on their cytochrome b. This part of the genome is the one which controls and regulates the extraction of oxygen in marine, brackish and fresh waters via the cellular membrane of the unicellular organisms or the cellular tissues of the respiratory organs of the multicellular organisms<sup>\*</sup>.

\*Including the Vertebrata. See Bibliography-Systematics: Bernardi & Powers 1992.

# 16.3. Synthesis of the proposals concerning the higher Taxa of the extant Selachii

The criteria that have allowed proposing diverse super-Orders were detailed in the preceding Volumes of the electronic Series *Géominpal Belgica* (*Géominpal Belgica*. **2.1**. to *Géominpal Belgica*. **2.4**., *Géominpal Belgica*. **3**, *Géominpal Belgica*. **4** and *Supplement to Géominpal Belgica*. **4**.

See these proposals on the on-line and freely accessible Website:

#### http://www.geominpal.be

# 1. Preliminary remark concerning the extant Elasmobranchii

## **Objective data**

Comparatively to the majority of the other group of fishes, the extant Elasmobranchii are a small group which regroups less than two thousand\* species.

\*Numerous of these species require a determination of their genetic code to be validated.

But this small group of marine vertebrates presents an extraordinary diversity of anatomical structures. They may possess five, six or seven pairs of gill slits, five being the more primitive. They may possess dorsal fins or not. They may be in possession of dorsal fin spines or not. Their caudal fin may present different types of morphology. They may possess a vertebral column composed only by vertebrae presenting a circular centrum or by a more complex composition presenting anterior vertebrae with an oval-shaped section. They may be oviparous, ovoviviparous or aplacental viviparous. They may be in possession of a rostrum or not. They present a huge diversity of morphology, of innervation-vascularisation modes and of dental histology.

This phenomenon is the result of more than three hundred millions of years of evolution and has made it quite impossible to reconstitute their phylogenetic relationships without an integration of all their paleontological data. All their Orders, Families and Genera presenting extant populations are the ultimate survival branches of one huge tree.

### Conclusion

To make their relations understandable they required a Systematics integrating all these particularities but also diverse sudden genetic modifications, and dispersal of their populations resulting from climatic and tectonic Events.

The following proposals are temporary attempts requiring future modifications but they result from forty-five years of research on the field and the seas.

It is for all these reasons that the senior-author, desirous to respect the bi-nominal nomenclatural system of von Linné and Artedi, has proposed so many Super Orders, because only such high taxomic ranks give the possibility to integrate characteristics so diversified.

# **Detailed example**

The choice of the Super Order Echinorhinomorphii is a good example for explaining the progressive understanding of the phyletic relationships which could have linked the extant Families Echinorhinidae GILL, 1862, Hexanchidae GRAY, 1851 and Heptranchidae HERMAN & VAN WAES, 2012.

The extant representatives of the Family *Echinorhinidae* have six pairs of gill slits, anaulacorhyzid dental roots and symmetric dental crowns presenting no central cuspid but paired cuspids orientated, half of these in the distal direction and half of these in the proximal direction.

By lack of skeletal remains, the anatomical characteristics of the ancestors of the extinct representatives of the Family Echinorhinidae are unknown, but their principal odontological characteristics are these of their extant representatives. As presumed ancestors, these taxa could have been in possession of only five pairs of gill slits.

The extant representatives of the Family Hexanchidae have six pairs of gill slits, anaulacorhyzid dental roots, dis -symmetric dental crowns presenting large cuspids decreasing in size and inclined in the direction of the commissure of their jaws. The first cuspid of their dental crowns presents a strong serration composed of large elements which may be considered as former cuspids, orientated such as the anterior cuspids of the Echinorhinidae.

The extant representatives of the Family Hexanchidae have conserved true commissural teeth, allowing specific determinations and demonstrating their relationship with hybodont-like Chondrichthyes.

By lack of skeletal remains, the anatomical characteristics of the ancestors of the extinct representatives of the Family Hexanchidae are unknown, but their principal odontological characteristics are these of their extant representatives.

The extant representatives of the Family Heptranchidae have seven pairs of gill slits, anaulacorhyzid dental roots and dissymmetric dental crowns presenting large cuspids decreasing in size and inclined in the direction of the commissure of their jaws. The first cuspid of their dental crowns presents a fine serration which may be considered as former cuspids orientated such as the anterior cuspids of the Echinorhinidae.

The extant representatives of the Family Heptranchidae have conserved true commissural teeth, allowing specific determinations and demonstrating their relationship with hybodont-like Chondrichthyes.

By lack of skeletal remains, the anatomical characteristics of the ancestors of the extinct representatives of the Family Heptranchidae remain unknown, but their principal odontological characteristics are these of their extant representatives.

## **Final conclusion**

Their principal anatomical extern characteristics, their anaulacorhyzid roots, their multi-cuspid dental crowns, the serrated morphology of their dental crowns, smooth on both sides and their successive increase of number of gill slits seem sufficient to propose their grouping in one taxon of a rank higher than an Order.

# 2. Biodiversity of the extant Families of Chondrichthyes

## **Objective data**

Without paleontological discoveries, twenty of the fifty-three extant Families of Chondrichthyes (Holocephali not included), would be considered as mono-generic: Family Chlamydoselachidae, Family Echinorhinidae, Family Heptranchidae, Family Heterodontidae, Family Squatinidae, Family Alopiidae, Family Cetorhinidae, Family Pristiophoridae, Family Mitsukurinidae, Family Megachasmidae, Family Pseudocarchariidae, Family Potamotrygonidae, Family Rhinidae, Family Platyrhinidae, Family Rhinobatidae, Family Rhynchobatidae, Family Narcinidae, Family Torpedinidae, Family Gymnuridae and Family Rhinopteridae.

And nine other Families of this group are only represented by two extant Genera: Family Hexanchidae, Family Centrophoridae, Family Etmopteridae, Family Brachaeluridae, Family Ginglymostomatidae, Family Hemiscylliidae, Family Pristidae, Family Urolophidae and Family Mobulidae.

### Deduction

Only twenty-four of the Families of these primitive vertebrates include more than two extant generic taxa and only some of their Genera\*, such as the Genus *Scyliorhinus*, the Genus *Apristurus*, the Genus *Raja*, the Genus *Mobula* and the Genus *Potamotygon* seem, presently, to continue to increase their diversification.

\*List not exhaustive.

This fact demonstrates that the large majority of their extant representatives constitute final ramifications of one huge phylogenetic tree, extending from the lowermost Triassic Period to the Present Times.

# Monophyly or Polyphyly

The monophyly or the polyphyly of each proposed Chondrichthyes' lineage remains a constant problem for both Paleontologists and Biologists, but, once more the principal causes of these permanent controversial discussions result from the diverse approaches used and from the lack of a Synthesis of all these approaches and from the difficulties to obtain reliable genetic data\*.

\*Because all the former modes of preservation have destroyed or seriously damaged the DNA of their holotype.

# **3.** Generic taxa proposed after the publication of the new Parasystematics proposals presented in the Series *Géominpal Belgica*. **2.1**. to Addition to *Géominpal Belgica*. **4**.

# Systematics remark

The inventors of the new taxa proposed after December 2012 did not take into account the proposals mentioned in the Series *Géominpal Belgica*, which obliges them *ipso facto* to attribute their new taxa to Families and Orders being completely revised\*.

\*Example: The attribution of a new fossil taxon to the Family Scyliorhinidae *sensu* CAPPETTA, 2012 makes it impossible to know if its nearest parents were, really, *Scyliorhinus*-like, or *Cephalurus*-like, or *Apristurus*-like, or *Halaelurus*-like, or *Pentanchus*-like or *Galeus*-like etc.

## **New Families**

Two new extinct Families: The Family Pseudorhinidae KLUG & KRIWET, 2013 which was attributed to the Order Squatiniformes *sensu* COMPAGNO, 1973 and the Family Crassonotidae KLUG & KRIWET, 2013 which was attributed to the Order Hexanchiformes *sensu* COMPAGNO, 1973.

## New Genera

Two extant generic taxa: Genus *Planonasus* WEIGMANN, STEHMANN & THIEL, 2013 and Genus *Keasius* WELTON, 2013 and the thirteen following extinct generic taxa: Genus *Tingitanius* CLAESON, UNDERWOOD & WARD, 2013, Genus *Potobatis* CAPPETTA & GAYET, 2013, Genus *Argoubia* ADNET, CAPPETTA, GUINOT & NOTARBARTOLO DI SCIARA, 2012, Genus *Oromobula* ADNET, CAPPETTA, GUINOT & NOTARBARTOLO DI SCIARA, 2012, Genus *Thiesius* GUINOT, CAPPETTA & ADNET, 2014, Genus *Antrigoulia* GUINOT, CAPPETTA & ADNET, 2014, Genus *Gladioserratus* UNDERWOOD, GOSWANI, PRASAD, VERMA & FLYNN, 2011, Genus *Occitanodus* GUINOT, CAPPETTA & ADNET, 2014, Genus *Magistrauia* GUINOT, CAPPETTA & ADNET, 2014, Genus *Magistrauia* GUINOT, CAPPETTA & ADNET, 2014, Genus *Parahemiscyllium* GUINOT, CAPPETTA & ADNET, 2014, Genus *Archaeogaleus* GUINOT, CAPPETTA & ADNET, 2014, and Genus *Cadiera* GUINOT, CAPPETTA & ADNET, 2014 were proposed after December 2012.

The Genus *Keasius* WELTON, 2013 was attributed to the Family Cethorhinidae GILL, 1862 and the Genus *Planonasus*\* was attributed to the Family Triakidae *sensu* COMPAGNO, 1974.

\*The anatomical characteristics of this taxon demonstrate that the Genus *Planonasus* is, without any doubt, a new representative of the Family Triakidae, but the illustration of its teeth does not allow recognizing their own odontological characteristics and, consequently, does not allow specifying which fossil taxon could be its ancestor.

The two Genera Argoubia and Oromobula were attributed to the Family Mobulidae sensu CAPPETTA, 2012.

The Genus *Tingitanius* was attributed to the Family Platyrhinidae *sensu* CAPPETTA, 2012 and the Genus *Thiesius* was attributed to the Family Scyliorhinidae *sensu* CAPPETTA, 2012.

The Genus Antrigoulia was attributed to the Family Paleospinacidae sensu REGAN, 1906, the Genus Gladioserratus was attributed to the Family Hexanchidae sensu COMPAGNO, 1984 and the Genus Occitanodus was attributed to the Family Orthacodontidae sensu GLYCKMAN, 1957.

The three Genera *Garrigascyllium*, *Magistrauia* and *Parahemiscyllium* were attributed to *Families incertae sedis* of the Order Orectolobiformes *sensu* CAPPETTA, 2012.

The Genus Archaeogaleus was attributed to the Family Carcharhinidae sensu CAPPETTA, 2012 and the Genus Cadiera was attributed to the Family Scyliorhinidae sensu CAPPETTA, 2012.

In Guinot, Cappetta & Adnet 2014, histological descriptions\* and comparisons with the dental morphology\* of the extant representatives of the three principal extant Orders concerned: The Order Hexanchiformes *sensu* HERMAN & VAN WAES, 2012, the Order Orectolobiformes *sensu* COMPAGNO, 1984 and the Order Heterodontiformes *sensu* COMPAGNO, 1984 are lacking, but the careful odontological descriptions and the quality of their illustrations allow suggesting the following systematics adjustments for the following generic taxa.

\*Thoroughly detailed in the twenty fascicules of the Series: Herman, Hovestadt-Euler & Hovestadt: *Contribution to the study* of the comparative morphology of teeth and other relevant ichthyodurilites in living supraspecific taxa of Chondrichthyan Fishes, published in the Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Série Biologie. Brussels. Belgium, between 1987 and 1999.

The teeth attributed to the Genus *Gladioserratus* present all the odontological characteristics of representatives of the Family Hexanchidae HERMAN & VAN WAES, 2002, but isolated teeth, not allowing to precise the number of the pairs of the gill slits they possessed, the attribution of this Genus to the Family Hexanchidae must be considered as hypothetical.

The far ancestors of the representatives of the Family Hexanchidae were unknown Chondrichthyes, but they

must have been in possession of only five pairs of gill slits. As these lower cretaceous fossil remains do not include skeletal remains it is impossible to guarantee any attribution.

All the teeth attributed to the Genus *Squatirhina* present all the odontological characteristics of the members of the new super Order Squatinomorphii.

The teeth attributed to the Genus *Heterodontus* present all the odontological characteristics of the members of the Super Order Heterodontomorphii HERMAN & VAN WAES, 2012 and these of the extant Genus *Heterodontus* de BLAINVILLE, 1816, or the extinct Genus *Paracestracion*\* KOKEN *in* ZITTEL, 1911.

\*Erratum: Typographied as Paracestration in Géominpal Belgica. 4.

The teeth attributed to the Genus *Paracestracion* KOKEN *in* ZITTEL, 1907 present all the typical odontological characteristics of the members of the Super Order Heterodontomorphii HERMAN & VAN WAES, 2012 and more precisely these of the extinct Genus *Paracestracion*.

The teeth attributed to the Genus *Garrigascyllium* present all the odontological characteristics of the members of the new Family Phorcinidae.

The teeth attributed to the Genus *Parahemiscyllium* present all the odontological characteristics of the members of the Family Hemiscylliidae GILL, 1862.

This Genus could be the common ancestor of the two Genera *Hemiscyllium* MÜLLER & HENLE, 1837 and *Chiloscyllium* MÜLLER & HENLE, 1837.

# 4. Systematic Inventory

## **Preliminary explanation**

Extant Order, extant Family or extant Genus, means that this taxon has extant representatives.

# **Class Chondrichthyes HUXLEY, 1880**

# Euselachii HAY, 1902

In this volume, all the representatives of the following Families: Family Hybodontidae OWEN, 1896, Family Acrodontidae CASIER, 1959, Family Polyacrodontidae GLYCMAN, 1964, Family Lonchidiidae HERMAN, 1977, Family Homalodontidae MUTTER, NEUMAN & DE BLANGER, 2008, Family Ptychodontidae JAEKEL, 1898 *rev.*, Family Hylaeoebatidae HERMAN & VAN WAES, 2012 and Family Distobatidae WERNER, 1989 are considered as Euselachii.

Many Genera of the Families Hybodontidae, Acrodontidae, Homalodontidae and Lonchidiidae are based on skeletons. These skeletons demonstrate that the mode of articulation of their jaws was orbitostylic, and that they were in possession of two dorsal fins with a fin-spine, two pectoral fins, two pelvic fins and one anal fin.

On some skeletons, the cartilaginous elements of five pairs of gill slits are preserved.

The large majority of their generic representatives were in possession of teeth presenting, at least, one high cuspid. This fact guarantees that these ones were active predators, feeding preferentially on fishes than on benthic invertebrates.

Skeletons of representatives of the Family Ptychodontidae JAEKEL, 1898 *rev.*, Family Hylaeoebatidae HERMAN & VAN WAES, 2012 and Family Distobatidae WERNER, 1989 remain unknown, but their isolated, or grouped, crushing teeth guarantee that they were predators of mainly benthic invertebrates.

The following Genera considered as *incertae sedis* (Cappetta 2006: pp.: 393-394 and Cappetta 2012: pp.: 49 to 83): Genus *Gobiodus* GLYCKMAN, 1980, Genus *Aegyptobatis* WERNER, 1989, Genus *Glickmanodus* NESSOV, GLYCKMAN & MERTINIENE *in* MERTINIENE & NESSOV, 1997, Genus *Acrorhizodus* CAPPETTA, BUFFETAUT, CUNY & SUTEETHORN, 2006 are also considered as Euselachii on basis of their odontological characteristics.

For references, see: Bibliography-Systematics: Family Acrodontidae CASIER, 1959: *Géominpal Belgica*. **2**: p.: 40 Family Polyacrodontidae GLYCMAN, 1964: *Géominpal Belgica*. **2**: p.: 41 Family Ptychodontidae JAEKEL, 1898 *rev.*: *Géominpal Belgica*. **2** (Supplement): p.: 6

# Super Order Hybodontomorphii nov.

This Super Order is proposed for regrouping the three Orders: Order Hybodontiformes OWEN, 1846, Order Acrodontiformes nov. and Order Ptychodontiformes rev.

# **Order Hybodontiformes OWEN**, 1846

This Order is based on the single Family Hybodontidae OWEN, 1896, it regroups also all the representatives of the Family Lonchidiidae HERMAN, 1977.

# Family Hybodontidae OWEN, 1846

This Family regroups the six following extinct taxa: Genus *Hybodus* AGASSIZ, 1837, based on *Hybodus reticulatus* AGASSIZ, 1837, discovered in strata of Sinemurian Age (Lower Lias) in Dorsetshire (England), Genus *Leptacanthus* AGASSIZ, 1837, based on *Leptacanthus tenuispinis* AGASSIZ, 1837, discovered in strata of lower Lias Age in southern England, Genus *Priohybodus* d'ERASMO, 1960, based on *Priohybodus arambourgi* d'ERASMO, 1960, discovered in strata of upper Jurassic Age in Somaliland, Genus *Pororhiza* CASIER, 1969, based on *Pororhiza molimbaense* CASIER, 1969, discovered in strata of Albian Age (Upper Cretaceous) in the R. D. Congo, Genus *Egertonodus* MAISEY, 1987, based on *Egertonodus* basanus MAISEY, 1987, discovered in strata of Wealdian Age in southern England and Genus *Thaiodus* CAPPPETTA, BUFFETAUT & SUTEETHORN, 1990, based on *Thaiodus ruchae* CAPPPETTA, BUFFETAUT & SUTEETHORN, 1990, discovered in one level of Aptian-Albian Age in Thailand.

According to Cappetta 2006 (p.: 325), the Genus Leiosphen AGASSIZ, 1837 is a nomen nudum.

According to Cappetta 2006 (pp.: 330-331), the Genus *Meristodon* AGASSIZ, 1843, based on *Meristodon paradoxa* (AGASSIZ, 1843) is a synonym of the Genus *Hybodus* AGASSIZ, 1837.

According to Cappetta 2006 (p.: 378), the Genus *Sphenonchus* AGASSIZ, 1843, based on *Sphenonchus hamatus* discovered in strata of Liassic Age of southern England, is a synonym of the Genus *Hybodus* AGASSIZ, 1837.

According to Cappetta 2006 (p.: 316), the Genus *Hybodonchus* FRAAS, 1889, based on *Hybodonchus cloacinus* FRAAS, 1889, discovered in strata of Liassic Age in southern Germany is a synonym of the Genus *Hybodus* AGASSIZ, 1837.

For references, see: Bibliography-Systematics: Agassiz 1837, Cappetta 2006, Cappetta, Buffetaut & Suteethorn, 1990, Casier 1969, d'Erasmo 1960 and Owen 1846

# **Order Acrodontiformes nov.**

This Order regroups the Family Acrodontidae CASIER, 1959 and the Family Polyacrodontidae GLYCMAN, 1964.

# Family Acrodontidae CASIER, 1959

This Family regroups the four following extinct taxa: Genus *Acrodus* AGASSIZ, 1838, based on *Acrodus gaillardoti* AGASSIZ *in* GEINITZ, 1837 discovered in strata of Middle Triassic Age in Lorraine (France), Genus *Bdellodus* QUENSTEDT, 1882, based on *Bdellodus bollensis* QUENSTEDT, 1882 discovered in strata of lower Lias Age in Baden-Würtemberg (Germany), Genus *Curtodus* SAUVAGE, 1867, based on *Curtodus rigauxi* discovered in strata of Batthonian Age (Middle Jurassic) in northern France and Genus *Asteracanthus* AGASSIZ, 1837, based on *Asteracanthus ornatissimus* AGASSIZ, 1837 discovered in strata of Kimmeridgian Age (Upper Jurassic) in southern England.

According to Cappetta 2006 (p.: 384), the Genus *Strophodus* AGASSIZ, 1838, based on *Strophodus longidens* AGASSIZ, 1838 discovered in strata of Bathonian Age (Middle Jurassic) in Normandy (France) is a synonym of the Genus *Asteracanthus* AGASSIZ, 1837.

According to Cappetta 2006 (p.: 386), the Genus *Thectodus* PLIENINGER *in* MEYER & PLIENINGER, 1844, based on *Thectodus cloacinus* (QUENSTEDT, 1856), discovered in strata of Rhaetian Age in southern Germany is a synonym of the Genus *Acrodus* AGASSIZ, 1838.

According to Cappetta 2006 (p.: 272), the Genus *Acrodonchus* FRAAS, 1889, based on *Acrodonchus minimus* AGASSIZ, 1839 discovered in strata of the Lias in southern England is a synonym of the Genus *Acrodus* AGASSIZ, 1838.

Recent odontological studies have demonstrated that all the diverse generic taxa of Euselachii in possession of acrodont-like teeth may be regrouped in only one Genus: Genus Acrodus AGASSIZ, 1837.

For references, see: Bibliography-Systematics: Agassiz 1838, Cappetta 2006, Casier 1959, Quenstedt 1882 and Sauvage 1867.

# Family Polyacrodontidae GLYCKMAN, 1964

This Family regroups the three following extinct taxa: Genus *Polyacrodus* JAEKEL, 1889, based on *Polyacrodus polycyphus* (AGASSIZ, 1837) discovered in strata of Anisian to Ladinian Age (Middle Triassic) in Lorraine (north-eastern France), Genus *Priscavolucris* GOMEZ-PALLEROLA, 1979, based on *Priscavolucris montsechi* discovered in strata of Berriasian to Valanginian Age (Lower Cretaceous), in Lerida Province (Spain), Genus *Astodontus* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, GLYCKMAN & MERTINIENE, 1991, based on *Astodontus shuvalovi* NESSOV, Based

For references, see: Bibliography-Systematics: Agassiz 1837, Cappetta 2006, Glyckman 1964 and Jaekel 1883.

# **Order Ptychodontiformes rev.**

This Order regroups the Families: Family Ptychodontidae JAEKEL, 1898 and Family Hylaeobatidae HERMAN & VAN WAES, 2012.

The principal odontological characteristics of all the representatives of this Order were dealt with in *Géominpal Belgica*. **2**.

The representative taxa of this Order are considered as hyper-specialized Hybodontiformes.

## Family Ptychodontidae JAEKEL, 1898

This Family regroups the four following extinct Genera: Genus *Ptychodus* AGASSIZ, 1838, Genus *Heterotychodus* YABE & OBATA, 1930, Genus *Boelodus* HERMAN & VAN WAES, 2012 and Genus *Landemainodus* HERMAN & VAN WAES, 2012.

> For references and illustrations: See Bibliography-Systematics: Agassiz 1838, Cappetta 2012: pp.: 78-81 and figs.: 65 and 66, Hamm 2008, Herman 1977, Herman & Van Waes 2012, Jaekel 1898 and Yabe & Obata 1930

# Family Hylaeobatidae HERMAN & VAN WAES, 2012

This mono-generic Family is based on its type Genus: Genus Hylaeobatis WOODWARD, 1916.

For references and illustrations: See Bibliography-Systematics: Cappetta 2012: pp.: 68-69 and fig.: 55, Herman & Van Waes 2012 and Woodward 1916.

# Super Order Chlamydoselachomorphii HERMAN & VAN WAES, 2012

## **Systematics**

This Super Order has only one representative extant Order, the Order Chlamydoselachiformes HERMAN & VAN

WAES, 2012, represented by the extant Family Chlamydoselachidae GARMAN, 1884 based on the Genus *Chlamydoselachus* GARMAN, 1884 regrouping the two extant taxa: *Chlamydoselachus anguineus* GARMAN, 1884 and *Chlamydoselachus africana* EBERT & COMPAGNO, 2009.

## **Odontological criteria selected**

The extant and extinct representatives of this Super Order are characterized by their radicular type, by the position of the five elements of their dental crown above the surface of their root, by the polycuspidity of their dental crown, by the presence of diastema separating all elements of the dental crown and by the placement of their teeth in parallel rows, which represents five fundamental odontological criteria.

## **Biological criteria selected**

The extant representatives of this Super Order are characterized by the orbitostylic mode of suspension of their jaws, the possession of six pairs of gill slits\*, the absence of dorsal fin spines, the absence of a rostrum, the normal degree of calcification of their anterior vertebrae, the normal degree of calcification of their pectoral girdle and their ovoviviparous mode of reproduction, or seven fundamental biological criteria.

\*The first pair being joined across their throat.

## **Determination Problem**

The holotype of *Chlamydoselachus* is an individual of a Japanese population of this Genus. The discovery of a second species of this Genus, of which the populations occupy the major part of the deep zones surrounding the southern part of the African Continent, requires a control of the genetic codes of all the North Atlantic populations attributed to *Chlamydoselachus anguineus* GARMAN, 1884 by ignorance of the potential diversity of this Genus.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2.1**.: p.: 35.

# Super Order Echinorhinomorphii HERMAN & VAN WAES, 2012

This Super Order was proposed for regrouping the three following Orders: The extant Order Echinorhiniformes de BUEN, 1926, the extant Order Hexanchiformes de BUEN, 1926 and the extant Order Heptranchiformes HERMAN & VAN WAES, 2012.

For reference, see Bibliography-Systematics: Herman, Hovestadt-Euler & Herman 1989: pp.: 105-106, Txt.-pl.: 1 and Plate 1 and Herman & Van Waes 2012: *Géominpal Belgica* **2. 1**.: p.: 37.

# Order Echinorhiniformes de BUEN, 1926

This Order is based on the Family Echinorhinidae GILL, 1862, itself based on the extant Genus *Echinorhinus* de BLAINVILLE, 1816.

The two extant members of the Genus *Echinorhinus* are: *Echinorhinus brucus* (BONNATERRE, 1788) and *Echinorhinus coockei* PIETSCHMANN, 1928. These two extant species have the following characteristics in common.

# Principal anatomical characteristics

All the individuals of these two species have two small dorsal fins, without fin-spine and they lack an anal fin. They have five pairs of gill slits of which the fifth pair is the longest.

The suspension of their jaws is orbitostylic. Their vertebral column is exclusively constituted by vertebrae having centrae presenting a vertical circular section. Both species are aplacental viviparous.

They possess large\*, thorn-like dermal denticles scattered over their body, some of which may be fused together. The dermal denticles of mature embryos are minute spines located within small holes in their skin.

\*The dermal denticles of *Echinorhinus coockei* are obviously smaller than these of *Echinorhinus brucus* and not overlapping.

# Principal odontological characteristics

## Composition of the dentition of the Echinorhiniformes

Contrarily to the jaws of the Hexanchiformes and the Heptranchiformes, the jaws of the extant representatives of the Echinorhiniformes present teeth placed in free parallel rows and they lack symphyseal tooth rows and commissural tooth rows.

## Characteristics of the dental root of the extant Echinorhiniformes

Their dental roots are flat and relatively high. They do not overlap the top of the base of their crowns and present one or two intern elongated furrows.

## Characteristics of the dental crown of the extant Echinorhiniformes

Their dental crowns present one to five large cuspids. The anterior ones are orientated to the anterior part of the jaw; the posterior ones are orientated to the commissure of the jaws. Their extern and intern faces are absolutely smooth. Their cutting edges present no serration. They possess no apron.

# Habitat

The diverse populations of *Echinorhinus brucus* live close to the sea bottom and may be encountered principally on continental and insular shelves and slopes at depths comprised between 400 to 900 metres\*.

\*Where intensive bottom trawlings have destroyed all forms of sessile animals. Depth record (2012): 1.214 metres.

In areas presenting up-wellings of deep cold waters, such as the south American coasts, it may be encountered between 10 to 20 metres depth.

The diverse populations of *Echinorhinus brucus* are scattered in dispersed areas of the world, separated by thousands of kilometres. The single common point of these areas is to be located in tropical and temperate waters.

The diverse populations of *Echinorhinus coockei* are also scattered in dispersed areas of the world, separated by thousands of kilometres, but they are absent along all the Pacific American coasts and in all the Atlantic Ocean.

It is, geologically important, to point out that the populations of *Echinorhinus coockei* inhabit both extremities of the Pacific Ocean, which means that they had the possibility to occupy these areas before the submersion of some central Pacific Plates.

And, geologically, it is also important to point out that the populations of *Echinorhinus brucus* inhabit only the western side of the Pacific Ocean, which means that they were isolated before the submersion of some central Pacific Plates.

See: Distribution map of *E. brucus* on: <u>www.nl.wikipedia.org</u> See: Distribution map of *E. coockei* on: <u>www.en.wikipedia.org</u>

# Singularity

The two extant species of this Genus feed on diverse invertebrates\* but also on other Chondrichthyes such as species of the Genera *Callorynchus* CUVIER, 1816 (Callorhynchidae, Holocephali), juveniles of the Genus *Squalus* LINNAEUS, 1758 (Squalidae, Selachii), the Genus *Hexanchus* RAFINESQUE, 1810 (Hexanchidae, Selachii), and egg-capsules of the Genera *Apristurus* GARMAN, 1813 and *Galeus* CUVIER, 1816 (Scyliorhinomorphii, Selachii).

\*Principally cephalopods.

# Fossil Genera attributed to the Family Echinorhinidae

According to Cappetta (2006: p.: 195 and 2012: pp.: 108-111) this Family also includes the four following extinct Genera: Genus *Paraechinorhinus* WELTON *in* PFEIL, 1983, Genus *Pseudoechinorhinus* PFEIL, 1983, Genus *Gibbechinorhinus* CAPPETTA, 1990 and Genus *Orthechinorhinus* ADNET, 2006.

Except for the morphology and the structure of their dental root, it is difficult to consider these fossil taxa as representatives of the extant Family Echinorhinidae GILL, 1862.

# Principal odontological characteristics of the Genus Echinorhinus

The jaws of the two extant species, *Echinorhinus brucus* and *Echinorhinus coockei*, present a strict homodont dentition. The dental root of these two species has an echinorhyzid structure. Some juvenile individuals present a row of small symphyseal teeth.

All the teeth are dissymmetric, have no principal cuspid, but present two or three pairs of large knife-like cusplets.

The extremities of half of these cusplets are orientated in the anterior direction, and the extremities of the other half of the cusplets in the commissural direction. Commissural tooth rows are absent\*.

\*Except on jaws of juvenile specimens, were some distorted late posterior teeth may be present.

For illustration: See Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt 1989: pl.: 1.

# Family Echinorhinidae GILL, 1862

## Fossil taxa attributed to the Genus Echinorhinus

According to Cappetta (2012: p.: 107), the 9 following extinct taxa\* are representatives of this Genus: *E. blakei*<sup>1</sup> AGASSIZ, 1856, from the middle Miocene of the Sierra Nevada (California, U.S.A.), *E. pozzii* AMEGHINO, 1906, from a Miocene level of Patagonia (Argentina), *E. australis* (CHAPMAN, 1909), from an Albian level (lower part of the Upper Cretaceous) of Queensland (Australia), *E. priscus*<sup>1</sup> ARAMBOURG, 1952, from different levels of the Ypresian of the Ouled Abdoun Basin (Morocco), *E. caspius*<sup>2</sup> GLUCKMAN, 1964, from the Aday Formation (lower Priabonian or uppermost Eocene) of Kazakhstan (central Asia, Russia), *E. eyrensis* PLEDGE, 1992, from a Maastrichtian level encountered in a bore-hole off South Australia, *E. pfauntschi* PFEIL, 1983, from a Burdigalian level in Austria, *E. weltoni*<sup>1</sup> PFEIL, 1983, from a middle Eocene level of Oregon (U.S.A.) and *E. lapaoi* ANTUNES & CAPPETTA, 2002, from a level marking the separation between the upper Campanian and the lower Maastrichtian (Upper Cretaceous) in the Benguela Basin (Angola).

\*List presented in function of the year of their description. Species<sup>1</sup> is a species of which the senior-author has himself collected specimens in its type locality and Species<sup>2</sup> is a species of which the senior-author has received specimens.

A re-examination of the three Cretaceous taxa of this list: *E. australis* (CHAPMAN, 1909), *E. eyrensis* PLEDGE, 1992 and *E. lapaoi* ANTUNES & CAPPETTA, 2002 will surely allow their attribution to other extinct Genera of the Family Echinorhinidae, according to its present redefinition.

These three specific extinct taxa having no representatives in Belgium, their reconsideration is not realizable in the Series *Géominpal Belgica*.

Two other species were recently (2013-2014) added to the original list: One from the Upper Cretaceous of Japan: *Echinorhinus wadonohaensis*\* KITAMURA, 2013 and one from the Lower Cretaceous of southern France: *Echinorhinus vielhus*\* GUINOT, CAPPETTA & ADNET, 2014.

\*These two taxa were attributed to the Genus *Echinorhinus*. According to their description and figuration, they could be representatives of other generic Mesozoic taxa but, doubtfully, representatives of the extant Genus *Echinorhinus* de BLAINVILLE, 1816.

Diverse isolated teeth were mentioned as *Echinorhinus* sp. from diverse parts of the world.

Their principal importance is the fact that they contribute to demonstrate that the Echinorhinomorphii initiated their diversification\* in the southern part of the Tethys and the western part of the Pacific Ocean.

\*Such as suggested by Dr. Kitamura in 2013.

### Echinorhinus vielhus GUINOT, CAPPETTA & ADNET, 2014

This species is based on a lot of twenty isolated teeth discovered in a limestone of Valanginian Age (Lower Cretaceous) in the Gard Department (southern France).

#### For references, see Bibliography-Systematics: Guinot, Cappetta & Adnet 2014.

#### Echinorhinus wadonohaensis KITAMURA, 2013

This species is based on isolated teeth discovered in a level of Santonian Age (Upper Cretaceous) of southwestern Japan.

Their dental crowns present a principal central cuspid flanked by one pair of lateral cusplets, one of this being distally oriented, the other being proximally oriented.

Their dental roots present no vertical groove, but discrete vertical furrows.

This species may be considered a member of the Family Orthechinorhinidae nov.

### For references, see Bibliography-Systematics: Kitamura 2013.

#### Other discoveries of fossil remains attributable to the Echinorhinomorphii

Diverse authors have mentioned the discovery of fossil remains attributable to undetermined taxa of this Super Order, but preferred to signalize their discovery as *Echinorhinus* sp\*.

\*See: PÖLLENSTOCK, J. 2014: *Echinorhinus* sp. In: Database of fossil elasmobranch teeth www.shark-references.com, World Wide Web electronic publication, Version 01/2014.

All these isolated data are fundamental for a better conception of the Natural History of this Super Order.

All these data were regrouped by Jürgen Pöllenstock and have led to the presentation of a map illustrating the paleodistribution of all the fossil representatives of this Genus.

See: Paleodistribution map of the Echinorhiniformes on the Website: <u>http://shark-references.com/species/view/Echinorhinus-sp</u>.

#### Echinorhinus sp.

The list of these isolated discoveries is the following: One dermal denticle discovered in a Pliocene level of Las Palmas (Balearic Islands, Spain), four dermal denticles discovered in a clay pit near Todtglüsingen, (Harburg, Germany), three teeth discovered in the Marnes de Donzacq Formation (Lower Lutetian) of southern France, three teeth discovered in a Maastrichtian level at Algarrobo, San Antonio Province (Chile), one tooth discovered in the level marking the separation of the Upper Campanian and the Lower Maastrichtian of Loanco cove, (Chanco, Maule, Chile) and one tooth fragment in the Fish Clay Formation at Roedvig (Denmark).

Even if quantitatively very poor, these data indicate diverse additional presences of representatives of this Genus.

### Fossil Genera attributed to the Family Echinorhinidae

Except for the morphology and the structure of their dental root, it is difficult to conceive that all these fossil taxa are representatives of the extant Family Echinorhinidae.

Here follows a detailed examination of the singularities of all these extinct Genera

## Genus Gibbechinorhinus CAPPETTA, 1990

This mono-specific Genus, represented by its type species *G. lewyi* CAPPETTA, 1990, is based on isolated teeth discovered in an upper Cretaceous level marking the transition between the Upper Campanian and the Lower Maastrichtian (Cretaceous Period) in the Oron Syncline in the Negev Desert (Israel).

This taxon is represented by about 30 teeth, or fragments of teeth. Their size, their proportions and their similar preservation allow supposing that these teeth represent a part of the dentition of one single individual.

The only objective data concerning this extinct taxon is the complex morphology of some of the dental crowns of its teeth\* presenting a, more or less pronounced, gibbosity and cutting edges presenting a serrulation and a morphology mixing the morphologies of the teeth of the Genus *Echinorhinus* and the Genus *Anacorax*. \*Except the last lateral teeth.

These data turn this Genus into one of the most aberrant Genera of all the extinct Chondrichthyes.

The sudden apparition of this aberrant taxon, mono-specific and so poorly represented, could find a plausible explanation in the occasional crossing of individuals of two distinct Genera, always producing sterile individuals\*, always difficult to classify.

\*Because of the mixing of morphological and anatomical characteristics of the two Genera.

Reference and illustrations: See Bibliography-Systematics: Cappetta 1990: p.: 742 and Cappetta 2012: p.: 108.

## Genus Orthechinorhinus ADNET, 2006

This mono-specific Genus, represented by its type species *O. pfeili* ADNET, 2006, is based on isolated teeth discovered in a level marking the transition between the Ypresian (Lower Eocene) and the Lutetian (Middle Eocene) in the Aquitaine Basin (southwestern France).

Reference and illustrations: See Bibliography-Systematics: Adnet 2006, Cappetta 1990: p.: 742 and Cappetta 2012: pp.: 108-109.

#### Genus Pseudoechinorhinus PFEIL, 1983

The type species of this mono-generic Genus is *Pseudoechinorhinus mackinnoni* PFEIL, 1983 based on isolated teeth discovered in a Danian level (lowermost Paleocene) of the Waikiri region (northern New-Zealand).

The dental crown of all the teeth of this species presents only one large central cuspid. Both sides of their dental crown are perfectly smooth.

The discovery of this fossil taxon in this area suggests a possible phyletic relation between this Genus and the extant Genus *Echinorhinus*\* of which most posterior teeth are also monocuspid.

\*Presently represented in this area by its extant species E. coockei PIETSCHMANN, 1928.

This fossil taxon may be considered as an extinct member of the Family Echinorhinidae GILL, 1862 and allows supposing that all the fossil relatives of the Genus *Echinorhinus* were in possession of teeth presenting a lower number of cusplets than its extant representatives.

Reference and illustrations: See Bibliography-Systematics: Cappetta 2012: pp.: 110 -111 and Pfeil 1983: p.: 258.

#### Genus Paraechinorhinus WELTON in PFEIL, 1983

The Genus *Paraechinorhinus* WELTON *in* PFEIL, 1983 has for generotype *P. hornesi* WELTON *in* PFEIL, 1983, Cappetta (2012: pp.: 109-110). It was based on isolated teeth discovered in the Monterey Formation (Middle Eocene) of Orange County (California, U.S.A.).

Symphyseal teeth of this Genus remain unknown. The absence of anterior radicular notches induces to consider that their teeth were not interlinked but placed in parallel rows.

This Genus includes a second species: *P. riepli* PFEIL, 1981, based on isolated teeth discovered in a Lutetian level (Middle Eocene) at Schlössbruch, near Salzburg (Salzburg, Austria).

Reference and illustrations: See Bibliography-Systematics: Cappetta 2012: pp.: 109 -110 and Welton *in* Pfeil 1983: p.: 301.

#### New Systematics proposals for these Echinorhiniformes

The odontological characteristics of these four Genera suggest to distribute three of these four Genera into two new Families and to consider the fourth one as a natural anomaly.

## Family Pseudoechinorhinidae nov.

This new Family is proposed for including the four following extinct Genera: Genus *Pseudoechinorhinus* PFEIL, 1983, Genus *Paraechinorhinus* WELTON *in* PFEIL, 1983, Genus *Gibbechinorhinus* CAPPETTA, 1990 and Genus *Priohybodus* d' ERASMO, 1960.

#### **Derivation nominis**

The name Pseudoechinorhinidae is proposed because the Genus *Pseudoechinorhinus* is considered as its generotype and to remind the considerable contribution to the knowledge of the Echinorhiniformes furnished by Dr. Fritz Pfeil (München, Germany) who was the inventor of this Genus.

Symphyseal teeth of its two Genera remain unknown. The absence of anterior radicular notches makes the consideration that their teeth were placed in parallel rows plausible.

This Family could also include some other taxa of upper Cretaceous Age, momentarily, attributed to the extant Genus *Echinorhinus*.

For description and illustrations of these two Genera: See Bibliography-Systematics: Cappetta 2012: pp.: 107-111, Pfeil 1983: p.: 258 and Welton *in* Pfeil 1983: p.: 301.

#### **Odontological characteristics of this new Family**

## Characteristics of their dental root

According to Pfeil 1983 and Cappetta 2012, the dental root of all the teeth of these two Genera present the following characteristics: A flat and high root with a variable number of intern furrows\* and the absence of anterior notches allowing their imbrication.

\*Hexanchoid morphology.

## Characteristics of their dental crown

According to Pfeil 1983 and Cappetta 2012, the dental crowns of all the teeth of these two Genera present the following characteristics: A large triangular form, with in some of these a lightly pronounced anterior hump\* and a narrow and elongated cuspid. Their extern and intern faces are smooth and their cutting edges are not serrated.

\*Present only on lateral to posterior teeth.

For description and illustrations, see Bibliography-Systematics: Cappetta 2012: pp.: 107, fig.: 94 and Pfeil 1983.

#### Remark

In fact, this Family could also include some other taxa of upper Cretaceous Age attributed to the extant Genus *Echinorhinus*. This problem concerning specific taxa having no representatives in Belgium does not concern this Series.

## Family Orthechinorhinidae nov.

This new Family has for generotype the mono-specific Genus *Orthechinorhinus* ADNET, 2006, based on isolated teeth discovered in a level marking the transition between the Ypresian (Lower Eocene) and the Lutetian (Middle Eocene) of the Aquitaine Basin (southwestern France).

Symphyseal teeth of this Genus remain unknown. The absence of anterior radicular notches indicates that the teeth were placed in parallel rows.

## **Derivation nominis**

The name Orthechinorhinidae is proposed because the Genus *Orthechinorhinus* is considered as its generotype and to remind its principal odontological characteristics: The orthogonal position of the single narrow and elon-gated cuspid (anterior teeth) or shorter and distally inclined cuspid (lateral to posterior teeth). This Family could also include some other taxa of upper Cretaceous Age, momentarily, attributed to the extant Genus *Echinorhinus*.

For description and illustrations: See Bibliography-Systematics: Adnet 2006, Cappetta 1990: p.: 742 and Cappetta 2012: pp.: 108-109.

## **Odontological characteristics of the Family Orthechinorhinidae**

#### Characteristics of its dental root

According to Adnet 2006 and Cappetta 2012, the dental root of all the teeth of this mono-generic Family presents the following characteristics: A flat and high root\* with a single intern furrow and the absence of anterior notches allowing their imbrication.

\*Presenting a nearly hemi-circular base (on the symphyseal and anterior teeth) or a distally elongated base (on the lateral teeth).

#### Characteristics of its dental crown

According to Adnet 2006 and Cappetta 2012, the dental crowns of all the teeth of these two Genera present the following characteristics: A narrow and elongated cuspid without lateral cusplets. Their extern and intern faces are smooth and their cutting edges are not serrated.

For description and illustrations, see Bibliography-Systematics: Cappetta 2012: pp.: 108-109, fig.: 96 and Pfeil 1983.

#### Remark

This Family could also include some other taxa of upper Cretaceous Age attributed to the extant Genus *Echino-rhinus*. The problem concerning specific taxa having no representatives in Belgium does not concern this Series.

#### Genus Gibbechinorhinus CAPPETTA, 1990

This 'abnormal' Genus may be included in the Family Pseudoechinorhinidae.

Even if the Genus *Gibbechinorhinus* CAPPETTA, 1990 is based on an important lot of isolated teeth, it seems obvious that these teeth come from the jaws of a single abnormal individual. This subjective reflection does not help to precise its systematics position.

Except for the last posterior teeth, all the dental crowns are serrated and present a, more or less pronounced and irregular hump. These humps, as well as a light serrulation, are observable on the lateral teeth of *Paraechinorhinus barnesi* WELTON *in* PFEIL, 1983 discovered in Miocene strata of California (U.S.A.).

The lower jaw of this taxon presents a central erect cuspid, which constitutes their sole common characteristic with the Genera *Orthechinorhinus* ADNET, 2006.

The Genus *Priohybodus* d' ERASMO, 1960, represented by isolated teeth of Upper Jurassic to Lower Cretaceous Age is a plausible ancestor of this Genus.

For reference and illustrations, see Bibliography-Systematics: Adnet 1906, Cappetta 2012: p.: 107, fig.: 94 F-J.

### The Genus Gibbechinorhinus and its local signification

According to CAPPETTA, 1990 and CAPPETTA, 2012, the single representative of this Genus is *Gibbechinorhinus lewyi* CAPPETTA, 1990 based on a lot of thirty teeth or fragments of teeth discovered in a lower Maastrichtian level in the Oron Syncline in the Negev Desert.

The fossil invertebrates assemblages discovered in the deposits of Upper Cretaceous Age of this region suggest that their paleoenvironment was representative of relatively shallow waters of very variable hyalinity.

In such an environment, the isolation of poorly diversified fish populations is a common phenomenon. Their last living populations frequently include a high concentration of abnormal individuals.

In northern France, at Hardivillers (Oise Department) and Hallencourt (Somme Department) the senior-author has discovered in an upper Campanian (Upper Cretaceous) horizon with very high phosphate concentration, small areas with thousands of same-sized teeth of *Squalicorax kaupi* (AGASSIZ, 1843) of which 45% presented a similar dissymmetry and an abnormal hump.

Such places are considered as large isolated marine areas where the salinity increases to a concentration inducing, primarily, progressive and irreversible alterations of the genetic code of their inhabitants and, finally. their death.

For reference and illustrations, see Bibliography-Systematics: Cappetta 1990 and Cappetta 2012: p.: 108, fig.: 95.

# Order Hexanchiformes de BUEN, 1926 rev.

This Order rev. is based on the Order Hexanchiformes de BUEN, 1926, but its extant representatives are restricted to the Genus *Hexanchus* RAFINESQUE, 1810.

The name of this taxon is based on its most primitive extant representative: The Genus *Hexanchus* RAFINESQUE, 1810.

# Principal anatomical characteristics of the Hexanchiformes

The principal anatomical characteristics of all the extant representatives of this Order rev. are: The possession of two dorsal fins without fin-spine, the possession of one anal fin and the absence of the massive radiating dermal denticles, typical for the Echinorhinomorphii.

The suspension of their jaws is orbitostylic. Their vertebral column is exclusively constituted by vertebrae having centrae that present a vertical circular section. All their extant representatives are ovoviviparous.

The extant representatives of the Hexanchomorphii are all in possession of six pairs of gill slits.

# Principal odontological characteristics of the Hexanchiformes

The principal odontological characteristics of all the extant representatives of this Order rev. are: the presence of a discrete anterior radicular notch, the presence of numerous commissural tooth\* rows, and the possession of one lower symphyseal tooth row.

\*Allowing a specific determination. See: Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt 1987.

### For reference, see Bibliography-Systematics:

Bigelow & Schroeder 1948, Cadenat & Blache 1963, Cappetta 2012 and de Buen 1926.

# Family Hexanchidae GRAY, 1851

According to Cappetta 2006 (p.: 299), the Family Hexanchidae\*regroups the twelve following nominal Genera: Genus *Hexanchus*\*\* RAFINESQUE, 1810, Genus *Notidanus*\*\*\* CUVIER, 1816, Genus *Notorhynchus*\* AYRES, 1855, Genus *Notidanion* JORDAN & HANNIBAL, 1923, Genus *Notidanodon* CAPPETTA, 1975, Genus *Weltonia* WARD, 1979, Genus *Eonotidanus* PFEIL, 1983, Genus *Notidanoides* MAISEY, 1986, Genus *Paranotidanus* WARD & THIES, 1987, Genus *Pachyhexanchus* CAPPETTA, 1990, Genus *Welcommia* CAPPETTA, 1990 and Genus *Pseudonotidanus* UNDERWOOD & WARD, 2004.

\*These two Genera are the sole valid extant taxa of this list, the number of pairs of gill slits of the others being unknown.

\*\*This taxon is a synonym of the Genus *Hexanchus* RAFINESQUE, 1810.

\*\*\*This taxon is a synonym of the Genus *Hexanchus* RAFINESQUE, 1810.

An additional extinct Genus: Genus *Gladioserratus* UNDERWOOD, GOSWAMI, PRASAD, VERMA & FLYNN was proposed in 2011.

# Reconsideration of the Systematics position of these taxa

The fact that all the representatives of the extant Genus *Notorhynchus* AYRES, 1855 are in possession of seven pairs of gill slits allows excluding this one immediately from the list of the representatives of the Family Hexanchidae.

The taxon *Eonotidanus* is a synonym of the Genus *Pachynotinadus* (Cappetta 2006: p.: 303) and the taxon *Paranotidanus* WARD & THIES, 1987 is another synonym of the Genus *Pachynotinadus* (Cappetta 2006: p.: 351).

The Kimmeridgian Genus *Notidanoides* MAISEY, 1986 is represented by isolated teeth but also by some skeletal remains which, apparently, do not allow specifying the number of its pairs of gill slits.

Consequently it is impossible to guarantee its attribution to the Family Hexanchidae. The general morphology of its teeth allow considering this Genus as a possible ancestor of the Genus *Notidanodon* CAPPETTA, 1975.

The Oxfordian Genus *Eonotidanus* PFEIL, 1983, synonym of the Genus *Pachynotidanus* CAPPETTA, 1990 is also represented by skeletal remains.

The number of its pairs of gill slits could allow specifying its systematics position, but neither Pfeil nor Cappetta mentioned their number.

The attribution of all the other fossil taxa only based on isolated teeth is purely speculative. The far ancestors of the Hexanchidae were surely in possession of only five pairs of gill slits. Some of the oldest Genera of this list represented may be some of these.

# **Order Heptranchiformes nov.**

This Order is based on the extant Family Heptranchidae BARNARD, 1925 which regroups all the extant Selachii in possession of seven pairs of gill-slits.

## Family Heptranchidae BARNARD, 1925

According to Cappetta (2006: p.: 395), this Family based on the extant Genus *Heptranchias* RAFINESQUE, 1810 includes also the extant Genus *Notorynchus* AYRES, 1855 and the extinct Genus *Paraheptranchias*\* PFEIL, 1981.

\*This extinct taxon being based on isolated teeth, this attribution remains hypothetical.

The principal anatomical characteristic of this extant Family is the possession of seven pairs of gill slits.

For reference, see Bibliography-Systematics: Barnard 1925, Cadenat & Blache 1963, Cappetta 2012 and Compagno 1984.

## Systematic position of the Family Pseudonotidanidae Underwood & WARD, 2003

# Family Pseudonotidanidae UNDERWOOD & WARD, 2004

This Family has for generotype the Genus *Pseudonotidanus* UNDERWOOD & WARD, 2004, based on skeletal remains of its type species *Pseudonotidanus*\* *politus* (THIES, 1992), discovered in the *Posidonia* Shale Formation of Lower Toarcian Age (End of the Lower Jurassic) at Holzmaden (southern Germany).

\*Described, in 1992, as Paleospinax politus by Thies.

A second species *Pseudonotidanus semirugosus* UNDERWOOD & WARD, 2004, based on isolated teeth discovered in the Watton Beds\* of Bathonian Age and in the Oxford Clay Formation of Oxfordian Age in southern England was later described (See Cappetta 2012 p.: 104, fig.: 91).

\*Thanks to Dr. David Ward, the senior-author had the possibility to collect some teeth of this taxon.

Considering the geological Age of the levels in which the teeth of these taxa were discovered, diverse suggestions may be advanced.

These generic taxa are representatives of an extant Order and, logically, of the Hexanchiformes, the oldest one. Other possibility, they are representatives of members of a more primitive Order being, of course, in possession of only five pairs of gill slits.

> For references and illustrations: See Bibliography-Systematics: Cappetta 2012 (p.: 104, fig.: 91), Thies 1992 and Underwood & Ward 2004 (p.: 476, pl.: 9, figs.: 1-7 and pl.: 10, figs.: 1-2)

## Passage from a synechodontid tooth to a notidanoid tooth (A virtual hypothesis)

A primitive synechodontid tooth is characterized by a short and arched polyhemiaulacorhyzid root and a dental crown presenting one main cuspid flanked by multiple pairs of lateral cusplets in vertical or subvertical position. Cuspid and cusplets present vertical extern and intern striations.

A notidanoid tooth is characterized by a high and flat root, with a variable number of intern furrows and a strongly serrated smooth dental crown presenting a short anterior part more massive than its distal part. All its cusplets are distally oriented.

On a 3D screen it must be possible to pass from the morphology of a synechodontoid (*Paleospinax*-like) tooth to the morphology of a hexanchid (*Notidanodon*-like) tooth.

This passage from a synechodontoid tooth to a notidanonoid tooth requires the principal following modifications: The complete flattening of the base of its dental root\*, the magnification of the basal surface of its dental root, the appearance of elongated furrows, replacing the variable polyhemiaulacorhyzid structure.

\*The placement in parallel rows, however, remains preserved.

After a rotation of 90° of the root, the dental crown and the dental root are placed in the same plane.

After an additional relatively strong oblique anterio-posterior compression of the tooth, the anterior part of the tooth becomes more massive and its anterior cusplets are considerably reduced in size, while the other cusplets are pushed in distal direction.

The dental crowns of the Elasmobranches teeth are constituted by apatite molecules which need the oxygen that is furnished by the complex vascularization of their dental roots.

A possible cause of the change in the supply of oxygen could be an important modification of their cytochrome b, responsible for the extraction of oxygen from marine waters.

Cytochrome b is a very vulnerable part of the genetic code. Geologist-paleontologists are able to precise when it was damaged.

## Passage from a notidanonoid tooth to some lower squaloid teeth (A virtual hypothesis)

The additional formation of an obvious anterior notch on the extern side of all the dental roots, allowing a solid imbrication of all the teeth of the dental series, produces the morphology of the lower teeth of the majority of the extinct and extant Squalomorphii.

# Remark

This scheme is only valid for some representatives of the super Order Squalomorphii HERMAN & VAN WAES, 2012, but it is not valid for the representatives of the Order Etmopteriformes and the Order Aculeoliformes which have conserved the primitive, parallel, mode of placement of their tooth rows.

It is the complexity of the composition of the Super Order Squalomorphii which caused problems to the conclusions formulated by the genetic researchers Bernardi & Powers 1992\*.

\*See Bibliography-Systematics: Bernardi & Powers 1992.

# Super Order Heterodontomorphii HERMAN & VAN WAES, 2012

This Super Order regroups the two Orders: The Order Heterodontiformes BERG, 1937 and the Order Paracestracioniformes HERMAN & VAN WAES, 2012.

> For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **3**: p.: 7.

# **Order Heterodontiformes BERG**, 1937

The Order Heterodontiformes is based on the single Family Heterodontidae GRAY, 1851. This Family was proposed by Gray to highlight the extreme singularities of the dentition of the extant as well as the extinct representatives of this Family.

# **Order Paracestracioniformes HERMAN & VAN WAES, 2012**

The Order Paracestracioniformes is based on the single Family Paracestracionidae HERMAN & VAN WAES, 2012.

This Family was proposed to point out the supposed lack of lateral molariform teeth of the Genus *Paracestracion on Noken in ZITTEL*, 1911 signalized by Cappetta in 1986.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **3**: p.: 11.

# Super Order Squatinomorphii rev.

## **Taxonomic modification**

The Super Order Orectolobomorphii HERMAN & VAN WAES, 2012 was proposed for regrouping the Order Orectolobiformes *sensu* Applegate 1972 and the Order Squatiniformes COMPAGNO, 1973.

The Super Order Squatinomorphii, such as presently proposed, regroups all the Neoselachii presenting teeth in possession of an apron and allow distinguishing five different lineages: the Squatiniformes, the Orectolobiformes reduced to the three Genera\* which constituted the Family Orectolobidae GILL, 1896, the Hemiscylliiformes nov., the Ginglymostomatiformes nov. and the Stegostomiformes nov.

\*Genus Orectolobus, Genus Sutorectus and Genus Eucrossorhinus.

The odontological characteristics of the Orders, the Families and the Genera included in this Super Order were detailed in *Géominpal Belgica*. 2012: **2**.

This new Super Order regroups the two extant Orders: Order Squatiniformes COMPAGNO, 1973 and the Order Orectolobiformes\* rev.

\*Equivalent of the Family Orectolobidae GILL, 1896: Genus Orectolobus, Genus Sutorectus and Genus Eucrossorhinus.

# **Order Squatiniformes de BUEN**, 1926

This Order is based on the single Family Squatinidae BONAPARTE, 1838 based on the extant Genus *Squatina* (LINNAEUS, 1758).

For reference, see Bibliography-Systematics: Compagno 1984, de Buen 1926 and Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 44.

# Order Orectolobiformes HERMAN & VAN WAES, 2012 rev.

This Order is presently reconsidered and restricted to the single Family Orectolobidae *sensu* GILL, 1896 which regroups the three extant Genera: Genus *Orectolobus*, Genus *Sutorectus* and Genus *Eucrossorhinus* and some extinct Genera.

For reference, see Bibliography-Systematics: Gill 1896 and Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 45.

# Super Order Hemiscylliomorphii nov.

This Super Order is based on the Order: Order Hemiscylliiformes nov., which regroups the six following Families: Family Porcynidae, Family Agaleidae, Family Hemiscylliidae, Family Brachaeluridae, Family Parascylliidae and Family Ginglymostomatidae.

# Order Hemiscylliiformes nov.

This Order regroups the five Families: Family Phorcynidae, Family Agaleidae, Family Hemiscylliidae, Family Brachaeluridae and Ginglymostomatidae.

# Spatio-temporal distribution of the Order Hemiscylliiformes

This Order regroups the five following Families: Family Porcynidae nov., Family Agaleidae REES, 2000,

Family Hemiscylliidae, Family Brachaeluridae APPLEGATE, 1974, and Family Ginglymostomatidae. GILL, 1862.

## Data concerning the Family Phorcynidae nov.

The mono-specific Genus *Phorcynis* THIOLLIERE, 1852, based skeletons of *Phorcynis catulina* THIOLLIERE, 1852 discovered in one level of Kimmeridgian Age (Lower Jurassic) in the Jura (France).

The mono-specific Genus *Mesiteia* GORJANOVIC-KRAMBERGER, 1855, based skeletal remains of *Mesiteia emiliae*, GORJANOVIC-KRAMBERGER, 1885 discovered in one level of Campanian Age (Upper Cretaceous) in Lebanon. Other specimens were in possession of private merchants. Their examination, in 1973, confirmed the general morphology of their dentition. The lower jaw of one of these specimens allowed guaranteeing the presence of one symphyseal tooth-row.

The senior-author had the possibility to examine, in 1973, another skeleton in a Lebanese private Collection. This very well preserved specimen showed its two dorsal fins, without spine, its two pectoral fins, its two pelvic fins and its five pairs of gill-slits. The dental crown of its lower lateral teeth presented a second pair of very short lateral cusplets.

The mono-specific Genus *Doratodus* SCHMID, 1861 is based on isolated teeth of its type-species *Doratodus tricuspidatus* SCHMID, 1861 discovered in a level of Triassic Age in Germany.

The mono-specific Genus *Heterophorcynis* UNDERWOOD & WARD, 2004 is based on isolated teeth of its generotype *Heterophorcynis microdon* discovered in a level of Bathonian Age (Middle Jurassic) in southern England. The mono-specific Genus *Dorsetoscyllium* UNDERWOOD & WARD, 2004 is based on *Dorsetoscyllium terraefullonicum*, represented by numerous isolated teeth discovered in a level of Bathonian Age (Middle Jurassic) in southern England.

The mono-specific Genus *Garrigascyllium* GUINOT, CAPPETTA & ADNET, 2014 is based on *Garrigascyllium aganticensis* represented by numerous isolated teeth discovered in a level of Valanginian Age (Lower Cretaceous) in south-western France.

### Conclusion

This Family had specific representatives ranging from Triassic Age in northern Germany to Valanginian Age (Lower Cretaceous) in south-western France.

All its representatives were discovered in sediments attributable to coastal and continental shelf environments.

## Data concerning the Family Agaleidae REES, 2000

The mono-generic Family Agaleidae includes only its mono-specific Genus *Agaleus* DUFFIN & WARD, 1983 represented only by its type species *A. dorsetensis* DUFFIN & WARD, 1983 based on isolated teeth discovered in a level of lower Sinemurian Age (Lower Jurassic) in southern England.

The fossil invertebrates discovered in the same level demonstrate that its paleoenvironment was representative of shallow water.

### Data concerning the Family Hemiscylliidae GILL, 1862

This Family regroups the two extant Genera: Genus *Hemiscyllium* MÜLLER & HENLE, 1837 and Genus *Chiloscyllium* MÜLLER & HENLE, 1837 and two extinct Genera: Genus *Acanthoscyllium* CAPPPETTA, 1980 and Genus *Almascyllium* CAPPPETTA, 1980.

The Genus *Hemiscyllium* based on *Hemiscyllium ocelllatum* (BONNATERRE, 1788), regroups all the populations of the diverse extant species scattered along the coasts of the Indo-Pacific Ocean, Indonesia, Papua and Australia.

This Genus includes also two extinct taxa: *Hemiscyllium bruxelliensis* HERMAN, 1977, based on hundreds isolated teeth discovered in levels of Middle and Upper Eocene Ages in Belgium and *Hemiscyllium hermani* MÜLLER, 1989, based on numerous isolated teeth discovered in one level of upper Campanian Age in Westfalia (Germany).

The Genus *Chiloscyllium* MÜLLER & HENLE, 1837 based on *Chiloscyllium plagiosum* (BENNETT, 1830) regroups all the populations of the diverse extant species scattered along the coasts of the Indo-Pacific Ocean, Indonesia,

Papua and Australia.

This Genus includes also nine extinct taxa: *Chiloscyllium humboldti* (REUSS, 1845), based on some isolated teeth of Turonian Age discovered in the Czech Republic, *Chiloscyllium broennimani* CASIER, 1958, based on some isolated teeth of Maastrichtian Age (Upper Cretaceous) from Trinidad Island, *Chiloscyllium daimeriesi* (HERMAN, 1973), based on hundreds of isolated teeth of Selandian Age (Middle Paleocene discovered in Belgium, *Chiloscyllium greeni* (CAPPETTA, 1973), based on some isolated teeth of Turonian Age discovered in Dakota (U.S.A.), *Chiloscyllium missouriense* CASE, 1979, based on some isolated teeth of Campanian Age discovered in Montana (U.S.A.), *Chiloscyllium gaemersi* MÜLLER, 1989, based on some isolated teeth of upper Campanian Age discovered in Westtfalia (southern Germany), *Chiloscyllium mereretiae* WERNER, 1989, based on isolated teeth of upper Cenomanian Age in Egypt, *Chiloscyllium meraense* NOUBHANI & CAPPETTA, 1997, based on numerous isolated teeth of upper Ypresian Age in central Morocco and *Chiloscyllium salvani* NOUBHANI & CAPPETTA, 1997, based on numerous isolated teeth of upper Campanian Age in central Morocco.

The two American taxa require re-examination, because members of a Genus regrouping only small benthic sharks could not cross the North Atlantic after the Upper Cretaceous Period.

The Genus Acanthoscyllium CAPPETTA, 1980 based on Acanthoscyllium sahelalmae (PICTET & HUMBERT, 1866) is represented by numerous skeletons and skeletal remains discovered in levels of upper Santonian Age in Lebanon.

The Genus *Almascyllium* CAPPETTA, 1980 based on *Almascyllium cheikeliasi* (SIGNEUX, 1952) is represented by numerous skeletons and skeletal remains discovered in levels of upper Santonian Age in Lebanon.

#### Conclusion

This Family had specific extinct representatives ranging from upper Cenomanian Age (in Egypt, northern Africa) to the Middle and Upper Eocene Ages (in Belgium, Europa) and extant representatives scattered along the coasts of of the Indo-Pacific Ocean, Indonesia, Papua and Australia.

Fossil or extant representatives were never encountered eastern more than the Great Pacific Barrier.

### Data concerning the Family Brachaeluridae APPLEGATE, 1974

The Family Brachaeluridae regroups the two extant Genera: Genus *Brachaelurus* OGILBY, 1908 and *Heteros-cyllium* REGAN, 1908 and the two extinct Genera: Genus *Paraginglymostoma* HERMAN, 1982 and Genus *Palaeobrachaelurus* THIES, 1983.

The mono-specific Genus *Brachaelurus* is based on *Brachaelurus waddi* (BLOCH & SCHNEIDER, 1801), inhabiting the north-eastern coasts of Australia.

The mono-specific Genus *Heteroscyllium* is based on *Heteroscyllium colcloughi* (OGILBY, 1908), inhabiting some northern and eastern coasts of Australia.

The mono-specific Genus *Paraginglymostoma* HERMAN, 1982 is based on *Paraginglymostoma bloti* HERMAN, 1982, represented by some teeth discovered in one level of Maastrichtian Age in Nieder-Elbe (northern Germany).

The mono-specific Genus *Palaeobrachaelurus* THIES, 1983 is based on *Palaeobrachaelurus bedfordensis* THIES, 1983, represented by some teeth discovered in one level of Callovian Age (Middle Jurassic) in southern England.

### Conclusion

This Family has extinct representatives ranging from Callovian Age (Middle Jurassic) in southern England to Maastrichtian Age (uppermost Cretaceous) in northern Germany and extant representatives endemic to Australia.

# **Order Stegostomatiformes nov.**

This Order regroups the two Families: Family Stegostomatidae GILL, 1862 and Family Rhincodontidae MÜLLER & HENLE, 1839.

The odontological characteristics of the Families and the Genera included in this Super Order were detailed in the preceding chapter: **13.5**.

## Spatio-temporal distribution of the Order Stegostomatiformes

This Order has representatives in levels of Cenomanian Age (Upper Cretaceous) in central Europe, in levels of Ypresian to Bartonian Age (Lower to Upper Eocene) in central Europe and central Asia and is still represented by one large mono-specific benthic Genus\* and by one huge filter-feeding Genus\*\*.

\*Genus Stegostoma. \*\*Genus Rhincodon.

# Family Stegostomatidae GILL, 1862

## Genus Stegostoma Müller & Henle, 1837

The extant mono-specific Genus *Stegostoma* is based on *Stegostoma fasciatum* (HERMANN, 1783). This Genus has for holotype *Eostegostoma angustum* HERMAN, 1977.

The species *Eostegostoma angustum* was represented by diverse European, northern African and northern American populations inhabiting shallow waters with energetic sea bottom currents between the Lower Eocene and the Middle Eocene.

# Family Archaeobatidae DELSATE & CANDONI, 2001

This Family regroups the three extinct Genera: Genus *Cristabatis* DELSATE & CANDONI, 2001, Genus *Doliobatis* DELSATE & CANDONI, 2001 and Genus *Toarcibatis* DELSATE & CANDONI, 2001.

## Genus Cristabatis DELSATE & CANDONI, 2001

The type-species of this Genus is *C. exudans* DELSATE & CANDONI, 2001, based on isolated teeth discovered in a level of Toarcian Age (uppermost Lias) of the Nièvre Department (France).

A second species: *C. crescentiformis* DELSATE & CANDONI, 2001 also based on isolated teeth discovered in the Toarcian is attributed to this Genus.

For description and figuration: See Bibliography-Systematics: Delsate & Candoni 2011.

# Genus Doliobatis DELSATE & CANDONI, 2001

The type-species of this mono-specific Genus is *D. weisi* DELSATE & CANDONI, 2001, based on isolated teeth discovered in a level of middle Toarcian Age (uppermost Lias) of the Luxembourg Province (Belgium).

For description and figuration: See Bibliography-Systematics: Cappetta 2012 and Delsate & Candoni 2011.

# Genus Toarcibatis DELSATE & CANDONI, 2001

The type-species of this Genus is *T. elongata* DELSATE & CANDONI, 2001, based on isolated teeth discovered in a level of middle Toarcian Age (uppermost Lias).

This Genus includes three other species: *T. alcarinata* DELSATE & CANDONI, 2001, *T. brevicristata* DELSATE & CANDONI, 2001 and *T. multicristata* DELSATE & CANDONI, 2001.

All these taxa are of Toarcian Age, but the first one was discovered in the Nièvre Department (France) and the two others in the Sarthe Department (France).

# **Systematics reflection**

This Family has a very short spatio-temporal distribution. Its four Genera are represented only during the sedimentation of some Toarcian Formations, and were only discovered in a very restricted area of southernmost Belgium and northern France.

The teeth of all its representatives have some superficial similarities with the Rhinobatoid Chondrichthyes, but also numerous fundamental criteria of the representatives of the Super Order Squatinomorphii: A hemiaulacorhy -zid root, a dental crown overlapping the top of its dental root, the possession of an apron\* and the presence of a principal smooth cuspid flanked by one pair of short smooth cusplets.

\*It is the morphology of this apron which allows suggesting the existence of a phyletic relation between this extinct Family and these of the Order Hemiscylliformes.

For description and figuration: See Bibliography-Systematics: Cappetta 2012 and Delsate & Candoni 2011.

# Super Order Squalomorphii HERMAN & VAN WAES, 2012

This Super Order was proposed for regrouping the seven following extant Orders: Order Squaliformes HERMAN & VAN WAES, 2012, Order Etmopteriformes HERMAN & VAN WAES, 2012, Order Oxynotiformes HERMAN & VAN WAES, 2012, Order Aculeoliformes HERMAN & VAN WAES, 2012, Order Centrophoriformes\* HERMAN & VAN WAES, 2012, Order Dalatiformes HERMAN & VAN WAES, 2012 and Order Somniosiformes HERMAN & VAN WAES, 2012.

\*Originally cited as Centrophoriiformes instead of Centrophoriformes.

## **Remark concerning their Systematics**

Other extinct Genera may be included in each of these seven Orders, but that is not the aim of this short Synthesis.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin).: p.: 4.

# Order Squaliformes sensu HERMAN & VAN WAES, 2012

This Order is based on the Family Squalidae BONAPARTE, 1834, based on the extant Genus *Squalus* LINNAEUS, 1758.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin).: p.: 4.

# **Order Etmopteriformes HERMAN & VAN WAES, 2012**

This Order is based on the Family Etmopteridae FOWLER, 1834, based on the extant Genus *Etmopterus* RAFINESQUE, 1810.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin).: p.: 6.

# Order Oxynotiformes HERMAN & VAN WAES, 2012

This Order is based on the Family Oxynotidae GILL, 1872, based on the extant Genus *Oxynotus* RAFINESQUE, 1810.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin).: p.: 6.

# **Order Aculeoliformes HERMAN & VAN WAES, 2012**

This Order, erroneously named Aculeoloformes, is based on the Family Aculeolidae HERMAN & VAN WAES, based on the extant Genus *Aculeola* de BUEN, 1959.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin).: p.: 7.

# **Order Centrophoriformes HERMAN & VAN WAES, 2012**

This Order is based on the Family Centrophoridae BLEEKER, 1859, based on the extant Genus *Centrophorus* MÜLLER & HENLE, 1837.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin).: p.: 8.

# Order Dalatiiformes HERMAN & VAN WAES, 2012

This Order is based on the Family Dalatiidae GRAY, 1851, based on the extant Genus *Dalatias* RAFINESQUE, 1810.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin).: p.: 9.

# **Order Somniosiformes HERMAN & VAN WAES, 2012**

This Order is based on the Family Somniosidae JORDAN, 1888, based on the extant Genus *Somniosus* LESUEUR, 1818.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2** (Fin): p.: 10.

# Super Order Scyliorhinomorphii HERMAN & VAN WAES, 2012

This Super Order, based on the Order Scyliorhiniformes HERMAN & VAN WAES, 2012, is itself based on the extant Family Scyliorhinidae GILL, 1862.

This Super Order was proposed for the regrouping of five Orders: The Order Scyliorhiniformes, already mentioned, the Order Atelomycteriformes HERMAN & VAN WAES, 2012, based on the Family Atelomycteridae HERMAN & VAN WAES, 2012, the Order Halaeluriformes HERMAN & VAN WAES, 2012, based on the Family Halaeluridae HERMAN & VAN WAES, 2012, the Order Pentanchiformes, based on the Family Pentanchidae HERMAN & VAN WAES, 2012 and the Order Triaenodoniformes, based on the Family Triaenodonidae HERMAN & VAN DEN EECKHAUT, 2010.

Five new Families were proposed in the same Publication: The Family Proscylliidae, the Family Atelomycteridae, the Family Halaeluridae, the Family Schroederichthydae and the Family Pentanchidae.

All these new Families were based on extant Genera. The Family Atelomycteridae was based on the extant Genus *Atelomycterus* GARMAN, 1913. The Family Halaeluridae was based on the extant Genus *Halaelurus* GILL, 1862. The Family Proscylliidae was based on the extant Genus *Proscyllium* HILGENDORF, 1904. The Family Schroederichthydae was based on the extant Genus *Schroederichthys* SPRINGER, 1966.

The extant Genus *Cephalurus* GILL, 1862 was integrated into the Family Triaenodonidae HERMAN & VAN DEN EECKHAUT, 2010.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **4**: p.: 46.

According to their odontological characteristics and some of their anatomical characteristics, the senior-author proposes to include a sixth Order in this Super Order: the Order Triakiformes nov. Ord.

## **Remark concerning their Systematics**

Other extinct Genera may be included in each of these six Orders, but that is not the aim of this short Synthesis. For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **4**: pp.: 46 to 53.

# **Order Scyliorhiniformes HERMAN & VAN WAES, 2012**

This Order is based on the Family Scyliorhinidae de BLAINVILLE, 1816 and also includes the Family Paleoscylliidae HERMAN & VAN WAES, 2012 regrouping nineteen extanct Genera and eigth extinct Genera.

## **Remark concerning its Systematics**

Other extinct Genera may be included in each of these two Families, but that is not the aim of this short Synthesis.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **4**: pp.: 46 to 53.

# **Order Atelomycteriformes HERMAN & VAN WAES, 2012**

This Order is based on the single Family Atelomycteridae HERMAN & VAN WAES, 2012, based on the sole extant Genus *Atelomycterus* GARMAN, 1913.

## **Remark concerning its Systematics**

Other extinct Genera may be included in this Family, but that is not the aim of this short Synthesis.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **4**: p.: 50.

# **Order Halaeluriformes HERMAN & VAN WAES, 2012**

This Order is based on the single Family Halaeluridae regrouping the three extant Genera: Genus *Halaelurus*, GILL, 1862, Genus *Holohalaelurus* FOWLER, 1934 and Genus *Galeus* CUVIER, 1816.

## **Remark concerning its Systematics**

Other extinct Genera may be included in this Family, but that is not the aim of this short Synthesis.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **4**: p.: 51.

# Order Pentanchiformes HERMAN & VAN WAES, 2012

This Order is based on the single Family Pentanchidae *sensu* HERMAN & VAN WAES, 2012 itself represented by the single Genus *Pentanchus* SMITH & RADCLIFFE, 1912.

The principal distinctive anatomical characteristic of this Genus is its possession of only one dorsal fin.

### **Remark concerning its Systematics**

Other extinct Genera could be included in this Family, but that is not the aim of this short Synthesis.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **4**: p.: 51.

# **Order Triaenodoniformes HERMAN & VAN WAES, 2012**

This Order is based on the Family Triaenodonidae HERMAN & VAN DEN EECKHAUT, 2010 which regroups the two extant Genera: Genus *Triaenodon* MÜLLER & HENLE, 1837 and Genus *Cephalurus* BIGELOW & SCHROEDER, 1944.

## **Remark concerning its Systematics**

Other extinct Genera could be included in this Family, but that is not the aim of this short Synthesis.

For reference, see Bibliography-Systematics:

Herman & Van Waes 2012: Géominpal Belgica. 4: p.: 51.

# **Order Triakiformes nov.**

This Order is proposed for regrouping the two extant Families, the Family Triakidae *sensu* COMPAGNO, 1984 and the Family Pseudotriakidae *sensu* GILL, 1893 as well as their plausible ancestors, presently suggested.

All the extant representatives of this Order possess five pairs of gill slits, two dorsal fins without fin-spine, a vertebral column composed only of vertebrae presenting a cylindrical centrum. They are aplacental viviparous fish.

The base of their dental crown overlaps, more or less intensively, the extern side of the top of their dental root. All their dental crowns present extern and intern costulae of variable height. Their dental crowns present one principal cuspid flanked by two or three lateral cusplets.

The Family Triakidae *sensu* COMPAGNO, 1984 is considered as the ancestor of the Family Pseudotriakidae *sensu* GILL, 1893.

# Family Triakidae GRAY, 1851

The Family Triakidae GRAY, 1851 is based on the Genus *Triakis* MÜLLER & HENLE, 1838 and, according to Compagno 1984, the ITIS' list, and FishBase (version of January 2009), includes the eight other following extant Genera: Genus *Mustelus* LINCK, 1790, Genus *Galeorhinus* de BLAINVILLE, 1816, Genus *Hemitriakis* HERRE, 1923, Genus *Scylliogaleus* BOULENGER, 1902, Genus *Furgaleus* WHITLEY, 1951, Genus *Hypogaleus* SMITH, 1957, Genus *Iago* COMPAGNO & SPRINGER, 1971 and Genus *Gogolia* COMPAGNO, 1973.

This conception is difficultly conceivable for paleontologists because it seems to mix generic taxa of numerous different phyletic lineages. The complete revision of this strange assemblage is not the aim of this Publication.

# **Odontological characteristics of the members of the Family Triakidae**

The odontological characteristics of the three\* extant generic representative taxa of the Family Triakidae *sensu* GRAY, 1851 were thoroughly described and illustrated in Herman, Hovestadt-Euler & Hovestadt 1987 (See Bibliography-Systematics).

\*Gray never integrated the Genus *Galeorhinus* de BLAINVILLE, 1816 in his Family Triakidae.

# Anatomical characteristics of the members of the Family Triakidae

The most characteristic anatomical criteria of all the extant members of this Order are: The possession of five pairs of gill slits, the possession of two dorsal fins without fin-spine, the possession of one anal fin and the possession of a vertebral column composed only of vertebrae presenting a cylindrical centrum. They are aplacental viviparous fish\*.

\*See Bibliography-Systematics: Lopez, Ryburn, Fedrigo & Naylor 2006.

According to Cappetta 2006 (p.: 405), this Family could also include the ten following extinct taxa: Genus *Palaeoscyllium* WAGNER, 1857, Genus *Protogaleus* MOLIN, 1860, Genus *Pseudogaleus* JAEKEL, 1894, Genus *Palaeogaleus* GURR, 1962, Genus *Paratriakis* HERMAN, 1977, Genus *Archaeotriakis* CASE, 1978, Genus *Pachygaleus* CAPPETTA, 1992, Genus *Squatigaleus* CAPPETTA, 1992, Genus *Kouribgaleus* NOUBHANI & CAPPETTA, 1997 and Genus *Xystrogaleus* ADNET, 2006.

For reference, see Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt, 1988.

# Data and comments

### Genus Palaeoscyllium WAGNER, 1857

This Genus is based on the skeleton of *Palaeoscyllium formosum* WAGNER, 1857 discovered in a level of the Lower Jurassic Period at Solnhofen (Bavaria, Germany) presenting typical scyliorhinomorphoid teeth.

The senior-author agrees with the opinions of Leidner & Thies 1999 and Underwood 2002 who concluded that
this Genus may be excluded from this Family.

#### Genus Protogaleus MOLIN, 1860

This Genus is a synonym of Genus Galeorhinus de BLAINVILLE, 1816, a typical carcharhinomorphoid taxon.

This taxon may be excluded from this Family.

#### Genus Pseudogaleus JAEKEL, 1894

This Genus is a synonym of Genus Galeorhinus de BLAINVILLE, 1816, a typical carcharhinomorphoid taxon.

This taxon may be excluded from this Family.

#### Genus Palaeogaleus GURR, 1962

This Genus is based on isolated teeth of its type species *Palaeogaleus vincenti* DAIMERIES, 1888 of Selandian Age (Middle Paleogene Period).

This taxon remains a representative taxon of the Family Triakidae as presently restricted.

# Genus Paratriakis HERMAN, 1977

This Genus is based on isolated teeth of its type species *Paratriakis bettrechiensis* HERMAN, 1977 of Cenomanian and Turonian Ages and represented by diverse skeletons of *P. curtirostris* (DAVIS, 1887) of Santonian Age discovered in northern Lebanon.

Cappetta (2012, pp.: 289-290) already considered this taxon as a member of the Family Triakidae, but diverse odontological considerations\* and diverse anatomical characteristics observable on the skeletal remains of this Genus induce the senior-author to consider that the Genus *Paratriakis* is a member of another carcharhiniform lineage and not an extinct representative of the Family Triakidae.

\*E.g.: The teeth of the diverse representatives of this Genus are flat and antero-distally elongated; their single cuspid is never in a vertical position.

#### Genus Archaeotriakis CASE, 1978

The type species of this Genus is *Archaeotriakis rochelleae* CASE, 1978, based on isolated teeth discovered in Campanian levels (Upper Cretaceous) of Montana (U.S.A.). A second species, *Archaeotriakis ornatus* CASE, 1978 was described from Campanian levels of Wyoming (U.S.A.).

This Genus seems to have been endemic of the North American Continent.

The Genus *Archaeotriakis* may be considered as an extinct representative of the Family Triakidae, or integrated in the Family Pseudotriakidae GILL, 1895.

But, the close similarities of its dental characteristics with these\* of the extant mono-generic Genus *Pseudotriakis* de BRITO CAPELLO, 1868 of the Family Pseudotriakidae GILL, 1895 suggest to include the Genus *Archaeotriakis* CASE, 1978 in this last Family.

\*See Plates 8 and 9 of Herman, Hovestadt-Euler & Hovestadt 1991.

The teeth of the representatives of the Genus *Pseudotriakis* differ from the teeth of the representatives of the Genus *Archaeotriakis*\* by the three principal following criteria: They are obviously anterio-distally more compressed; their crown presents a second anterior cusplet and costulations reaching the top of their cuspid.

\*See Cappetta 2012: p.: 292, fig.: 275.

The fact that, at the end of the Upper Cretaceous, the Genus *Archaeotriakis* inhabited the North American Continent helps to understand the present distribution of the two extant representatives of the Genus *Pseudotriakis*.

#### Genus Pachygaleus CAPPETTA, 1992

The type species of this Genus is *Pachygaleus lefevrei* (DAIMERIES, 1888), or *Galeus lefevrei* DAIMERIES, 1888, based on isolated teeth discovered in the Ypresian (Lower Eocene) at Saint-Gilles (Brussels, Belgium).

Middle Eocene deposits exist at Saint-Gilles, but no Ypresian deposits were accessible at this epoch.

This Genus is a member of the former Family Carcharhinidae *sensu* Compagno 1984 and not a member of the Family Triakidae *sensu* GRAY, 1851.

For references, see: Bibliography-Systematics: Cappetta 2006: p.: 345.

#### Genus Squatigaleus CAPPETTA, 1992

The type species of this Genus is *Squatigaleus atlasi* CAPPETTA, 1989 based on isolated teeth discovered in the lower Maastrichtian (Upper Cretaceous) of central Morocco. This Genus includes three additional species, one from the northern American Continent, *S. sulphurensis*, one from the lower Campanian of Morocco, *S. vianeyi*, and a last one, *S. grandjeani*, from the lower Maastrichtian of Egypt.

This Genus is represented in diverse fossiliferous strata of Campanian and Maastrichtian Ages (Upper Cretaceous) from North Africa (Morocco to Egypt) and strata of Maastrichtian Age from North America and Near-East.

Their teeth differ from the teeth of the extant Genera *Mustelus* LINCK, 1790 and *Scylliogaleus* BOULENGER, 1902 only by their more elongated single cuspid and by their finer and higher extern and intern costulations.

The extinct Genus *Squatigaleus* may be considered as a fossil representative of the Family Triakidae and could be a common ancestor of these two extant Genera.

For references, see: Bibliography-Systematics: Cappetta 2012: p.: 294, fig.: 277.

#### Genus Kouribgaleus NOUBHANI & CAPPETTA, 1997

The type species of this mono-generic Genus is *Kouribgaleus gomphorhiza* NOUBHANI & CAPPETTA, 1997 based on isolated teeth discovered in only one Thanethian level (Paleocene) of central Morocco.

The teeth of this species differ only from the teeth of the Genus *Palaeogaleus* GURR, 1962 by the fact that their dental crowns present shorter costulae.

This Genus is considered as a representative of the revised Family Triakidae.

For references, see: Bibliography-Systematics: Noubhani & Cappetta 1997 and Cappetta 2012: p.: 287, fig.: 270.

#### Genus Xystrogaleus ADNET, 2006

The type species of this mono-generic Genus is *Xystrogaleus cappettai* ADNET, 2006, based on isolated teeth discovered in only one level of Middle Eocene Age from the Aquitaine Basin (southwestern France).

The teeth attributed to this taxon, presently known from only one precise level in only one fossiliferous locality may be considered as malformations.

Their dissymmetry and the presence of a reticulate, zoecia-like, ornamentation on the faces of their crown suggest a possible affinity with the extant Genus *Galeus* RAFINESQUE, 1810.

For references, see Bibliography-Systematics: Adnet 2006 and Cappetta 2012: p.: 295, fig.: 278.

#### Conclusions

Only the five Genera commonly attributed to this Family: Genus *Triakis* MÜLLER & HENLE, 1838, Genus *Mustelus* LINCK, 1790, Genus *Hemitriakis* HERRE, 1923, Genus *Scylliogaleus* BOULENGER, 1902 and Genus *Archaeotriakis* CASE, 1978 may be considered as extant or extinct representatives of the Family Triakidae *sensu* GRAY, 1851.

# Family Pseudotriakidae GILL, 1893

According to Compagno 1984, this Family is based on the extant Genus *Pseudotriakis* de BRITO CAPELLO, 1868 and also includes the two extant Genera: Genus *Gollum* COMPAGNO, 1973 and Genus *Planonasus* WEIGMANN, STEHMANN & THIEL, 2013.

#### For reference, see Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt 1991: pls: 8 to 10. and Weigmann, Stehmann & Thiel 2013.

#### Genus Pseudotriakis de BRITO CAPELLO, 1868

The Genus *Pseudotriakis* de BRITO CAPELLO, 1868 is represented by numerous scattered small populations\* regrouping two extant species, *Pseudotriakis microdon* de BRITO CAPELLO, 1868, its generotype and *Pseudotriakis acrales* JORDAN & SNYDER, 1904. Its precise origin remains unknown, but the Genus *Archaeotriakis* CASE, 1978 seems to be a plausible ancestor.

\*See Distribution map of Pseudotriakis microdon on: www.en.wikipedia.org

#### Remark

This map regroups all the populations of *Pseudotriakis microdon* as well as all these of *Pseudotriakis acrales*.

The extant individual representatives of this Genus are generally signalized as close bottom inhabitants of continental and insular slopes, encountered between 450 and 1.550 metres depth.

All the representatives of all the populations of *P. microdon* and *P. acrales* have five pairs of gill slits. They have no nictitating membrane\*. They are aplacental viviparous Chondrichthyes and intra-uterus oophagy seems to be a common rule.

\*This is the single anatomical difference between the Genera *Pseudotriakis* and *Triakis*.

The most singular odontological characteristic of this Genus is the very high number\* of its tooth rows and the small size of its teeth.

\*The senior-author has counted 256 to 284 tooth rows, of 2.5 to 4 millimetres of height in the jaws of the twelve North Atlantic specimens he had the possibility to examine.

If *P. microdon* and *P. acrales* are considered as synonyms, the Genus *Pseudotriakis* has a worldwide distribution, but if *P. acrales* is considered as a distinct species, the distribution of the Genus *Pseudotriakis* requires another consideration which would better concord with the geological history of the Indo-Pacific Ocean.

Phylogenetic analyses, using protein-coding genes, have demonstrated that the genetic divergence between P. *microdon* and P. *acrales* is less marked than the one observed between some other shark species of the same Genus.

The scientific attribution of the two extant representatives to this Genus was preceded by the biological comprehension of the fishermen who called these: False cat-sharks. Cat-sharks is the vernacular name covering all the extant Scyliorhinomorphii. The qualitative 'False' means that some anatomical differences exist between them and the other cat-sharks.

For references, see: Bibliography-Systematics: Brito Capello (de) 1868: 314-317, Castro (de) 2011: 352-354, Compagno 1984: 378-379, Herman, Hovestadt-Euler & Hovestadt 1991: pls.: 8 to 10, Yano 1992: 460-468 and Yano & Musick: 877-886.

# Genus Gollum COMPAGNO, 1973

This Genus regroups the two extant species: *Gollum attenuatus* (GARRICK, 1954) and *Gollum suluensis* LAST & GAUDIANO, 2011. The existence of some other species is supposed.

The representatives of this Genus are benthic inhabitants of the south-western part of the Pacific Ocean: Off New Zealand coasts and off Sulu coasts (The Philippines).

Distribution map of *Gollum attenuatus*: See: <u>www.commons.wikimedia.org</u>

# Family Proscylliidae sensu COMPAGNO, 1973

According to Compagno 1973, this Family regrouped the three following extant Genera: The Genus *Proscyllium* HILGENDORF, 1904, the Genus *Eridacnis* SMITH, 1913 and the mono-specific Genus *Ctenacis* COMPAGNO, 1973.

#### Genus Proscyllium HILGENDORF, 1904

This Genus includes the three extant taxa: *P. habereri* HILGENDORF, 1904, *P. venustum* (TANAKA, 1912) and *P. magnificum* LAST & VONGPANICH, 2004.

These three species are benthic inhabitants of the northern and central Pacific Ocean.

Distribution map of *Proscyllium habereri* See: <u>www.commons.wikimedia.org</u> Distribution map of *Proscyllium venustum* See: <u>www.ceb.wikipedia.org</u> Distribution map of *Proscyllium magnificum* See: <u>www.en.wikipedia.org</u>

#### Genus Eridacnis SMITH, 1913

This Genus includes the three extant benthic species: *E. radcliffei* SMITH, 1913, *E. barbouri* (BIGELOW & SCHROEDER, 1944) and *E. sinuans* (SMITH, 1957).

The diverse populations of *E. sinuans* are endemic to the southwestern Indian Ocean (off South Africa, off Mozambique and off Tanzania), these of *E. radcliffei* are scattered along some eastern coasts of Africa, south Arabia, more southern India to the Philippines Archipelago and these of *Eridacnis barbouri*, inhabiting the northern coasts of Cuba, are supposed to have crossed the Cordilleras de los Andes at the Pliocene Period.

Distribution map of *Eridacnis radcliffei* See: <u>www.commons.wikimedia.org</u> Distribution map of *Eridacnis barbouri* See: <u>www.commons.wikimedia.org</u> Distribution map of *Eridacnis sinuans* See: www.commons.wikimedia.org

# Family Leptochariidae GRAY, 1851

According to Compagno 1984, this extant Family is only represented by its type Genus, *Leptocharias* SMITH, 1838.

#### Genus Leptocharias SMITH, 1838

Its type species, *Leptocharias smithii* MÜLLER & HENLE, 1839 is an eastern Atlantic Ocean benthic species inhabiting waters of a depth comprised between 10 to 90 metres, from northern Mauritania to southern Angola. Its mode of reproduction is aplacental viviparity.

This species is particularly abundant on muddy bottoms in the vicinity of river mouths.

Distribution map of *Leptocharias smithii* See: <u>www.commons.wikimedia.org</u>

# Genus Ctenacis COMPAGNO, 1973

This mono-specific extant Genus is represented by *Ctenacis fehlmanni* (SPRINGER, 1968), which is represented by a single very dense population concentrated along the coasts of the Corner of Africa.

Distribution map of *Ctenacis fehlmanni* See: <u>www.commons.wikimedia.org</u>

# **Important Systematics additions**

The five following Super Orders: Ganopritomorphii nov., Anacoracomorphii nov., Isuromorphii nov., Lamnimorphii nov. and Odontaspididomorphii nov. are proposed to make the new Parasystematics of the Selachii presented in the Series *Géominpal Belgica* coherent.

Except for the four Orders Anacoraciformes\*, Isuriformes, Lamniformes and Odontaspididiformes, all the Orders having extant representatives were included in the Super Orders already examined.

\*Order, presently, represented by its sole extant Genus: Genus Galeocerdo MÜLLER & HENLE, 1837.

Each of these four Super Orders includes also diverse extinct Genera distributed between their extant and extinct Families and Orders.

The senior-author was surprised that very few of his potential biologist or paleontologist reviewers has signalized to him the absence of one taxon allowing the grouping of all these, more or less, large predators\*.

\*Including one pacific huge filter-feeding extant taxon.

In fact, it was more and more obvious that they represented four distinct lineages only distinguishable by two odontological criteria not yet detected: the global morphology of their dental crown and this of their dental root.

# Super Order Anacoracomorphii nov.

This Super Order is based on its extinct Genus *Anacorax* WHITE & MOY THOMAS, 1940, generotype of the Family Anacoracidae CASIER, 1947 included in the Order Anacoracifomes HERMAN & VAN WAES, 2012.

# **Derivatio nominis**

The fact that the Anacoracomorphii includes the extant Genus *Galeocerdo* gives a possibility to geneticists to make a comparison of the genomes of extant taxa\* of the four new Super Orders presently proposed and to validate or invalidate these propositions.

\**Galeocerdo cuvier* PERON & LE SUEUR, 1822, *Isurus oxyrhynchus* RAFINESQUE, 1810, *Odontaspis ferox* (RISSO, 1826) and *Lamna nasus* (BONNATERRE, 1788) are four extant species.

# Taxa included in this Super Order

This taxon is proposed for the Order Anacoracifomes HERMAN & VAN WAES, 2012 which regroups the two extinct Families Anacoracidae CASIER, 1947 and Pseudocoracidae CAPPETTA, 2012 and the extant Family Galeocerdidae HERMAN & VAN DEN EECKHAUT, 2010.

# Anatomical characteristics of the Anacoracomorphii

This Order has many extinct Genera, but only one extant generic taxon, the Genus Galeocerdo.

The tenuous link between this extant Genus and its supposed ancestor, the extinct Genus *Eugaleocerdo* HERMAN & VAN WAES, 2012, is represented by isolated teeth of *Eugaleocerdo jaekeli*\* (WOODWARD, 1895), its sole representative.

\*Discovered in levels of Santonian and Campanian Age (Upper Cretaceous) of southern England.

# **Odontological characteristics of the Anacoracomorphii**

Their dental roots have a tripod form, they do not overlap the top of their dental root, they possess no apron, they are in possession of one pair of flat and tongue-like lateral cusplets of which the anterior one is resorbed by the crown, forming an anterior hump and the cutting edges of their dental crown are serrated.

# **Order Anacoraciformes HERMAN & VAN WAES, 2012**

This Order regroups the three following Families: The two extinct Families: Family Anacoracidae CASIER, 1947 and Family Ptychocoracidae HERMAN & VAN WAES, 2012, and the extant Family Galeocerdidae HERMAN & VAN DEN EECKHAUT, 2010.

For reference, see Bibliography-Systematics:

Herman & Van Waes 2012: Géominpal Belgica. 2: p.: 63.

# Family Anacoracidae CASIER, 1947

The extinct Family Anacoracidae CASIER, 1947 regroups the three following Genera: Genus *Anacorax* WHITE & MOY-THOMAS, 1940, Genus *Pseudocorax* PRIEM, 1897 and Genus *Squalicorax* WHITLEY, 1939.

# Family Galeocerdidae HERMAN & VAN DEN EECKHAUT, 2010

The Family Galeocerdidae HERMAN & VAN DEN EECKHAUT, 2010 regroups only two Genera: the extinct Genus *Eugaleocerdo*\* HERMAN & VAN WAES, 2012 and the extant Genus *Galeocerdo* MÜLLER & HENLE, 1837. \*The Genus *Eugaleocerdo* HERMAN & VAN WAES, 2012 was electronically published in early June 2012.

The structure of the root of the teeth of *Eugaleocerdo jaekeli* (WOODWARD, 1895) and the serration of its dental crowns prefigure these of the extinct and extant representatives attributed to the Genus *Galeocerdo*.

# Family Ptychocoracidae HERMAN & VAN WAES, 2012

The Family Ptychocoracidae HERMAN & VAN WAES, 2012 is, presently, restricted to its single extinct taxon: Genus *Ptychocorax* GLYCKMAN & ISTCHENKO *in* GLYCKMAN, 1980.

Ignoring the extraordinary monognathic heterodonty of the dentition of its type and unique representative, the Genus *Nanocorax*\* CAPPETTA, 2012 was included by the senior-author in this Family.

\*Originally described as Genus *Microcorax* CAPPETTA & CASE, 1975, by ignorance of the existence of the avian Genus *Microcorax* SHARPE, 1877.

#### Virtual reconstitution of the ancestor of the Genus *Ptychocorax*

The generotype of the Genus *Ptychocorax* GLYCKMAN & ISTCHENKO *in* GLYCKMAN, 1980 is *Ptychocorax dolloi* (LERICHE, 1911).

The very strange morphology of the last posterior and the commissural teeth of this species were supposed to represent the dentition of a distinct species, successively named *Acrodus dolloi* by Leriche in 1911 and *Hermanodus dolloi* by Landemaine in 1991.

This species is based on isolated anaulacorhyzid teeth discovered in a thin shelly level marking the transition between the Coniacian and Santonian Stages (Upper Cretaceous) in the Namur Province (Belgium).

Proceeding to a virtual tri-dimensional anterio-posterior elongation of one of these commissural teeth, its small apex, curved in the direction of the commissure, will progressively take a vertical position in the central part of the dental crown.

Proceeding, simultaneously, to a virtual increase of its size, it will take the morphology of the crown of an acrodontiform Chondrichthyes similar to the Liassic species *Acrodus gaillardoti* AGASSIZ, 1839. Its longitudinal striations, originally oriented in the commissural direction become the extern and intern vertical striations of their dental crown.

This last virtual operation reveals which was the possible ancestor of the Genus Ptychocorax.

For references, see Bibliography-Systematics:

Cappetta 2006: p.: 313, Cappetta 2012: p.: 247-248 and fig.: 227, Landemaine 1991: p.: 7, Leriche 1911: p.: 7 and Leriche 1929: p.: 228, figs.: 6-7.

#### Genus Nanocorax CAPPETTA, 2012

The Genus *Nanocorax* CAPPETTA, 2012 is based on isolated teeth of Cenomanian Age discovered in the Tarrant County (Texas, U.S.A.).

The anaulacorhyzid root and the distorted form of the smooth crown of its teeth could allow considering this Genus as a possible ancestor of the Family Parascylliidae GILL, 1862 and, more precisely, of the Genus *Pararhincodon* HERMAN *in* CAPPETTA, 1976.

#### Systematics position of the Genus Nanocorax

This Genus must be excluded from the Order Anacoraciformes.

#### Family Paracoracidae CAPPETTA, 2012

The Family Paracoracidae CAPPETTA, 2012 was based on the single extinct Genus *Paracorax* CAPPETTA, 1977. This extinct Genus is in fact a synonym of an Avian taxon (See Cappetta 2006: p.: 349).

After having contacted its inventor\*, who however did not react, the senior-author proposed the generic name *Eugaleocerdo* instead of *Paracorax*.

\*In early May 2012.

The Genus *Eugaleocerdo* being considered as the oldest representative of the Family Galeocerdidae, the Family Paracoracidae CAPPETTA, 2012 has lost any systematics' signification and may be considered as invalidated.

# Super Order Isuromorphii nov.

# Taxa included in this Super Order

This Super Order is based on the extant Order Isuriformes HERMAN & VAN WAES, 2012.

# Anatomical characteristics of the Isuromorphii

All the representatives of this Super Order have five pairs of gill slits, two dorsal fins without fin-spines, one anal fin, and a vertebral column constituted by cylindrical vertebrae having a centrum presenting a circular section. For more details: see Compagno 1984.

# **Odontological characteristics of the Isuromorphii**

Their dental roots have a tripod form, they have a secondary anaulacorhyzid structure, they possess two, more or less, elongated root lobes.

Their dental crowns are monocuspid. Traces of any eventual lateral mini-cusplets are absent, even on embryos or neonate individuals. They are curved into the central part of the mouth. Their extern and intern faces are absolutely smooth.

# **Order Isuriformes HERMAN & VAN WAES, 2012**

The odontological characteristics of the extinct and extant representatives of this Order were dealt with in *Géominpal Belgica* **2**.: p.: 47.

# Taxa included in this Order

This Order regroups the three following Families: Family Paraisuridae HERMAN & VAN WAES, 2012, Family Cretoxyrhinidae rev., and Family Isuridae rev. For reference and description of the odontological criteria of its representatives: see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 47.

The two Families: Family Parotodontidae HERMAN & VAN WAES, 2012, based on the Genus *Anotodus* LE HON, 1871 and Family Anotodontidae HERMAN & VAN WAES, 2012, based on the Genus *Parotodus* CAPPETA, 1980 are suppressed because these two valid extinct Genera are presently considered as final huge representatives of this Order but having as possible common ancestor the Genus *Usakias* ZHELEZKO & KOZLOV, 1999.

Its anatomical and odontological characteristics are these of the Super Order Isuromorphii.

These two Families were proposed in *Géominal Belgica* 2: 2012 on p.: pp.: 49-52.

# Family Isuridae rev.

This Family is based on the extant Genus *Isurus* RAFINESQUE, 1810, included the extant Genus *Carcharodon* SMITH *in* MÜLLER & HENLE, 1838 and the two extinct Genera: *Genus Anomotodon* ARAMBOURG, 1952 and *Genus Cosmopolitodus* GLYCKMAN, 1964.

After having had the possibility to examine numerous teeth of *Woellsteinia oligocaena*, the senior-author also includes one additional generic taxon, the Genus *Woellsteinia* REINNECKE, STAPF & RAISCH, 2001 in this Family.

The Genus Anomotodon has for generotype Anomotodon plicatus ARAMBOURG, 1952, the Genus Woellsteinia has for generotype Woellsteinia oligocaena REINECKE, STAPF & RAISCH, 2001 and the Genus Cosmopolitodus has for generotype Cosmopolitodus hastalis AGASSIZ, 1843.

The revision of this Family consists in the integration of the Upper Eocene to Middle Oligocene Genus *Woellsteinia* having representatives discovered in strata ranging from the Upper Eocene to the Middle Oligocene in Germany to central Asia.

The diverse specific taxa included in the three Genera: Genus *Isurus* RAFINESQUE, 1810, Genus *Cosmopolitodus* GLYCKMAN, 1964 and Genus *Carcharodon* SMITH, 1838 are mentioned in this Publication, but the evolution of the diverse populations of the first representatives of the Genus *Carcharodon* required a fundamental revision. This revision\*, based on the evolution of the morphology of the serration of the cutting edges of the dental crown, allows adding the following data.

\*Partially realized by Lutz Andres: Im Steingarten 8 – 35460 – Staufenberg – Germany.

The frequency of partial perturbations of the Earth's magnetic Field between the end of the Miocene and the end of the Pliocene was so important that the senior-author thinks that the apparition of the numerous diverse first populations of the Genus *Carcharodon*, such as *C. xyphyodon*, *C. patagonicus*, and *C.escheri* is the genetic odontological manifestation of these phenomena.

For references: See: Bibliography- Systematics: Cappetta 2012: p.: 190, fig.: 179, Reinecke, Stapf & Raisch 2001 and Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 49.

# Genus Carcharodon SMITH, 1838

This Genus, based on *Carcharodon carcharias* (LINNAEUS, 1758), regroups, at least, two extinct taxa: *Carcharodon escheri* (AGASSIZ, 1843) and *Carcharodon xiphodon* (AGASSIZ, 1843).

The senior-author agrees with the conclusions of the thorough studies realized by Lutz Andres\* which have demonstrated that the populations of *C. escheri* (AGASSIZ, 1843) were the northern Mio-Pliocene representatives of this Genus and that these of *C. xiphodon* (AGASSIZ, 1843) were the southern Mio-Pliocene representatives of this Genus.

\*See Andres Lutz 2002: Isurus escheri on Internet.

*C. escheri* and *C. xiphodon* are considered as two distinct groups of populations having for common ancestor the lower Miocene species *Cosmopolitodus hastalis* (AGASSIZ, 1843).

# Genus Woellsteinia REINNECKE, STAPF & RAISCH, 2001

This extinct Genus has for holotype *Woellsteinia oligocaena* REINNECKE, STAPF & RAISCH, 2001 and is based on isolated teeth of Rupelian Age (Middle Oligocene) from the Mainz Basin (southwestern Germany).

This Genus regroups three other specific taxa: *Woellsteinia hermani* KOZLOV *in* ZELEZSKO & KOZLOV, 1999 from the Lower Bartonian (Upper Eocene) in western Kazakhstan (central Asia), *Woellsteinia kozlovi* ADNET, 2006 from Lower and Middle Eocene levels in the Aquitaine Basin (southwestern France) and *Woellsteinia palatasi* (KOZLOV, 2001) from the Upper Eocene in western Kazakhstan (central Asia).

For references and illustrations, see: Bibliography-Systematics: Cappetta 2012: p.: 190, fig.: 179 and Reinnecke, Stapf & Raisch, 2001.

# Family Cretoxyrhinidae GLYCKMAN, 1958

The odontological characteristics of the extinct and extant representatives of this Order were dealt with in *Géominpal Belgica* 2.: p.: 48.

This Family includes the two extinct Genera: Genus *Cretoxyrhina* GLYCKMAN, 1958 and Genus *Dallasiella* CAPPETTA and CASE, 1999.

For references: See: Bibliography- Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 48.

# Family Paraisuridae HERMAN & VAN WAES, 2012

This Family is based on the Genus Paraisurus GLYCKMAN, 1957.

The odontological characteristics of the extinct and extant representatives of this Order were dealt with in *Géominpal Belgica* **2**.: p.: 47.

See: Bibliography- Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 47.

#### **Reflection concerning the Genus** *Xiphodolamia* LEIDY, 1877

The Genus *Xiphodolamia* LEIDY, 1877 is generally included in this Family, but it is not sure that its generotype and sole representative: *Xiphodolamia ensis* LEIDY, 1877 presented a monognathic heterodonty.

Attempts of reconstitution of its dentition, based on the principle of a dignathic heterodonty, allow suggesting a relationship with the Squalomorphii rather than with the Isuromorphii.

This Genus which regroups the two extinct specific taxa: *X. ensis* and *X. barbadica* (CASIER, 1958) has a very short temporal distribution. It is restricted to some Eocene levels of both north Atlantic coasts.

It disappeared just before the Eocene-Oligocene Transition.

See: Bibliography-Systematics: Cappetta 2012: p.: 228-229, Glyckman 1964 and Leidy 1877.

# Order Alopiiformes HERMAN & VAN WAES, 2012

This Order was proposed to regroup the two extant Families: The Family Alopiidae BONAPARTE, 1838 and the Family Cetorhinidae GILL, 1862 and the two extinct Families: Family Anodontidae and Family Parodontidae.

The odontological characteristics of these two Families are insufficient to consider them as valid.

Considering the global morphology\* of a symphyseal tooth of the holotype of the taxon *Ostenoselache steno-soma*\*\* DUFFIN, 1998, the Family Ostenalachidae DUFFIN, 1998 could be considered as a plausible ancestor of the Genus *Keasius* WELTON, 2013, the oldest representative of the Family Cetorhinidae.

\*See: Cappetta 2012: p.: 329, fig.: 318.

\*\*This species is based on a skeleton, partially preserved, discovered in a Sinemurian level (Lower Jurassic) in the Come Province (Lombardy, Italy).

For reference and description of the odontological criteria of its representatives: see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 50.

This Order is based on the Family Alopiidae BONAPARTE, 1838 rev.

According to Cappetta (2012: pp.: 241-243), this Family regroups the five following Genera: The extant Genus *Alopias* RAFINESQUE, 1810 and thee four extinct Genera: Genus *Paranomotodon* HERMAN *in* CAPPETTA & CASE, 1975, Genus *Parasquatina* HERMAN, 1982, Genus *Usakias* ZHELESKO & KOSLOV, 1999 and Genus *Anotodus* LE HON, 1871. Cappetta did not mention the Genus *Parotodus* CAPPETTA, 1980, considered as valid by the senior-author.

# Family Alopiidae sensu BONAPARTE, 1838

This Family regroups the extant Genus *Alopias* RAFINESQUE, 1810 and the four extinct Genera: Genus *Anotodus* LE HON, 1871, Genus *Paranomotodon* HERMAN *in* CAPPETTA & CASE, 1975, Genus *Usakias* ZHELEZKO & KOZLOV, 1999 and Genus *Parasquatina* HERMAN, 1982.

# Genus Alopias RAFINESQUE, 1810

This Genus regroups the three extant taxa: A. superciliosus LOWE, 1840, A. macrourous RAFINESQUE, 1810 and A. vulpinus (BONNATERRE, 1788) and the four extinct taxa: A. exigua (PROBST, 1879), A. hassei (NOETLING, 1885), A. latidens LERICHE, 1901, A. denticulatus CAPPETTA, 1981.

Contrarily to opinion of Cappetta (2012: p.: 242), the two taxa *Alopias crochardi* WARD, 1979 and *Alopias leensis* WARD, 1979 are not representatives of the Genus *Alopias* RAFINESQUE, 1810, but, such as explained in *Géominpal Belgica* **2**: (p.: 54) the ancestors of the two Genera: Genus *Anotodus* LE HON, 1871 and Genus *Parotodus* CAPPETTA, 1980.

A. exigua (PROBST, 1879) is based on numerous isolated teeth discovered in numerous levels of Chattian Age (Lower Oligocene) to Rupelian Age (Middle Oligocene) in southwestern Germany, in northern Belgium and in France.

For references: See Bibliography-Systematics: Cappetta 2012: p.: 242 and Probst 1879.

A. *latidens* LERICHE, 1901 is based on numerous isolated teeth discovered in diverse levels of Chattian Age Chattian Age (Lower Oligocene) to Serravalian Age (Middle Miocene) in northern Belgium, in Italy and in Carolina (U.S.A.).

For references: See Bibliography-Systematics: Cappetta 1970, Cappetta 1975, Cappetta 1987, Cappetta 2012: p.: 242, Menessini 1969.

*A. hassei* (NOETLING, 1885) is based on a small lot of isolated teeth discovered in one level of unspecified Age (Eocene or Miocene) in the Kalingrad Oblast (Former Tannenberg, eastern Prussia).

For references: See Bibliography-Systematics: Cappetta 2012: p.: 242 and Noetling 1885.

*A. denticulatus* CAPPETTA, 1981 is based on numerous isolated teeth discovered in levels of lower Ypresian Age (Lower Eocene) in the Ouled Abdoun Basin (central Morocco).

The presence of one pair of lateral cusplets on the dental crowns of this taxon allows supposing that it was not a member of the Genus *Alopias*. See further considerations.

For references: See Bibliography-Systematics: Cappetta 1981 and Cappetta 2012: p.: 242.

*A. superciliosus* is also represented by numerous isolated teeth discovered in diverse levels of Miocene Age in southern France, Portugal and Barbados Islas.

For references: See Bibliography-Systematics: Antunes & Jonet 1970, Cappetta 2012: p.: 242 and Casier 1958.

# Genus Anotodus LE HON, 1871

This Genus is based on numerous isolated teeth of *Anotodus benedenii* LE HON, 1871 discovered in levels of Rupelian Age (Middle Oligocene) to Zanclian Age (Lower Pliocene) of Lower to Middle Eocene Periods.

The Oligocene-Pliocene species Anotodus benedenii has for Eocene ancestor A. leensis (WARD, 1978).

For reference and description of the odontological criteria of its representatives: see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 52.

For references: See Bibliography-Systematics: Ward 1978 and Herman & Van Waes 2012.

#### Genus Parotodus CAPPETTA, 1980

This Genus is based on *Parotodus retroflexus* is based on numerous isolated teeth discovered in levels of Burdigalian Age (Lower Miocene) to Tortonian Age (Upper Miocene).

The Miocene species *Parotodus retroflexus* has for ancestor *A. crochardi* (WARD, 1978) of Lower to Middle Eocene Periods.

For reference and description of the odontological criteria of its representatives: see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 52.

For references: See Bibliography-Systematics: Ward 1978 and Herman & Van Waes 2012.

#### Genus Paranomotodon HERMAN in CAPPETTA & CASE, 1975

This mono-specific extinct Genus has for generotype *Paranomotodon angustidens* REUSS, 1845, based on isolated teeth discovered in a level of Turonian Age (Upper Cretaceous) in Czech Republic.

All its odontological characteristics, such as its monocuspid smooth dental crown overlapping a holaulacorhyzid dental root, guarantee its attribution to the Family Alopiidae.

#### Spatio-temporal distribution of the Genus Paranomotodon

This mono-specific taxon is represented by numerous isolated teeth in strata ranging from upper Cenomanian Age (Upper Cretaceous) to upper Maastrichtian Age (end of the Upper Cretaceous) in Europe, central Asia, Japan, northern and western Africa and North America.

For references: See Bibliography-Systematics: Albers & Weiler 1964, Cappetta 2012 (pp.: 260-261 and fig.: 239), Dalinkevicius 1935, Herman 1977, Leriche 1902 and Reuss 1845.

#### Genus Usakias ZHELEZKO & KOZLOV, 1999

#### Systematic remark

The taxon *Usakias* is a good example of the numerous generic taxa proposed with the justified conviction to be in possession of a new taxon, but described without revision of the Family and the Order in which it will be inserted.

This extinct Genus, having for generotype *Usakias wardi* ZHELESKO & KOZLOV, 1999, was based on numerous isolated teeth discovered in a level of Bartonian Age (uppermost Eocene) in western Kazakhstan (central Asia).

Despite the dental root structure and the presence of lateral cusplets on the dental crown of all its representatives, this taxon was considered (Cappetta 2006: p.: 389) as a junior synonym of the Genus *Alopias* RAFINESQUE, 1810 and inserted in the Family Alopiidae BONAPARTE, 1838 which was considered as a member of the Order Lamniformes BERG, 1937.

Cappetta (2012: pp.: 242-243) signalized that, except their robustness, the significant odontological difference between the Genera *Alopias* and *Usakias* is that the members of the last one are in possession of one or two pairs of lateral cusplets.

One of the most important conclusions imposed by the systematic revision\* of all the extant and extinct representatives of the Order Lamniformes was the distinction between the large predators of the Neoselachii in possession of teeth presenting dental crown with lateral cusplets (E.g.: Order Scapanorhynchiformes, Order Odontaspididiformes) and large predators of the Neoselachii in possession of teeth presenting dental crown without lateral cusplets (Order Isuriformes)

\*See Bibliography-Systematics: HERMAN, J. & VAN WAES, 2012. *Géominpal Belgica*. **2**. p.: 52. Full text on-line since end of March 2012: <u>http://www.geominpal.be</u>.

The two other specific taxa of the Genus Usakias: Usakias asiaticus ZHELESKO & KOZLOV, 2000 Usakias lerichei ZHELESKO & KOZLOV, 2000 as well as the two sub-species Usakias wardi gracilis ZHELESKO & KOZLOV, 1999 and Usakias wardi shorymensis ZHELESKO & KOZLOV, 1999 were reconsidered as valid taxa of the revalidated Genus Usakias.

#### Species regrouped in the Genus Usakias

*U. wardi* ZHELESKO & KOZLOV, 1999 is based on numerous teeth discovered in a level of lower Bartonian Age (Upper Eocene) in western Kazakhstan (central Asia).

For references and illustrations, see: Cappetta 2012: p.: 244, fig.: 224 and Zhelesko & Kozlov, 1999: p.: 164, pl.: 31, figs.: 1 to 9.

*U. asiaticus* ZHELESKO & KOZLOV, 2000 is based on numerous teeth discovered in a level of Ypresian Age (Lower Eocene) in Uzbekistan (central Asia).

For references and illustrations, see: Zhelesko & Kozlov 1999: p.: 142, pl.: 1, figs.: 1 to 3.

*U. lerichei* KOZLOV, 2000 is based on numerous teeth discovered in a level of Rupelian Age (Middle Oligocene) in western Kazakhstan (central Asia).

For description and illustrations, see: Kozlov 2000: p.: 143, pl.: 1, figs.: 4 to 8.

*Usakias wardi* var. *gracilis* ZHELESKO & KOZLOV, 1999 is based on numerous teeth discovered in a level of Bartonian Age (uppermost Eocene) in western Kazakhstan (central Asia).

For description and illustrations, see: Zhelesko & Kozlov 1999.

*Usakias wardi* var. *shorymensis* ZHELESKO & KOZLOV, 1999 is based on numerous teeth discovered in a level of Bartonian Age (uppermost Eocene) in western Kazakhstan (central Asia).

For references and illustrations, see: Zhelesko & Kozlov 1999.

Dr. Zhelesko has given to the senior-author, some teeth of *U. lerichei*, *U.wardi*, *Usakias wardi* var. *gracilis* and *Usakias wardi* var. *shorymensis*. These perfectly preserved and slightly radioactive teeth allow suggesting that the teeth attributed to *U. wardi* var. *gracilis* were teeth of juvenile individuals of *Usakias wardi*.

#### Conclusion

The senior-author considers that the Genus *Usakias* is an extinct representative of the Order Odontaspididiformes HERMAN & VAN WAES, 2012 and more precisely a first ones of the Family Odontaspididae MÜLLER & HENLE, 1839.

#### Genus Parasquatina HERMAN, 1982

The Genus *Parasquatina* was considered as a member of the Family Squatinidae rev., and as its oldest representative.

#### Odontological characteristics of the Genus Parasquatina

The monocuspid dental crowns overlaps slightly the top of their hemiaulacorhyzid roots, their apron is very short and subcylindrical. See *Géominpal* 2.: p.: 44.

#### Anatomical characteristics of the Genus Parasquatina

In absence of skeletal remains, the size and the general morphology of its teeth allow drawing its profile.

The populations, presently attributable to the Genus *Parasquatina*, were constituted by small predators inhabiting coastal zones (Bettrechies, Nurlu, France) and continental shelf zones (Hemmoor, northern Germany).

# Spatio-temporal distribution of the Genus Parasquatina

Teeth attributable to the Genus *Parasquatina* HERMAN, 1982 were discovered in levels of Turonian Age at Bettrechies (North Department, France), in two levels of Lower Campanian Age at Trivières and Obourg (Hainaut Province, Belgium), in two levels of Lower Campanian Age at Nurlu (Somme Department, northern France), in one level of lower Maastrichtian Age at Hallembaye (Liège Province, Belgium) and the tooth of its generotype, *P. Cappettai* HERMAN, 1982, in one level of Maastrichtian Age at Hemmoor (northern Germany).

English friends have signalized the presence of teeth of this Genus in the Upper Campanian of southern England.

The oldest presences of this Genus were discovered in the lower Turonian of northern France, where it is extremely rare, the last presences of this Genus were discovered in the Maastrichtian of northern Germany, where it is also extremely rare.

For reference, see Bibliography-Systematics: Cappetta 2012: p.: 323, fig.: 312 and Herman 1982: p.: 325.

# **Order Cetorhiniformes HERMAN & VAN WAES, 2012**

This Order is based on the Family Cetorhinidae GILL, 1862. For reference and description of the odontological criteria of its representatives: see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 53.

This Family regroups the two Genera: the extant Genus *Cetorhinus* de BLAINVILLE, 1816 and the extinct Eocene Genus *Keasius* WELTON, 2013.

# Family Cetorhinidae GILL, 1862

This Family regroups the extant Genus *Cetorhinus* de BLAINVILLE, 1816 and the extinct Genus *Keasius* WELTON, 2013.

# Family Ostenoselachidae DUFFIN, 1998

This monogeneric extinct Family is based on skeletal remains of its generotype: Genus Ostenoselache DUFFIN, 1998.

# Super Order Odontaspididomorphii nov.

This Super Order is based on the extant Order Odontaspididiformes sensu HERMAN & VAN WAES, 2012.

# Taxa included in this Super Order

This Super Order regroups the three Orders: Order Odontaspididiformes HERMAN & VAN WAES, 2012, Order Alopiiformes HERMAN & VAN WAES, 2012 and Order Lamniformes *sensu* HERMAN & VAN WAES, 2012, all having extant representatives of Family, Genus and species ranks.

The odontological characteristics of the Orders, the Families and the Genera included in this Super Order were detailed in *Géominpal Belgica*. 2012: **2**: pp.: 60 to 64.

# **Order Odontaspididiformes HERMAN & VAN WAES, 2012**

This Order was proposed for regrouping the two extant Families: Family Odontaspididae MÜLLER & HENLE, 1837 and Family Mitsukurinidae JORDAN, 1898 and the three extinct Families: Family Serratolamnidae LANDEMAINE, 1991 and Family Eoptolamnidae KRIWET, KLUG, CANUDO & CUENCA-BENCOS, 2008 and Family Scapanorhynchidae HERMAN & VAN WAES, 2012.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 60

# **Family Odontaspididae rev.** (sensu HERMAN & VAN WAES, 2012)

This Family is based on the extant Genus Odontaspis AGASSIZ, 1838.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: Géominpal Belgica. 2: p.: 61.

This Family may also include the Genus Turania KOZLOV, 2001.

# Genus Turania KOZLOV, 2001

The mono-specific Genus *Turania* KOZLOV, 2001 represented by its type species *Turania andrusovi* KOZLOV, 2001 is based on isolated teeth discovered in a level of Bartonian Age (Upper Eocene) in western Kazakhstan, central Asia.

Considering the narrow odontological similarities existing between the teeth of this taxon and the teeth of the Genus *Roulletia* VULLO, CAPPETTA & NERAUDEAU, 2001, the senior-author agrees with his French colleague Cappetta (2012: p.: 208) and considers the validity of the Genus *Turania* as dubious.

For references and illustrations, see: Bibliography-Systematics: Cappetta 2012: p.: 207, fig.: 196, Kozlov 2001 and Vullo, Cappetta & Néreaudeau 2001.

# Family Mitsukurinidae rev.

This Family is based on the extant Genus Mitsukurina JORDAN, 1898.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 61.

# Family Pseudocarchariidae COMPAGNO, 1973

This extant mono-generic Family is only represented by its generotype, the Genus *Pseudocarcharias* CADENAT, 1963.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: Géominpal Belgica. 2: p.: 62.

#### Genus Pseudocarcharias CADENAT, 1963

This mono-specific Genus has for type species *Pseudocarcharias kamoharai* MATSUBARA, 1936.

# Biological characteristics of the Genus Pseudocarcharias

The possession of five pairs of gill slits, the possession of two dorsal fins without fin spine, the possession of a vertebral column constituted only by vertebrae presenting a cylindrical centrum, an anal fin and their aplacental viviparous mode of reproduction are its principal anatomical characteristics.

#### Dental root characteristics of the Genus Pseudocarcharias

The dental roots of all the representatives of its generotype are holaulacorhyzid and possess two root lobes moderately extended forming an inverted U.

Such a structure reducing the tripod form of the other Odontaspididiformes to a nearly single plane offers a maximum of power and resistance when attacking a prey.

#### Dental crown characteristics of the Genus Pseudocarcharias

The dental crown of this taxon has a nearly vertical position. Only the crown of the anterior teeth is slightly inclined towards the central part of the mouth. They present a huge principal cuspid flanked by one pair of minute lateral cusplets. Extern and intern sides of the dental crown are absolutely smooth.

The presence of the lateral cusplets of the fossil specimens of this species is a little more obvious than this of the recent ones.

#### Spatio-temporal distribution of the Genus *Pseudocarcharias*

Fide Cappetta (2012: p.: 209), the Genus *Pseudocarcharias* is also represented by isolated teeth discovered in some Japanese, Venezuelan, Italian and German levels of Miocene Age attributed to its extant representative. Recent\* phylogenetic analyses, based on mitochondrial DNA, have suggested that *Pseudocarcharias kamoharai* is closely related to either *Megachasma pelagios* or extant Odontaspididae.

\*Compagno & Musick 2005.

This extant species is represented by a very high number of populations world-widely scattered. Their sole common point is the water temperature, concentrating its populations between the Latitude 37°N and Latitude 44°S.

See its distribution map: <u>www.nl.wikipedia.org</u>, <u>www.commons.wikimedia.org</u> or on: <u>www.de.academic.ru</u> See images of its dentition on: <u>www.nifty2.com</u>

For references and illustrations, see: Bibliography-Systematics: Cadenat 1963, Cappetta 2012: p..: 209: fig.: 197, Compagno 1984, Compagno 2002: pp.: 71-74, Edwards 1993, Fujita 1981, Long & Seigel 1997, Matsubara 1936 and Melendez, Lopez & Yanez 2006.

# Super Order Lamnomorphii nov.

(Order Lamniformes sensu HERMAN & VAN WAES, 2012)

The odontological characteristics of the Orders, the Families and the Genera included in this Super Order were detailed in *Géominpal Belgica*. 2012: **2**: pp.: 54 to 60.

# Order Lamniformes *sensu* HERMAN & VAN WAES, 2012

This Order is based on the Family Lamnidae *sensu* HERMAN & VAN WAES, 2012, based on the extant Genus *Lamna* CUVIER, 1816, and includes two fossil Genera: Genus *Lethenia* BAUT & GENAULT, 1999 and Genus *Rhizoquandrangulus* BAUT & GENAULT, 1999, both of Lower to Upper Oligocene Age of western Europe.

This revised Order regroups the three Families: Family Lamnidae MÜLLER & HENLE, 1838 Fam. rev., Family Archaeolamnidae nov. Fam. and Family Otodontidae GLÜCKMAN, 1964.

This Order includes also the extant mono-generic Family Megachasmidae TAYLOR, COMPAGNO & STRUHSAKER, 1983.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**: p.: 54.

# Family Lamnidae rev.

(sensu HERMAN & VAN WAES, 2012)

# Ontogeny of the teeth of Lamna nasus

The growth of the teeth of embryos of *Lamna nasus* is easily observable on embryos at successive steps of maturation.

The younger ones possess only groups composed of one soft elongated cuspid flanked by a pair of soft short cusplets separated by two diastema. Just before hatching these three parts of their future dental crown fusion and their diastema are filled with apatite. This last phase induces the formation of a basal enforcement of the dental crowns.

# Family Archaeolamnidae UNDERWOOOD & CUMBAA, 2010

Despite their obvious polycuspidy, Cappetta 2006 (p.: 400), included the five extinct Genera constituting this Family in the Family Cretoxyrhinidae GLYCKMAN, 1958.

This new Family was proposed for regrouping the five following extinct polycuspid Genera : Genus *Acrolamna* ZHELELESKO, 1990, Genus *Archaeolamna* SIVERSON, 1992, Genus *Cretolamna* GLYCKMAN, 1958, Genus *Palaeocarcharodon* CASIER, 1967 and the Genus *Carcharoides* AMEGHINO, 1901.

After examination of the odontological characteristics of a lot of teeth of *Roulletia palatasi* the senior-author includes another Genus to this list: Genus *Roulletia* VULLO, CAPPETTA & NERAUDEAU, 2001

# Genus Roulletia VULLO, CAPPETTA & NERAUDEAU, 2001

This mono-specific Genus has for holotype *Roulletia palatasi* VULLO, CAPPETTA & NERAUDEAU, 2001 and is based on isolated teeth discovered in one level of Cenomanian Age (Upper Cretaceous) in the Charente Department (southwestern France).

For references and illustrations, see: Bibliography-Systematics:

Cappetta 2012: p.: 206, fig.: 194, and Vullo, Cappetta & Néreaudeau 2001

#### Family Otodontidae GLYCKMAN, 1964

This Family regroups the six following extinct Genera: Genus *Otodus* AGASSIZ, 1843, Genus *Carcharocles* JORDAN & HANNIBAL, 1923, Genus *Cretolamna* GLYCKMAN, 1958, Genus *Megaselachus* GLYCKMAN, 1964, Genus *Cretodus* SOKOLOV, 1965, Genus *Parotodus* CAPPETTA, 1980 and the Genus *Dwardius* SIVERSON, 1999.

#### Systematics remarks

The Genus *Plicatolamna* HERMAN *In* CAPPETTA & CASE, 1975 is a synonym of the Genus *Cretodus* SOKOLOV, 1965, the Genus *Cretolamna* GLYCKMAN, 1958 is a synonym of the Genus *Cretolamna* GLYCKMAN, 1958, the Genus *Procarcharodon* CASIER, 1960 is a synonym of the Genus *Carcharocles* JORDAN & HANNIBAL, 192 and the Genus *Orpodon* CAPPETTA & NOLF, 2005 is a synonym of the Genus *Carcharoides* AMEGHINO, 1901.

The Genus *Palaeogenotodus* (HERMAN & VAN DEN EECKHAUT, 2010) is a synonym of the Genus *Otodus* AGASSIZ, 1843.

See Bibliography-Systematics:

Ameghino, 1901, Cappetta, 2012, Cappetta & Nolf, 2005, Casier 1960, Glyckman, 1958, Herman in Cappetta & Case, 1975, Herman & Van Den Eeckhaut 2010 (Géo. 1: 30), Hora, 1939, Jordan & Hannibal, 1923 and Sokolov, 1965.

# Family Megachasmidae TAYLOR, COMPAGNO & STRUHSAKER, 1983

This mono-generic Family is based on the extant Genus *Megachasma* TAYLOR, COMPAGNO & STRUHSAKER, 1983. Its anatomical and odontological characteristics are these of its type Genus.

#### Genus Megachasma TAYLOR, COMPAGNO & STRUHSAKER, 1983

This extant mono-specific Genus is based on the extant species *Megachasma pelagios* TAYLOR, COMPAGNO & STRUHSAKER, 1983. Its anatomical and odontological characteristics are these of its type species. It is also represented by two extinct taxa: *Megachasma comanchensis* SHIMADA, 2007, based on isolated teeth discovered in a Cenomanian level (Upper Cretaceous) from Japan and *Megachasma applegatei* SHIMADA, WELTON & LONG, 2014, based on isolated teeth discovered in different levels of the Oligocene to Lower Miocene Period.

See: Bibliography-Systematics: Shimada 2007 and Shimada, Welton & Long, 2014

#### Megachasma pelagios TAYLOR, COMPAGNO & STRUHSAKER, 1983

This huge\* nectic ovoviviparous filter-feeder species is represented by diverse populations\*\* inhabiting the Pacific, Indian and Atlantic Oceans. In 2012, only fifty-five individuals of *Megachasma pelagios* were caught or mentioned, all being found between 5 and 600 metres depth.

\*Size record: circa 5.5 metres of total length. \*\*Only discovered after November 1976.

For its distribution map: See <u>www.en.wikipedia.org</u>

For references and illustrations, see: Bibliography-Systematics: Berra 1997, Herman, Hovestadt-Euler & Hovestadt 1993: pls.: 45 to 48, Taylor, Compagno & Struhsaker, 1983

The discovery of fossil teeth attributable to this species in Belgium was signalized by De Schutter in 2013.

See: Bibliography-Systematics: De Schutter 2013.

# Super Order Carcharhinomorphii rev.

This emended Super Order, based on the former Order Carcharhiniformes COMPAGNO, 1973, is presently considered as represented by the single emended Order Carcharhiniformes COMPAGNO, 1973.

The odontological characteristics of the Orders, the Families and the Genera included in this Super Order were detailed in *Géominpal Belgica*. 2012: **2**.: p.: 46.

# Order Carcharhiniformes *sensu* HERMAN & VAN WAES, 2012

This partially revised Order was reconsidered as regrouping the five extant Families: Family Carcharhinidae *sensu* HERMAN & VAN WAES, 2012 based on the extant Genus *Carcharhinus* de BLAINVILLE, 1816, Family Hemigaleidae HASSE, 1879 based on the extant Genus *Hemigaleus* BLEEKER, 1852, Family Sphyrnidae GILL, 1862, based on the extant Genus *Sphyrna* RAFINESQUE, 1810, Family Loxodonidae HERMAN & VAN WAES, 2012, based on the extant Genus *Loxodon* MÜLLER & HENLE, 1838 and the Family Hemipristidae HERMAN & VAN WAES, 2012, based on the extant Genus *Hemipristis* AGASSIZ, 1843.

Diverse extinct taxa were also considered as ancestors of some extant representatives of this Order. But it is not the aim of this short taxonomical Synthesis, concerning the Systematics of all the principal extinct and extant Chondrichthyes, to enumerate once more all the taxa (Family and Genera) included by the senior-author in all the Orders proposed or revised in 2012.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica* **2**.: p.: 46.

# Super Order Scapanorhynchomorphii nov.

This Super Order is based on the Order Scapanorhynchiformes HERMAN & VAN WAES, 2012 and includes also the Order Odontaspididiformes HERMAN & VAN WAES, 2012.

The odontological characteristics of the Orders, the Families and the Genera included in this Super Order were detailed in *Géominpal Belgica*. 2012: **2.**: pp.: 47 to 51.

# **Order Odontaspididiformes HERMAN & VAN WAES, 2012**

This Order regroups the three following extant Families: Family Scapanorhynchidae HERMAN & VAN WAES, 2012, Family Odontaspididae Fam. rev. and Family Mitsukurinidae JORDAN, 1898 Fam. rev.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2:** p.: 60.

# Super Order Pristiophoromorphii nov.

This Super Order is based on the extant Order Pristiophoriformes BERG, 1958, itself based on the extant Family Pristiophoridae BLEEKER, 1859, based on the extant Genus *Pristiophorus* MÜLLER & HENLE, 1837.

The Family Pristiophoridae BLEEKER, 1859 also includes an extinct Genus, the Upper Cretaceous Genus *Propristiophorus* WOODWARD, 1932, presently revalidated.

This Super Order includes also the Family Pliotrematidae HERMAN & VAN WAES, 2012, based on the extant Genus *Pliotrema* REGAN, 1906. See Chapter **12.6**. of this Publication.

# **Order Ptychotrygoniformes rev.**

This Order is based on the Order Ptychotrygoniformes, represented by the sole Family Ptychotrygonidae KRIWET, NUNN & KLUG, 2009.

The placement in quincunx of their teeth allows considering all the taxa of this Order as Batoids.

# Family Ptychotrygonidae KRIWET, NUNN & KLUG, 2009

Considered as *Rajiformes incertae sedis* (Cappetta 2006: pp.: 408-409 and 2012: pp.: 389-392), these Chondrichthyes regroup the three following extinct Genera: Genus *Ptychotrygon* JAEKEL, 1894, Genus *Texatrygon* CAPPETTA & CASE, 1990 and Genus *Ptychotrygonoides* LANDEMAINE, 1991.

# **Odontological characteristics of the Family Ptychotrygonidae**

The odontological characteristics of all the representatives of this extinct Family of uncertain phyletic relationship may be summarized as follows: Teeth, wider than high, presenting a holaulacorhyzid root with two root-lobes horizontally extended and a massive monocuspid dental crown overlapping the top of their dental root.

The teeth of all the representatives of its three Genera are in possession of an apron and an ornamentation on both sides of their dental crown. The morphology of this ornamentation is the principal criterion that allows distinguishing its three Genera.

# Spatio-temporal distribution of the Ptychotrygonidae

This extinct Family regroups diverse populations of three Genera which inhabited shallow coastal waters of North America and occidental, southern and central Europe during the upper Cretaceous Period (lower Campanian to upper Maastrichtian). Their last representatives disappeared from the European coasts at the end of the lower Campanian and, in North America, at the end of the Cretaceous Period.

# Odontological criteria for distinguishing its three Genera

The dental crowns of the teeth of all the representatives of the Genus *Ptychotrygon* JAEKEL, 1894 present strong anterio-posterior ridges and, on both sides, a strong reticulate ornamentation.

The dental crowns of the teeth of all the representatives of the Genus *Texatrygon* CAPPETTA & CASE, 1990 present only one anterio-posterior ridge and an ornamentation, on both sides, but reduced to short folds at their lower margins.

The dental crowns of the teeth of all the representatives of the Genus *Ptychotrygonoides* LANDEMAINE, 1991 present only one anterio-posterior ridge and an ornamentation constituted by strong radial extern folds and a smooth intern face.

# Genus Ptychotrygon JAEKEL, 1894

The generotype of the Genus *Ptychotrygon* is *Ptychotrygon triangularis* (REUSS, 1845)\*, species based on isolated teeth discovered in a level of Turonian (or Cenomanian?) Age in Bohemia (Czech Republic).

\*Considered by Reuss as a member of the Genus *Ptychodus*.

This Genus includes also the eleven following species: P. vermiculata CAPPETTA, 1975, based on isolated teeth discovered in a level of lower Maastrichtian Age in Texas (U.S.A.), P. ellae CASE, 1987, based on isolated teeth discovered in a level of upper Campanian Age (Upper Cretaceous) in Wyoming (U.S.A.), P. greybullensis CASE, 1987, based on isolated teeth discovered in a level of upper Campanian Age (Upper Cretaceous) in Wyoming (U.S.A.), P. henkeli WERNER, 1989, based on isolated teeth discovered in a level of upper Cenomanian Age (Upper Cretaceous) in Egypt, P. winni CASE & CAPPETTA, 1997, based on isolated teeth discovered in a level of upper Maastrichtian Age in in Texas (U.S.A.), P. geyeri KRIWET, 1999, based on isolated teeth discovered in a level of upper Albian (Upper Cretaceous) in the Teruel Province (Spain), P. rugosa CASE, SCHWINNER, BORODIN & LEGGET, 2001, based on isolated teeth discovered in a level of upper lower-middle Santonian Age (Upper Cretaceous) in Georgia (U.S.A.), P. henningensis CASE, SCHWINNER, BORODIN & LEGGET, 2001, based on isolated teeth discovered in a level of lower-middle Santonian Age (Upper Cretaceous) in Georgia (U.S.A.), P. chattahoochensis CASE, SCHWINNER, BORODIN & LEGGET, 2001, based on isolated teeth discovered in a level of lower-middle Santonian Age (Upper Cretaceous) in Georgia (U.S.A.), P. eutawensis CASE, SCHWINNER, BORODIN & LEGGET, 2001, based on isolated teeth discovered in a level of upper lowermiddle Santonian Age (Upper Cretaceous) in Georgia (U.S.A.), and P. gueveli CAPPETTA, 2004, based on isolated teeth discovered in a level of upper Turonian Age (Upper Cretaceous) in Indre-et-Loire Department (France).

The co-existence of four species of the same Genus in the same geological horizon: *P. henningensis*, *P. ellae*, *P. eutawensis* and *P. rugosa* proposed by Case, Schwinner, Borodin & Leggett in 2001 is surprising and dubious, requiring a re-examination of these four specific taxa.

The existence of a sexual dental dimorphism between the Genus *Ptychotrygon* is a possibility which cannot be excluded and which would allow reducing this number to two species.

Teeth of *Ptychotrygon triangularis* (REUSS, 1845) are relatively frequent in the lower Turonian strata of Bettrechies (Nord Department, France), where oral and rostral teeth of one representative of one species, which may be attributed to the Genus *Libanopristis*, are sporadically discovered.

At Lonzée (Namur Province, Belgium), in the Glaucony of Lonzée Formation, a thin shelly horizon indicates the separation between the lower and the upper parts of the Santonian Age. The senior-author has observed in three different ancient private Collections the presence of some massive small teeth attributable to the Genus *Ptychotrygon*.

This, supposed, short interruption of sedimentation between the lower and the middle Santonian seems detectable in the U.S.A. (northern America), in Belgium (western Europe) and in Lebanon (the Near East) indicating the paleoenvironmental importance of this phenomenon.

#### Genus Texatrygon CAPPETTA & CASE, 1990

The type-species of the Genus *Texatrygon* is *Texatrygon hooveri* (McNULTY & SLAUGHTER, 1972), species based on isolated teeth discovered in a shelly level of upper Turonian Age (Upper Cretaceous) in Texas (U.S.A.).

This Genus includes a second species: *T. coopei* CAPPETTA & CASE, 1999 based on isolated teeth discovered in a level of lower Campanian Age in Texas (U.S.A.).

For references and illustrations, see Bibliography-Systematics: Cappetta 2012: p.: 392, fig.: 382 and Cappetta & Case 1990

#### Genus Ptychotrygonoides LANDEMAINE, 1991

The generotype of this mono-specific Genus *Ptychotrygonoides* is *Ptychotrygonoides pouiti* LANDEMAINE, 1991, species based on isolated teeth discovered in a level of Cenomanian Age (Upper Cretaceous) in the Charente-Maritime Department (France).

Teeth of this species were also discovered in one level of Turonian Age (Upper Cretaceous) of northern Spain.

For references and illustrations, see Bibliography-Systematics: Cappetta 2012: p.: 391, fig.: 381 and Landemaine 1991.

# **Research of ancestors of the Family Ptychotrygonidae**

In absence of any skeletal remains, only the common odontological characteristics of its three representative extinct Genera may furnish indications.

# **Objective data**

The three generic taxa regrouped in this Family are in possession of small massive teeth presenting a holaulacorhyzid root and a massive, non-cylindrical, apron. They were inhabitants of coastal shallow waters.

#### Hypothesis

Plausible ancestors of this Family must have been in possession of similar massive teeth with dental crowns having a non-cylindrical wider apron, dental roots presenting a more primitive root structure, which means a hemiaulacorhyzid root. They must have inhabited similar sea bottoms.

#### **Conclusion proposed**

The sole group of neoselachian Chondrichthyes presenting all these characteristics is the Order Hemiscylliiformes, such as defined in this Publication.

# Super Order Ganopristomorphii nov.

# **Preliminary remark**

The following Systematics proposals are based on the conviction of the senior-author that the sudden formation of a rostrum is considered as a consequence of a fundamental modification of the genetic code.

# **Order Ganopristiformes HERMAN & VAN WAES, 2012**

# **Systematics**

Cappetta (2006: pp.: 407-408 and 2012: pp.: 367) regrouped in a single Family, the Family Sclerorhynchidae CAPPETTA, 1974 the twenty-two following Genera: Genus *Ischyrhiza* LEIDY, 1856, Genus *Gigantichthys* DAMES, 1887, Genus *Sclerorhynchus* WOODWARD, 1889, Genus *Platyspondylus* HAUG, 1905, Genus *Onchopristis* STROMER, 1917, Genus *Onchopristis* STROMER, 1917, Genus *Schizorhiza* WEILER, 1930, Genus *Dalpiazia* CHECCHIA-RISPOLI, 1933, Genus *Ganopristis* ARAMBOURG, 1935, Genus *Marckrgrafia* WEILER, 1935, Genus *Ctenopristis*\* ARAMBOURG, 1940, Genus *Pucapristis* SCHAEFFER, 1963, Genus *Ankistrorhynchus* CASIER, 1964, Genus *Libanopristis* CAPPETTA, 1980, Genus *Micropristis* CAPPETTA, 1980, Genus *Baharapristis* WERNER, 1989, Genus *Renpetia* WERNER, 1989, Genus *Plicatopristis* CAPPETTA, 1991, Genus *Celtipristis* KRIWET, 1999, Genus *Kiesius* CAPPETTA & CASE, 1999 and Genus *Biropristis* SUAREZ & CAPPETTA, 2004.

\*Oral teeth identified by Herman in 1973. See Bibliography-Systematics: Herman 1973.

Cappetta added, with doubt, the two Genera: Genus *Titanichthys* DAMES, 1887 and Genus *Sechmetia* WERNER, 1989.

Cappetta (2012: p.: 367) reduced this list to the following twelve generic taxa, divided into two groups: The first one regroups the three Genera possessing rostral teeth of which the core of the capuchin contains osteodentine and the second one the nine Genera possessing rostral teeth of which the core of the capuchin consists of orthodentine and contains a pulp cavity.

The three Genera: Genus *Onchopristis* STROMER, 1917, Genus *Pucapristis* SCHAEFFER, 1963 and Genus *Schizo-rhyza* WEILER, 1930 constitute the first group.

The nine Genera: Genus Ischyrhiza LEIDY, 1856, Genus Sclerorhynchus WOODWARD, 1889, Genus Onchopristis STROMER, 1917, Genus Dalpiazia CHECCHIA-RISPOLI, 1933, Genus Ganopristis ARAMBOURG, 1935, Genus Marckrgrafia WEILER, 1935, Genus Ctenopristis ARAMBOURG, 1940, Genus Ankistrorhynchus CASIER, 1964, Genus Libanopristis CAPPETTA, 1980, Genus Micropristis CAPPETTA, 1980, Genus Borodinopristis CASE, 1987 and Genus Plicatopristis CAPPETTA, 1991 constitute the second group.

The Genus Kiesius CAPPETTA & CASE, 1999 is absent of both lists.

The senior-author pointed out that the Genus *Ganopristis* ARAMBOURG, 1935, generotype of the Family Ganopristidae HERMAN, 1977, was finally accepted and included in this list.

This fact enforces the proposal of the Order Ganopristiformes HERMAN & VAN WAES, 2012, based on this Family and the proposal of the new Super Order Ganopristomorphii.

The Family Sclerorhynchidae CAPPETTA, 1974, based on the Genus *Sclerorhynchus* WOODWARD, 1889, is considered as a synonym of the Family Ganopristidae HERMAN, 1977 because it was based on the specific taxon *Ganopristis leptodon* ARAMBOURG, 1935, a synonym of *Sclerorhynchus leptodon* (WOODWARD, 1935).

As a paleontologist, the senior-author prefers to use, as far as possible\*, the oral teeth as fundamental tool of classification for the Chondrichthyes.

\*Oral teeth of some Genera are quite impossible to distinguish at a specific level: E.g.: These of the Genera *Rhinobatos*, *Anoxypristis* and *Pristis*.

But the majority of the oral teeth of all the taxa of the Ganopristomorphii is easily distinguishable at a specific level and reveals their generic ancestor.

# Systematic proposal

This Super Order is based on the sole Order Ganopristiformes HERMAN & VAN WAES, 2012. The oral teeth of all

the representatives of this Super Order are characterized by the possession of an apron and a placement in quincunx. All the members of this Super Order are also in possession of a rostrum with rostral teeth.

#### Taxonomy

This Super Order is based on the Order Ganopristiformes\* HERMAN & VAN WAES, 2012, based on its sole Family, the Family Ganopristidae\* HERMAN, 1974 proposed in his PhD Thesis, 4<sup>th</sup> January 1974. The text of this Thesis was published in June1977 in the *Mémoires pour servir à l'explication des cartes géologiques et minières de Belgique*. **15**. (See Bibliography-Systematics: Herman 1977).

\*The Family Ganopristidae proposed in this Publication regrouped the same taxa as these included in the sub Family Ganopristinae proposed by Arambourg in 1952.

This designation was accepted by the members of the jury who included Dr. Jacques Blot (M.N.H.N., Paris, France) and Dr. Edgard Casier (I.R.S.N.B., Brussels, Belgium); both respecting the original proposal of Dr. Prof. Camille Arambourg (M.N.H.N., Paris, France) and admitting the elevation of this sub Family to the rank of a Family.

The senior-author would have preferred the proposal Ganopristidae, to the proposal Sclerorhynchidae, because the capuchin of their rostral teeth was enamelled, which seemed to be its most distinctive criterion. The reference to the Genus *Sclerorhynchus* WOODWARD, 1889 did not make this singularity explicit.

In 2012, Cappetta himself recognized\* the validity of the Genus *Ganopristis* ARAMBOURG, 1935, based on the species *Ganopristis leptodon* ARAMBOURG, 1935 but persisted to use the designation Family Sclerorhynchidae.

\*See Bibliography-Systematics: Cappetta 2012: p.: 367 and p.: 375. No additional comments.

# Anatomy of the Ganopristomorphii

A superficial observation of all the skeletal remains of this extinct taxon is sufficient to realize that all these individuals are in possession of two pectoral fins and two pelvic fins, which are well separated. These four fins are independent members of similar size.

The Genus *Sclerorhynchus* WOODWARD, 1889 was selected as generotype of the Family Sclerorhynchidae CAPPETTA, 1974. Its type species *Sclerorhynchus atavus* WOODWARD, 1889 is represented by numerous skeletal remains that also showed two dorsal fins\*.

\*Cappetta 2012: p.: 388.

Living representatives and skeletons of extinct representatives of Batomorphii do not have dorsal fins and their pectoral and pelvic fins are more or less interconnected.

The very flat appearance of their fossils results principally from the compaction of the sediments and partially from their own evolution.

After the sensible regression of the diverse populations of the Genus *Ptychodus* AGASSIZ, 1935 observable during the beginning of the lower Santonian, the possession of a rostrum seems to have been a real advantage for competition in their own zones of distribution or to replace the members of this Genus where they had already disappeared.

Two groups will immediately take advantage of this situation: The first representatives of the Family Pristiophoridae BLEEKER, 1859 and the first representatives of the Family Ganopristidae HERMAN, 1977.

# The oral teeth of the Ganopristomorphii

All the oral teeth of all the generic representatives of this Super Order present a crown overlapping the top of their holaulacorhyzid root and an apron. Such as these of all the members of the Order Ptychotrygonyformes, they are disposed in quincunx. The size, the morphology of their apron, the presence or the absence of a pair of lateral cusplets and the ornamentation of their crown are the principal criteria that allow distinguishing them.

# Family Ganopristidae HERMAN, 1977

The Super Order Ganopristomorphii as well as the Order Ganopristiformes are based on the extinct revalidated Family Ganopristidae HERMAN, 1977, which regroups the following twenty-one Genera.

The Family Sclerorhynchidae CAPPETTA, 1974 had as generotype the Genus Sclerorhynchus ARAMBOURG, 1935.

Arambourg had based this Genus on the species *Ganopristis leptodon* ARAMBOURG, 1935, which is presently a synonym of Sclerorhynchus leptodon ARAMBOURG, 1935.

#### Genus Ankistrorhynchus CASIER, 1964

The oral dentition of this lower Santonian Belgian Genus remains officially unknown but the senior-author has observed some ganopristiform oral teeth in the *Collection Coupatez* of the I.R.S.N.B. (Brussels, Belgium). The presence of the Ganopristomorphii in the Glauconie of Lonzée Formation only being guaranteed by the discovery of only one type of rostral teeth, it seems logical to suppose that these teeth are the oral teeth of this Genus.

#### Genus Baharipristis WERNER, 1989

The possession of a large apron, the presence of lateral cusplets on the dental crown of the anterior teeth, their absence on latero-anterior to posterior teeth, the strong ornamentation of the extern side of their dental crown and the fine ornamentation of the intern side of their dental crown are the principal characteristics of this Cenomanian northern African Genus. See Cappetta 2012: p.: 370, figs.: 359: A to M.

#### Genus Biropristis SUAREZ & CAPPETTA, 2004

The possession of a short angular to rounded apron, the monocuspidy of their crown and its reticulate ornamentation are the principal characteristics of this Maastrichtian southern American Genus. See Cappetta 2012: figs.: 359A to 359E.

#### Genus Borodinopristis CASE, 1967

The possession of a relatively long and rounded apron, one pair of lateral cusplets and the strong costulations on the base of the extern face of their dental crown are the principal characteristics of this Santonian-Campanian northern American mono-specific Genus. See Cappetta 2012: p.: 370, figs.: 359L to 359S.

#### Genus Celtipristis KRIWET, 1999

The possession of a short and blunt apron, the monocuspidy of all its dental crowns and the nearly smooth faces of these crowns are the principal characteristics of this Barremian (Lower Cretaceous) European mono-specific Genus. It is the oldest representative of this Super Order. See Cappetta 2012: p.: 371, figs.: 360A to 360H.

# Genus Columbusia CASE, SCHWIMMER, BORODIN & LEGGETT, 2007

The possession of a very long and narrow apron, the monocuspidy of the anterior and lateral teeth, the presence of some rounded lateral cusplets on their posterior teeth and the smooth\* surface of the extern face of their crown are the principal characteristics of this upper Campanian northern American Genus. See Cappetta 2012: p.: 372, figs.: 360A to 360K.

\*A discrete vertical carina is present on the extern face of the crown of their posterior teeth.

#### Genus Ctenopristis ARAMBOURG, 1940

The proportion of its teeth, longer than wide, the possession of a very short and rounded apron, the monocuspidy of their dental crown and the very poor ornamentation of the extern face of their crown are the principal characteristics of this Coniacian-Maastrichtian African and Near East Genus: See Cappetta 2012: p.: 373: figs.: 362E to 362H and Herman 1973.

# Genus Dalpizia CHECCHIA-RISPOLI, 1933

The possession of a strongly compressed monocuspid crown, the very short apron of variable forms and the very strong and short costulations\* presented by the extern side of their dental crown are the principal characteristics of this Cenomanian to Maastrichtian African and Asian Genus. See Cappetta 2012: p.: 374, fig.: 363. \*Only one axial to four symmetrically disposed.

#### Genus Ganopristis ARAMBOURG, 1935

The possession of a very short but wide apron of their monocuspid dental crown and the very fine, radial and rippled folds of the extern face of their crown are the principal characteristics of this Santonian to Maastrichtian

European, northern African and Near Eastern\* Genus. See Cappetta 2012: p.: 376, fig.: 364.

\*Israel, Lebanon and Jordan.

#### Genus Ischyrhiza LEIDY, 1856

The possession of a monocuspid crown presenting a very massive apron, elongated (anterior teeth) or short (lateral teeth) and the extern face of the dental crown always presenting one central and vertical discrete carina are the principal characteristics of this Turonian to Maastrichtian European, northern and southern American, northern and western African and Asian Genus. See Cappetta 2012: p.: 377, fig.: 365.

#### Genus Kiestus CAPPETTA & CASE, 1999

The presence of a pair of lateral cusplets on its anterior teeth, the possession of a short, large and oval-shaped apron and the ornamentation of its dental crowns reduced to one bifid (anterior teeth) or rectilinear (other teeth) carina are the principal characteristics of this lower Turonian to middle Coniacian north American mono-specific Genus. See Cappetta 2012: p.: 378, fig.: 366.

#### Genus Libanopristis CAPPETTA, 1980

The possession of a monocuspid dental crown presenting a well-developed apron and transversal\* parallel cristae are the principal characteristics of this Cenomanian Lebanese Genus. See Cappetta 2012: p.: 379, fig.: 368: A to N. See: Conclusions.

\*Typical ornamentation of ptychotrygonid teeth.

#### Genus Marckgrafia WEILER, 1935

The possession of a monocuspid dental crown presenting a massive, rounded and protuberant apron, the hemiaulacorhyzid structure of their lateral teeth and the rare massive bulbous excrescences situated on the base of their dental crown are the principal characteristics of this mono-specific Cenomanian Genus of Egypt. See Cappetta 2012: p.: 379, figs.: O to R and p.: 380, fig.: 369.

#### Genus Micropristis CAPPETTA, 1980

The possession of a monocuspid dental crown presenting a moderately protuberant apron, the monocuspidy of all its dental crowns and the ornamentation of its extern face, reduced to a discrete bifid central carena are the principal characteristics of this Cenomanian to lower Campanian European and Lebanese mono-specific Genus. See Cappetta 2012: p.: 381, fig.: 370A to 370Q. See: Conclusions.

#### Genus Onchopristis STROMER, 1917

The possession of a monocuspid dental crown presenting a long and compressed cylindrical apron and the ornamentation of its extern face, reduced to a discrete vertical carina are the principal characteristics of this Barremanian (lower Cretaceous) to Cenomanian northern African and northern American Genus. See Cappetta 2012: p.: 381, fig.: 370M to 370R.

#### Genus Onchosaurus GERVAIS, 1852

The oral teeth of this Turonian to Maastrichtian European, north-eastern and western African, northern and southern American and Asian Genus remain unknown. For recent illustration of a rostral tooth: See Cappetta 2012: p.: 382, fig.: 371 and p.: 383, fig.: 372. See conclusions.

# Genus Plicatopristis CAPPETTA, 1991

The possession of holaulacorhyzid teeth presenting one principal, triangular and massive cuspid flanked by one pair of short lateral cusplets, only present on anterior teeth, the size of their long and wide apron and the lateral short and massive costulations present on the base of the extern an intern sides of their crown and their simple, bifid or trifid extern carina are the principal characteristics of this Coniacian to Maastrichtian northern African and Lebanese mono-specific Genus. See Cappetta 2012: p.: 384, fig.: 373.

#### Genus Pucapristis SCHAEFFER, 1963

The possession of monocuspid massive and laterally compressed teeth, their short massive and rounded

protuberant apron and the presence of a central discrete and bifid carina are the principal characteristics of this Maastrichtian central southern American mono-specific Genus. See Cappetta 2012: p.: 385, fig.: 374.

# Genus Renpentia WERNER, 1989

The possession of monocuspid teeth (anterior and lateral teeth) or teeth presenting a large central cuspid flanked by a pair of short and rounded lateral cusplets (posterior teeth), a large, elongated and protuberant apron and an extern ornamentation constituted by a strong bifid central carina are the principal characteristics of this supposed mono-specific Cenomanian Egyptian Genus. See Cappetta 2012: p.: 386, fig.: 375.

Cappetta (2012, p.: 386) considers the second species attributed to this Genus as a member of the Orectolobiformes because the teeth of this northern American Danian\* species are in possession of an apron. See conclusions. \*These teeth were discovered in the Nacimiento Formation of Danian Age (Early Paleogene) in New Mexico (U.S.A.).

#### Genus Schizorhiza WEILER, 1930 in STROMER & WEILER, 1930

The possession of monocuspid, extremely laterally compressed, minute teeth presenting a secondary anaulacorhyzid root, absence of any ornamentation on both sides of the crown and a virtually absent apron are the principal characteristics of this Santonian to Maastrichtian northern and western African, northern and southern American and Lebanese mono-specific Genus. See Cappetta 2012: p.: 387, fig.: 377. See: Conclusions.

#### Genus Sclerorhynchus WOODWARD, 1889

The possession of monocuspid holaulacorhyzid teeth presenting a rounded protuberant apron and dental crowns presenting discrete radial folds are the principal characteristics of this Turonian to Maastrichtian northern American, northern African and Lebanese Genus. See Cappetta 2012: p.: 389, fig.: 379.

#### Conclusions

**1.** The Genus *Celtipristis* KRIWET, 1999 is the first representative of the Ganopristomorphii. It is represented by oral and rostral teeth of Barremian Age (Lower Cretaceous). The last Ganopristomorphii disappeared at the end of the Maastrichtian (uppermost Cretaceous).

The presence of antero-posterior parallel cristae on the occlusal face of the teeth of the Genus *Libanopristis* CAPPETTA, 1980 allow considering this Genus as a member of the Order Ptychotrygoniformes.

**2.** It seems possible that the skeletons of the Genus *Micropristis* CAPPETTA, 1980 were skeletons of juvenile individuals of the Genus *Sclerorhynchus* WOODWARD, 1889.

**3.** The very large paleodistribution of the rostral teeth of the Genus *Onchosaurus* GERVAIS, 1852 allows supposing that their oral teeth were discovered in diverse localities but attributed to another Genus and another Family.

**4.** The Genus *Renpentia* WERNER, 1989 could include a second species: *R. standthardtae* WILLIAMSON & LUCAS, 1993, based on isolated oral teeth of Danian Age.

The senior-author agrees with the interpretation of Cappetta (University of Montpellier 2, France) who considers this Genus as a member of the Order Orectolobiformes *sensu* APPLEGATE, 1974 and not as a representative of the Order Ganopristiformes HERMAN & VAN WAES, 2012.

**5.** Except for the Genus *Libanopristis* CAPPETTA, 1980 considered as a representative of the Ptychotrygoniformes, all the generic taxa of the Ganopristimorphii are in possession of oral teeth presenting a typical apron and they may have orectolobid ancestors.

# The rostral teeth of the Ganopristiomorphii

Their structure: an enamelled capuchin surmounting a calcified socle is very similar to this of the diverse representatives of the Super Order Pristiophoromorphii, but their morphology is very different.

The rostral teeth of all the extinct and extant species of the Family Pristiophoridae are straight. The morphology of the capuchin of the rostral teeth of the Ganopristomorphii is very variable\* and serves as principal distinctive generic criterion.

\*E.g.: Sigmoidal: *Ganopristis* and *Sclerorhynchus*, beak-like: *Ischyrhyza*, harpoon-like: *Dalpiazia* and *Pucapristis*, curved and saw-like: *Bordinopristis*, needle-like: *Ctenopristis*, massive and smooth: *Libanopristis* and *Ischyrhyza* or massive and striated: *Baharipristis* and *Marckgrafia*.

#### Conclusion

The Ganopristomorphii are representatives of the Selachii and not of the Batomorphii. The morphology of the apron of their oral teeth allows supposing, if not guaranteeing, that their ancestors were members of the Super Order Orectolobomorphii but not of the same lineage as this of the Pristiophoromorphii.

# **Preliminary remark**

The following Systematics proposals are based on the conviction of the senior-author that the sudden formation of a rostrum is considered as a consequence of a fundamental modification of the genetic code.

# Selachii: Enigmatic taxa

Till today, the Systematics' position of some generic taxa remains unknown. The senior-author may only add some personal reflections and field data.

#### Genus Odontorhytis BÖHM, 1926

This Genus is based on *O. pappenheimi* BÖHM, 1926 represented by isolated teeth discovered in an Eocene level of Namibia (South Africa).

The dental root of this extinct taxon is holaulacorhyzid, does not overlap the top of the dental crown of which the smooth cutting edge presents only two very short lateral extensions. Both sides of the dental crown present numerous high sub-vertical striations.

The anterior teeth of this species are seven times higher than wide, the posterior teeth known are four times higher than wide.

Later, supposed posterior teeth of this strange taxon, three times higher than wide, were also discovered in diverse levels of Lower and Middle Eocene Age in northern Africa: Morocco\* and Tunisia\*\*.

\*Prospections of Georges Wouters (1968 to 1974), Jacques Herman and Michel Girardot (1971). These materials are included in the *Crochard Collection* and the *Wouters-Picavez Collection* of the Vertebrate Section of the Department of Pale-ontology of the I.R.S.N.B. (Brussels, Belgium).

\*\*Prospections of Dr. Henri Neybergh, former geologist of the Belgian Geological Survey.

Some teeth discovered by Georges Wouters\* in two different levels of Ypresian Age (Lower Eocene) at Khouribga (Ouled Abdoun Basin) from Morocco seemed to be last posterior and commissural teeth of this taxon.

\*In June 1969.

These teeth are smaller but larger than the specimens commonly illustrated and their dental crown presents a smooth extern side and minute lateral cusplets.

These lateral teeth remain three times higher than wide, which is insufficient to consider them as commissural teeth of a representative of the Genus *Striatolamia* GLYCKMAN, 1964, but sufficient to consider this Genus as a possible ancestor of the Genus *Odontorhytis*.

A virtual simulation would enable to reconstitute the successive phases of the morphological transformation, affirming the passage from the *Striatolamia* dental morphology to the *Odontorhytis* dental morphology.

For references and figuration: See Bibliography-Systematics: Böhm 1926 and Cappetta 2012: pp.: 326-327.

# 17. BATOIDEI

# (Sensu Compagno 1973)

The Batoidei regroup the two Super Orders: Super Order Rajomorphii HERMAN & VAN WAES, 2012 and Super Order Myliobatomorphii HERMAN & VAN WAES, 2012.

# Anatomical characteristics of the Batoidei

All the extant and extinct members of the Batoidei present a strongly dorso-ventrally flattened body, one pair of large to huge pectoral fins, one pair of strongly reduced pelvic fins, no dorsal fin and a more or less elongated caudal fin, with or without spines and tubercules.

Except for the extant members of the Family Hexatrygonidae HEEMSTRA & SMITH, 1980, all the extant representatives of the Batoidei present, on their ventral side, five pairs of gill slits. All their extinct representatives known by skeletal remains also present only five pairs of gill slits.

The evolution of their locomotion mode has induced many researches. See: Bibliography-Locomotion.

#### **Odontological characteristics of the Batoidei**

All the extant and extinct members of the Batoidei are in possession of teeth presenting a monocuspid dental crown overlapping a holaulacorhyzid or polyaulacorhyzid root. Their teeth are placed in parallel rows, in quincux or grouped in dental plates.

# Mode of reproduction of the Batoidei

Some have preserved the oviparity\*, the most primitive one, others are ovoviviparous\*\* and others are aplacental viviparous\*\*\*.

\*All the extant members of the Order Rajiformes.

\*\*The large majority of the extant members of the Order Dasyatiformes, uncertainty remains for some taxa.

\*\*\*The large majority of the extant members of the Order Myliobatiformes, uncertainty remains for some taxa.

# Super Order Rajomorphii HERMAN & VAN WAES, 2012

This Super Order was proposed for regrouping the two following Orders: The Order Rajiformes BERG, 1940, and the Order Torpediniformes de BUEN, 1926.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**.: p.: 69.

# Order Rajiformes BERG, 1940 rev.

# Systematic remark

The Genus *Pucabatis* CAPPETTA, 1975 and all the taxa which constituted the former Order Sclerorhynchiformes KRIWET, 2004 were extracted from this Order.

This Order regrouped the five following Families: Family Rajidae LINNAEUS, 1758, Family Platyrhinidae JORDAN, 1923, Family Hypsobatidae CAPPETTA, 1992, Family Parapalaeobatidae CAPPETTA, 1992 and the Family Archaeobatidae DELSATE & CANDONI, 2001.

According to its principal odontological characteristics, the Family Archaeobatidae DELSATE & CANDONI, 2001 is presently considered as a group of primitive taxa attributable to the Super Order Squatinomorphii, and, more precisely, of the Order Hemiscylliiformes.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012: *Géominpal Belgica*. **2**.: p.: 70.

# Family Rajidae BONAPARTE, 1831

Fide Cappetta (2006: p.: 407), this Family regrouped the eight following Genera : Genus *Raja* LINNAEUS, 1758, Genus *Actinobatis* AGASSIZ, 1843, Genus *Dipturus* RAFINESQUE, 1810, Genus *Mafdetia* WERNER, 1989, Genus *Pararaja* CAPPETTA, 1980, Genus *Rajitheca* STEININGER, 1966, Genus *Smithraja* HERMAN, 1986, Genus *Rajorhina* JAEKEL, 1894 and Genus *Walteraja* SIVERSON & CAPPETTA, 2001.

In 2012\*, Cappetta reconsidered the composition of this Family as follows: Genus *Raja* LINNAEUS, 1758, Genus *Dipturus* RAFINESQUE, 1810, Genus *Rajorhina* JAEKEL, 1894, Genus *Rajitheca* STEININGER, 1966, Genus *Smith*-

*raja*, HERMAN, 1986, Genus *Malacoraja* STEHMANN, 1970 and Genus *Walteraja*, SIVERSON & CAPPETTA, 2001, forming a group of seven Genera.

\*See Bibliography-Systematics: Cappetta 2012: pp.: 358 to 364.

The reasons allowing the elimination of the four Genera Actinobatis, Mafdetia, Pararaja and Rajorhina from this list are not explained.

#### Genus Smithraja HERMAN, 1986

The Genus *Smithraja*, HERMAN, 1986 must be integrated in this Family, and not in the Family Rhinopteridae. Some teeth attributable to this Genus were discovered in the upper Thanetian of northern France.

Concerning the Genus *Smithraja*: See Bibliography-Systematics: Herman 1982.

For illustrations concerning the dentition of supra-specific taxa of the Order Rajiformes: See Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt, 1994: pp.: 165-207 and pls.: 1 to 30. Herman, Hovestadt-Euler & Hovestadt, 1995: pp.: 237-307 and pls.: 1 to 56.

Herman, Hovestadt-Euler & Hovestadt, 1995. pp. 257-507 and pls. 1 to 50.

Herman, Hovestadt-Euler & Hovestadt, 1996: pp.: 179-236 and pls.: 1 to 41.

# Family Parapalaeobatidae CAPPETTA, 1992

This mono-specific Family is based on the Genus *Parapalaeobates* WEILER *in* STROMER & WEILER, 1930. This Genus has a temporal distribution extending from the Santonian to the Maastrichtian and a geographical distribution covering Europe, northern and western Africa, the near East, central Asia and Madagascar.

This Family is based on the Genus *Parapalaeobates* WEILER *in* STROMER & WEILER, 1930 and it also includes the Genus *Youssobatis* CAPPETTA, 1992.

The morphology of the dental crowns of the teeth of the representatives of the Genus *Youssobatis* makes it difficult to include this taxon in the Family Parapalaeobatidae (See Cappetta 2012: p.: 351, figs.: 339 and 340).

# Family Hypsobatidae CAPPETTA, 1992

Fide Cappetta, this Family regroups the three following extinct Genera: Genus *Angolaia* ANTUNES & CAPPETTA, 2002, Genus *Hypsobatis* CAPPETTA, 1992 and Genus *Youssoubatis* CAPPETTA, 1992.

Some isolated teeth discovered in the Tuffeau de Maastricht Formation (uppermost Cretaceous) of the Limburg Province (Belgium) could be attributed to the Genus *Youssoubatis*.

# Family Cyclobatidae CAPPETTA, 1980

The mono-generic Family Cyclobatidae CAPPETTA, 1980 is represented by its generotype: the Genus *Cyclobatis* EGERTON, 1844.

It was proposed\* that the Genus *Cyclobatis* EGERTON, 1844 could be considered as the ancestor of the Genus *Potamotrygon* GARMAN, 1877 and included in the Family Potamotrygonidae GARMAN, 1887.

\* Herman & Van Waes, 2012.

See Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt, 1999: pls.: 14 and 15. Herman & Van Waes, 2012: Géo. **2**.: p.: 75.

# Order Rhinobatiformes COMPAGNO, 1977 rev.

This Order, considered as a sub Order, regrouped (*fide* Cappetta, 2006: p.: 406) the six following Families: Family Platyrhinidae JORDAN, 1923, Family Rhinidae MÜLLER & HENLE, 1838, Family Rhinobatidae MÜLLER & HENLE, 1838 and Family Rhynchobatidae MÜLLER & HENLE, 1838. Family des Hypsobatidae CAPPETTA, 1992 and Family Parapaleobatidae CAPPETTA, 1992.

As well as Compagno 1977, Cappetta 2012 included the Family Rhinidae\* MÜLLER & HENLE, 1838 in this Order.

The general morphology of the teeth of the sole representative species of this extant mono-generic and mono-specific Family presents a sufficient number of similarities with the teeth of the extinct Genus *Ptychotrygon* REUSS, 1845 to constitute a distinct Order with this one: The Order Ptychotrygoniformes HERMAN & VAN WAES, 2012.

See Bibliography-Systematics:

Cappetta, 2006, Cappetta 2012, Compagno 1977 and Müller & Henle, 1838.

#### Family Rhinobatidae MÜLLER & HENLE, 1838 rev.

#### **General morphology**

Their minute teeth are twice wide as high.

Fide Cappetta (2006: pp.: 406-407), this Family regrouped its generotype, the Genus Rhinobatos LINCK, 1790 and the twelve nominal following Genera: Genus *Allelopos*<sup>3</sup> MÜNSTER, 1836, Genus *Arthtopterus*<sup>3</sup> AGASSIZ, 1843, Genus *Euryarthra*<sup>3</sup> AGASSIZ, 1843, Genus *Asterodermus*<sup>2</sup> AGASSIZ, 1843, Genus *Spathobatis*<sup>2</sup> THIOLLIERE, 1852, Genus *Belemnobatis*<sup>2</sup> THIOLLIERE, 1852, Genus *Aptychotrema*<sup>1</sup> NORMAN, 1926, Genus *Rhombopterygia*<sup>2</sup> CAPPETTA, 1980, Genus *Isidobatus*<sup>2</sup> WERNER, 1989, Genus *Iansan*<sup>1</sup> BRITO & SERET, 1996, Genus *Hermanobatos*<sup>3</sup> BERNARDEZ, 2002 and Genus *Nolfia*<sup>3</sup> BERNARDEZ, 2002.

Genus<sup>1</sup>: Extant and valid taxon. Genus<sup>2</sup>: Extinct and valid taxon. Genus<sup>3</sup>: Taxon non valid.

Eleven Genera qualified '*incert. Fam.*' complete this list: Genus *Ataktobatis* CAPPETTA & CORRAL, 1999, Genus *Baibishihia* NESSOV *in* NESSOV & UDOVICHENKO, 1986, Genus *Engaibatis*, ARRATIA, KRIWET & HEINRICH, 2002, Genus *Jurobatos* THIES, 1983, Genus *Microbatis* CAPPETTA, 1993, Genus *Myledaphus* COPE, 1876, Genus *Parahypolophus* MEYER, 1974, Genus *Protoplatyrhina* CASE, 1978, Genus *Pseudohypolophus* CAPPETTA & CASE, 1975, Genus *Squatirhina* CASIER, 1947 and Genus *Vascobatis* CAPPETTA & CORRAL, 1999.

#### Genus Ataktobatis CAPPETTA & CORRAL, 1999

The mono-specific Genus *Ataktobatis* CAPPETTA & CORRAL, 1999 is based on isolated teeth of *A. variabilis* CAPPETTA & CORRAL, 1999 discovered in only one level of Maastrichtian Age (Upper Cretaceous) from northern Spain.

Such a specific name attributed to teeth of a mono-specific Genus of which the teeth are virtually indistinguishable, allows considering this taxon of dubious validity.

But the morphology of the lingula of the teeth figured by Cappetta (2002: p.: 352, fig.: 341) suggests that this taxon could be an ancestor of the extant Genus *Platyrhina* (Family Platyrhinidae).

#### Genus Baibishihia NESSOV in NESSOV & UDOVICHENKO, 1986

The mono-specific Genus *Baibishihia* NESSOV *in* NESSOV & UDOVICHENKO, 1986 is based on isolated teeth of its type species *B. baibishe* NESSOV *in* NESSOV & UDOVICHENKO, 1986 discovered in a Santonian level of central Asia (Russia).

In accordance with Cappetta 2006 (p.: 334), the senior-author considers this taxon as a junior synonym of the Genus *Myledaphus* COPE, 1876.

For description and illustration: See Bibliography-Systematics: Cappetta 2012 and Nessov & Udovichenko 1986.

#### Genus Engaibatis ARRATIA, KRIWET & HEINRICH, 2002

The mono-specific Genus *Engaibatis* ARRATIA, KRIWET & HEINRICH, 2002 is based on isolated teeth of its type species *B. schultzei* discovered in the Upper Jurassic of Tanzania.

Its millimetric-sized teeth present all the odontological characteristics\* of hemiscylliid Chondrichthyes. This taxon may be considered as a primitive member of the Family Hemiscylliidae GILL, 1862.

\*See Cappetta 2012: p.: 353, fig.: 342.

For description and illustration: See Bibliography-Systematics: Cappetta 2012 and Arratia, Kriwet & Heinrich 2002.

#### Genus Jurobatos THIES, 1983

The mono-specific Genus *Jurobatos* THIES, 1983 is based on *J. Cappettai* THIES, 1983, based on isolated teeth discovered in a level of Toarcian Age in northern Germany.

Its teeth\* possess a smooth dental crown overlapping the top of their dental root, a rounded and massive apron and one short principal cuspid flanked by one pair of large, more or less, rounded lateral cusplets. Their dental hemiaulacorhyzid root presents two root lobes which are horizontally extended.

\*See Cappetta 2012: p.: 325, fig.: 311.

Together, all these odontological characteristics allow considering this Genus as an evolved representative of the Super Order Squatinomorphii and, more precisely, as an ancestral representative of the Order Hemiscylliiformes.

For description and illustration: See Bibliography-Systematics: Cappetta 2012 and Thies 1983.

#### Genus Microbatis CAPPETTA, 1993

The mono-specific Genus *Microbatis* CAPPETTA, 1993 is based on isolated teeth of its type-species *M. sabatieri* CAPPETTA, 1993 discovered in only one Thanetian (Paleogene) level of northern Africa.

Its millimetric-sized teeth present all the odontological characteristics of dasyatiform Chondrichthyes. This Genus may be considered as a primitive member of the Order Dasyatiformes.

For description and illustration: See Bibliography-Systematics: Cappetta 1993 and Cappetta 2012: p.: 353, fig.: 343.

#### Genus Myledaphus COPE, 1876

The Genus *Myledaphus* COPE, 1876 is based on *M. bipartitus* COPE, 1876 represented by isolated teeth and some grouped teeth discovered in the Judith River Formation of Campanian Age (Upper Cretaceous) of northern America (Montana, U.S.A).

This Genus was considered as a representative taxon of the *Rhinobatoidei incertae sedis* of the Order Rajiformes by Cappetta (2006: p.: 406 and 2012: p.: 354), but is presently considered as a member of the Family Pastinachidae nov. of the Order Myliobatiformes *sensu* COMPAGNO, 1973.

For description and illustration: See Bibliography-Systematics: Cappetta 2012, Compagno 1973, Cope 1876 and Herman & Van Waes 2012.

#### Genus Parahypolophus MEYER, 1974

According to Cappetta (2006: p.: 350), the type-species of the extinct Genus *Parahypolophus* MEYER, 1974 is *Parahypolophus mcnultyi* (THURMOND, 1971), based on isolated teeth discovered in a level of the Paluxy Formation of Albian/Aptian Age (lowermost Upper Cretaceous) in northern Texas (U.S.A.).

Once more, because proposed in a PhD Thesis, this taxon is considered, by Cappetta as a *nomen nudum*, but as synonym of the Genus *Pseudohypolophus* CAPPETTA & CASE, 1975. No comments.

For references, see: Cappetta 2006: p.: 350, Cappetta & Case 1975 and Meyer 1974: p.: 149.

# Genus Protoplatyrhina CASE, 1978

The Generotype of this extinct Genus is *Protoplatyrhina renae* CASE, 1978, based on isolated teeth discovered in a level of the Judith River Formation of Campanian Age (Upper Cretaceous) in Montana (U.S.A.).

Cappetta (2006: p.: 361) considered this Genus is as a Rhinobatoidei incertae Fam.

This Genus of doubtful validity includes a second species *Protoplatyrhina hoopei* WILLIAMSON, KIRKLAND & LUCAS, 1993, based on isolated teeth discovered in a level of the Toreva Formation of middle Turonian Age (Upper Cretaceous) in Arizona (U.S.A.).

If valid, these two taxa could be regrouped in the Genus *Pseudohypolophodon* CAPPETTA & CASE, 1975, but surely not in the Genus *Squatirhina* CASIER, 1947 such as proposed by Cappetta (2012: p.: 355).

For principal references and illustrations, see: Case 1978: p.: 193, Cappetta 2012: p.: 355 and figs.: 344L to 344N and Williamson, Kirkland & Lucas 1993: p.: 460: figs.: 9.11 to 9.15.

#### Genus Pseudohypolophus CAPPETTA & CASE, 1975

The Genus *Pseudohypolophus* CAPPETTA & CASE, 1975 is based on *Pseudohypolophus mcNultyi* (THURMOND. 1971 and regroups three other taxa: *P. ellipsis* CASE, SCHWIMMER, BORODIN & LEGGET, 2001 from a level of Satonian Age in Georgia (U.S.A.), *P. elongatus* MUSTAFA, CASE & ZALMOUT, 2002 from a level of upper Satonian Age in central Jordany and *P. lapilliferus* NESSOV *in* NESSOV & UDOVICHENKO, 1996 from a level of upper Albian Age in Uzbekistan (Central Asia).

The structure of their dental root and the morphology of their dental crown are very similar to these of the extant Genus *Pastinachus sephen* FORSSKÄL, 1775 which is presently considered, by the majority of the ichthyologists, as a member of the Order Dasyatiformes.

#### Genus Vascobatis CAPPETTA & CORRAL, 1999

The mono-specific Genus *Vascobatis* CAPPETTA & CORRAL, 1999 is based on its type and unique species *Vascobatis albaitensis* CAPPETTA & CORRAL, 1999.

This taxon is based on a lot of isolated teeth discovered in a level of Maastrichtian Age (Upper Cretaceous) in the Condado de Trevido (northern Spain).

Some relatively similar teeth were discovered\* in two levels of Maastrichtian Age in the Limburg Province (Belgium).

\*By the senior-author and one of his field friends. According to the wish of this collaborator, these teeth are in repository of the N.H.M. of Maastricht (The Netherlands).

The teeth discovered in the Maastricht area could represent a second species of this Genus. These teeth only differ from these of the type species by their higher cuspid.

While the structure of the dental root of these teeth is hemiaulacorhyzid, the morphology of their dental crown is this of a primitive dasyatoid Batoidei and surely not this of any orectoloboid taxon.

The lack of any ornamentation on all its dental crowns is a second odontological characteristic of this Genus.

Momentarily, the Genus *Vascobatis* may be considered as one of the oldest representative taxa of the Family Dasyatidae JORDAN, 1888 of the Order Dasyatiformes.

For description and illustration of teeth of the Genus *Vascobatis*: See Cappetta 2012: p.: 357, fig.: 346.

For description and illustration of the extant generic representatives of the Family Dasyatidae: See Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt 1997: pp.: 107-162 and pls.: 1 to 30.

# Conclusion concerning the *Rhinobatidae incertae sedis* CAPPETTA, 2012

Except for the Genus *Squatirhina* CASIER, 1947, well represented and diversified in Belgium, and the rare discoveries of teeth attributable to the Genus *Vascobatis* CAPPETTA & CORRAL, 1999 none of these extinct Genera has ever been mentioned in Belgium.

The senior-author added one fossil Genus to this list: The Genus *Smithraja* HERMAN, 1986 which must be considered\* as a member of the Family Rhinobatidae MÜLLER & HENLE, 1837 and not as a member of the Family Rajidae BONAPARTE, 1831, such as suggested by Cappetta in 2006 (p.: 377) and in 2012 (p.: 333).

\*The strong lateral compression of its teeth and the height of their dental root are two odontological characteristics of this Family.

# Other incertae sedis Genus of the Super Order Squatinomorphii

#### Genus Parasquatina HERMAN, 1982

This mono-specific Genus is represented by its type-species *P. cappettai* HERMAN, 1982 based on one isolated tooth discovered in the Lower Maastrichtian of northern Germany.

Since 1982, teeth of this squatinomorphid taxon were discovered in diverse French localities\* of upper Campanian Age and in a Danish level of Danian Age (*fide* Cappetta 2012, p.: 325).

\*Hem (Pas-de-Calais Department, France) and Nurlu (Somme Department, France), Prospections of the senior-author during the Summer of 1983.

For description and illustration: See Bibliography-Systematics: Herman 1982 and Herman & Van Waes 2012.

#### Remark concerning the odontology of the Genus Rhinobatos LINCK, 1790

Numerous attempts to distinguish the diverse specific taxa present in diverse fossiliferous Belgian Eocene levels and attributable to this Genus have demonstrated the limit of the efficiency of the odontological criteria used to identify all these specific taxa.

These attempts were realized, separately, by the senior-author and some collaborators. The results were more than significant: Each participant was unable to guarantee the presence of six, seven or eight plausible morphotypes in one level of the Ypresian strata from Egem (Western Flanders).

A more significant experiment: After mixing the teeth of the jaws of three individuals of three extant species of this Genus, none of them was able to reconstitute the jaws of these valid\* different extant taxa.

\*Valid because their anatomical and genetic data confirmed their membership to three different species.

#### Family Platyrhinidae JORDAN, 1923

This Family regroups the extant Genus: Genus *Platyrhina* MÜLLER & HENLE, 1838 and the two extinct Genera: Genus *Narcopterus* AGASSIZ, 1835 and Genus *Tethybatis* CARVALHO, 2004.

#### Genus Platyrhina MÜLLER & HENLE, 1838

This extant Genus regroups the three extant species: *P. sinensis* BLOCH & SCHNEIDER, 1801 and the two, recently discovered, species: *P. hyugaensis* MIYAMOTO & NAKAYA, 2011 and *P. tangi* MIYAMOTO & NAKAYA, 2011. These three species are ovoviviparous and feed principally on shelled mollusks.

This last characteristic prefigures the feeding mode of the myliobatiform Batomorphii.

Distribution map of P. sinensis see on : www.discoverlife.org

Distribution map of *P. hyugaensis* see on: <u>http://shark-references.com/species/view/Platyrhina-hyugaensis</u> Distribution map of *P. tangi* see on: <u>http://shark-references.com/species/view/Platyrhina-tangi</u>

The dental morphology of *Platyrhina sinensis* BLOCH & SCHNEIDER, 1801 has been described and illustrated in 1997.

See Bibliography- Systematics: Herman, Hovestadt-Euler & Hovestadt, 1997: pl. : 23-25.

#### Genus Narcopterus AGASSIZ, 1835

The type species of the Genus *Narcopterus* AGASSIZ, 1835 is *N. bolcanus* AGASSIZ, 1835 represented by a skeleton discovered in the Lutetian (Middle Eocene) of northern Italy.

This Genus is considered as a junior synonym of the extant Genus *Platyrhina* MÜLLER & HENLE, 1831, but the skeleton of its holotype requires further deeper osteological studies before definitely accepting this proposal.

For description and illustrations see: See Bibliography-Systematics: Agassiz 1835 and Cappetta 2012: p.: 346.

# **Order Dasyatiformes nov.**

This Order is proposed for regrouping the six following Families: Family Dasyatidae JORDAN, 1888, Family Urolophidae MÜLLER & HENLE, 1841, Family Urotrygonidae McEACHRAN, DUNN & MIYAKE, 1996, Family Plesiobatidae NISHIDA, 1990, Family Potamotrygonidae GARMAN, 1877, Family Gymnuridae FOWLER, 1934 and Family Hexatrygonidae HEEMSTRA & SMITH, 1980.

The extinct Genus Vascobatis CAPPETTA & CORRAL, 1999 could be one of its oldest representatives.

# Anatomical characteristics of the Order Dasyatiformes

All the extant taxa of this Order possess five pairs of gill slits, have two large pectoral fins, no dorsal fin, the form of their body is rhombic to oblong. They do not possess a rostrum. None of them has preserved the oviparous mode of reproduction.

# **Odontological characteristics of the Order Dasyatiformes**

All the extant taxa of this Order have holaulacorhyzid teeth. The base of their monocuspid dental crown overlaps the top of their dental root. They are, generally\*, ornamented. Their dental roots present two root lobes the morphology of which helps to determine their parental Family.

\*It is not sure that the rare Genera without crown ornamentation classically attributed to this Order are really representatives of this Order.

# Singularities

Some of its members may possess caudal spines and some others caudal spines as well as large caudal denticles.

# Family Dasyatidae JORDAN, 1888

According to Cappetta (2006: pp.: 409-410), this Family regrouped the four following extant Genera: Genus *Dasyatis* RAFINESQUE, 1810, Genus *Pastinachus* RÜPPEL, 1828, Genus *Himantura* MÜLLER & HENLE, 1837, Genus *Taeniura* MÜLLER & HENLE, 1837 and the seven following extinct Genera: Genus *Heliobatis* MARSH, 1877, Genus *Xiphotrygon* COPE, 1879, Genus *Hypolophites* STROMER, 1910, Genus *Palaeodasyatis* FOWLER, 1937, Genus *Glyckmania* AVERIANOV & UDOVICHENKO, 1993, Genus *Ishaquia* NOUBHANI & CAPPETTA, 1995 and Genus *Asterotrygon* CARVALHO, MAISEY & GRANDE, 2004.

# Dasyatoid Incertae Family

The following eighteen taxa are simply mentioned as *Dasyatoid incertae Family*: Genus *Alexandrinum* MOLIN, 1860, Genus *Acanthobatis* LARRAZET, 1886, Genus *Hypolophodon* CAPPETTA, 1980, Genus *Coupatezia* CAPPETTA, 1982, Genus *Arechia* CAPPETTA, 1983, Genus *Merabatis* CAPPETTA, 1983, Genus *Heterotorpedo* WARD, 1983, Genus *Microbatis* CAPPETTA, 1993, Genus *Glickmania* AVERIANOV & UDOVICHENKO, 1993, Genus *Meridiana* CASE, 1994, Genus *Dasyrhombodus* NOUBHANI & CAPPETTA, 1997, Genus *Heterobatis* NOUBHANI & CAPPETTA, 1997, Genus *Heterobatis* CAPPETTA & CASE, 1999, Genus *Prosopodon* NOUBHANI & CAPPETTA, 1997, Genus *Eniantobatis* CAPPETTA & CASE, 1999, Genus *Prosopodon* NOUBHANI & CAPPETTA, 1997, Genus *Texabatis* CAPPETTA & CASE, 1997 and Genus *Vipericucullus* CASE, 1996.

In 2012, Cappetta (pp.: 352-356) reduced, without explanations, this list to the following taxa: Genus *Ataktobatis* CAPPETTA & CORRAL, 1999, Genus *Engaiabatis* ARRATIA, KRIWET & HEINRICH, 2002 and Genus *Microbatis* CAPPETTA, 1993.

# Family Rhynchobatidae GARMAN, 1913

According to the list of IT IS 2010 and to the list of FishBase 2013, this extant Family is represented by its single generotype: The Genus *Rhynchobatus* MÜLLER & HENLE, 1837.

# Family Rhinidae MÜLLER & HENLE, 1838

According to the list of IT IS 2010 and to the list of FishBase 2013, this extant Family is represented by its single generotype: The Genus *Rhina* BLOCH & SCHNEIDER, 1838.

The Genus *Pucabatis* SCHAEFFER, 1963 seems to be its direct ancestor and the Genus *Ptychotrygon* JAEKEL, 1894 a far ancestor. These three Genera constitute the Order Ptychotrygoniformes HERMAN & VAN WAES, 2012.

# Family Mobulidae GILL, 1862

This Family regroups the three extant Genera: Genus *Mobula* RAFINESQUE, 1810, Genus *Neotrygon* CASTELNAU, 1873 and Genus *Manta* BANCROFT, 1829 and the eight extinct Genera: *Plinthicus* COPE, 1861, *Burnhamia* CAPPETTA, 1976, *Archaeomanta* HERMAN, 1979, *Eomanta* PFEIL, 1981, *Paramobula* PFEIL, 1981, *Eomobula* HERMAN, HOVESTADT-EULER & HOVESTADT, 1989, *Cretomanta* CASE, TOKARYK & BAIRD, 1990 and *Eoplinthicus* CAPPETTA & STRINGER, 2002.

For description and illustration of the dentition of the extant Genera *Mobula* and *Manta*: See: Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt 2000.

#### Genus Mobula RAFINESQUE, 1810

This Genus has for type species *M. auriculata* RAFINESQUE, 1810 and includes eight other representatives: *M. mobular* BONNATERRE, 1788, *M. hypostoma* BANCROFT, 1831, *M. japonica* MÜLLER & HENLE, 1841, *M. eregoodootenkee* BLEEKER, 1859, *M. rochebrunei* VAILLANT, 1879, *M. tarapacana* PHILLIPPI, 1892, *M. thurstoni* LLOYD, 1908 and *M. munkiana* NOTARBALO di SCIARA, 1987. All these taxa request genetic analysis before to be considered valid taxa.

#### Genus Neotrygon CASTELNAU, 1873

This Genus has for type species *N. kuhlii* MÜLLER & HENLE, 1837 and includes five other extant representatives: *N. trigonoides* CASTELNAU, 1873, *N. 212anadens* (LAST, 1987), *N. leylandi* (LAST, 1987), *N. picta* LAST & WHITE, 2008 and *N. ningalooensis* LAST, WHITE & PUCKRIDGE, 2010.

#### Anatomical characteristics of the Genus Mobula

All the extant representatives of this Genus have five pairs of gill slits, a vertebral column constituted only by vertebrae having a cylindrical centrum.

The individuals of the diverse populations of the diverse species of this Genus were generally observed by divers between 30 and 50 metres of depth, but some were electronically followed to more than 1.000 metres depth.

They are able to effectuate spectacular jumps\* above the sea level and to migrate over long distances in accordance with the krill concentrations.

\*Jumping record observed: 14 metres.

#### **Odontological characteristics of the Genus** *Mobula*

All the extant or extinct representatives of this Genus are in possession of small teeth presenting a polycuspid ornamented dental crown overlapping the top of their polyaulacorhyzid dental root.

#### Differences between the Genera Mobula and Neotrygon

The differences that allow distinguishing members of these two generic taxa are only based on some differences observed between their genetic code. Fact demonstrating the limits of the identification of Batomorphii by odontological criteria.

For description and illustration: See Bibliography-Systematics: Castelnau 1873 and Last & White 2008.

Distribution map of N. kuhlii: see on www.wikimedia.commons.org

#### Genus Manta BANCROFT, 1829

This Genus has for type species *Manta birostris* BANCROFT, 1829 and also includes *M. alfredi* (KREFT, 1868). But he validity of this second taxon *M. alfredi* (KREFT, 1868) remains highly controversial.

This Genus is the single extant representative species of the Chondrichthyes having only teeth in its upper jaw. This demonstrates the loss of any nutritional function of their teeth. These teeth seem to perform only a sexual role.

For the distribution map of *Manta birostris*, See on: <u>www.commons.wikimedia.org</u>

For description and illustration: See Bibliography-Systematics: Bancroft 1829, Duffy & Abbott 2003, Herman, Hovestadt-Euler & Hovestadt 2000, Marshal, Compagno & Bennett 2009.

#### Genus Plinthicus COPE, 1861

This extinct Genus has for type species *Plinthicus stenodon* COPE, 1861 based on isolated teeth discovered in a level of Miocene Age in New-Jersey (U.S.A.) and includes a second species *P. kruibekensis* BOR, 1990 discovered, in Belgium, in the Boom Clay Formation of Middle Oligocene Age.

For description and illustration: See Bibliography-Systematics: Bor 1990: p.: 94, pl.: 1: figs.: 1 to 5 and Cope 1861: p.: 316.

#### Genus Burnhamia CAPPETTA, 1976

This extinct Genus has for type species *Burnhamia daviesi* (WOODWARD, 1889)\* based on teeth discovered in the London Clay Formation of Lower Eocene Age in the London Basin (England).

\*Described as *Rhinopera daviesi*.

This Genus includes two other species: *B. fetahi* CAPPETTA, 1985 based on teeth discovered in the upper Ypresian of the Ouled Aboun Basin (central Morocco) and *B. glickmani* PFEIL, 1981 based on teeth discovered in the Tasaran Formation (Eocene Age) of Kazakhstan (Russia).

This Genus seems to have a temporal distribution restricted to the Lower Eocene and Middle Eocene. Its geographical distribution includes only the occidental and the central parts of Europe as well as the occidental part of central Asia.

> For description and illustration: See Bibliography-Systematics: Capetta 1976: p.: 574, Cappetta 1985, Casier 1946, Casier 1966, Pfeil 1981: p.:159, pl. 4: fig.: 4 and Woodward 1889: p.: 366

#### Genus Archaeomanta HERMAN, 1979

This Genus has for type species Archaeomanta melenhorsti HERMAN, 1979 based on isolated teeth discovered in the Mons-en-Pévèle Sands Formation of upper Ypresian Age in Western Flanders Province (Belgium).

This Genus includes two other species: *A. priemi* HERMAN, 1979 based on isolated teeth discovered in a level of the Wemmel Sands Formation of Upper Eocene Age in the Flemish Brabant Province (Belgium) and *A. hermani* KOZLOV, 2001 based on isolated teeth discovered in a level of the Shoryn Formation of Upper Eocene Age in Kazakhstan (Russia).

This extinct Genus had a temporal distribution restricted to the Lower Eocene and the Middle Eocene. Its geographical distribution includes only the occidental and the central parts of Europe as well as the occidental part of central Asia.

> For description and illustration: See Bibliography-Systematics: Herman 1979 and Kozlov 2001.

#### Genus Eomanta PFEIL, 1981

This Genus has for type species *E. kowaldi* based on isolated teeth discovered in the Rupel Clay Formation of Oligocene Age. According to Cappetta (2006: p.: 333).

According to Cappetta 2012, this Genus is considered as a synonym of the extant Genus Mobula.

For description and illustration: See Bibliography-Systematics: Cappetta 2012 : p. : 462 and Pfeil 1981.

#### Genus Paramobula PFEIL, 1981

This Genus has for type species *P. fragilis* (CAPPETA, 1970)\*. According to Cappetta himself (2006: p.: 333), this Genus is a synonym of the extant Genus *Mobula*. Taxon suppressed by its inventor: No comments.

\*Described in 1970 as Manta fragilis.

#### Genus Cretomanta CASE, TOKARYK & BAIRD, 1990

This mono-specific Genus has for type species *C. 214anadensis* based on isolated teeth discovered in a single level of the Niobrara Formation of Coniacian Age (Upper Cretaceous) in Saskatchewan (Canada).

This species was considered as a *Lamniformes incertae sedis* (Cappetta 2006: p.: 44) and reconsidered as a *Myliobatiformes incertae sedis* (Cappetta 2012 : p. : 469).

For references and illustrations: See: Bibliography-Systematics: Cappetta 2012: pp.: 459-460 and fig.: 454 and Case, Tokaryk & Baird 1990: p.: 1092 and p.: 1093: fig.: 14.

#### Genus *Eoplinthicus* CAPPETTA & STRINGER, 2002

This Genus has for type species *E. yazooensis* CAPPETTA & STRINGER, 2002 based on isolated teeth discovered in a level of the Yazoo Formation of Priabonian Age (uppermost Eocene) in Louisiana (U.S.A.).

#### Genus Eomobula HERMAN, HOVESTADT-EULER & HOVESTADT, 1989

This mono-specific Genus has for type species: *E. stehmanni* HERMAN, HOVESTADT-EULER & HOVESTADT, 1989. It is based on isolated teeth discovered in two different levels of the Mons-en-Pévèle Sands Formation of Western Flanders Province (Belgium).

The low polyaulacorhyzid structure of their dental roots corresponds with this of the extant representatives of the Genus *Mobula*.

Teeth of this species were discovered in other levels of the same Age in northern Africa (Morocco and Tunisia) and in the Aquitaine Basin in France.

For references and illustrations: See: Bibliography-Systematics: Cappetta 2012: p.: 461: fig.: 455 and Herman, Hovestadt-Euler & Hovestadt 1989: p.: 176, pl.: 1, figs.: 1-2.

#### Family Pastinachidae nov.

(Plates 67 to 70)

This Family could be based on the extant Genus *Pastinachus* RÜPPEL, 1829\* and could regroup the other extant Genus *Neotrygon* and some extinct taxa such as *Hypolophodon* CAPPETTA, 1980 and *Pseudohypolophus* CAPPETTA & CASE, 1975, which present numerous similar odontological criteria such as a flat smooth rhombic-shaped crown completely overlapping the top of their holaulacorhyzid root.

\*Hypolophus MÜLLER & HENLE, 1837 is a junior synonym of Pastinachus RÜPPEL, 1829.

The Genus *Pastinachus* regroups *Pastinachus sephen* FORSSKÄL, 1775, its generotype, and four other extant species: *P. atrus* McLEAY, 1883, *P. solocirostris* LAST, MANJAJI & YEARSLEY, 2005, *P. stellurostris* LAST, FAHMI & NAYLOR, 2010 and *P. gracilicaudus* LAST & MANJAJI-MATSUMOTO, 2010.

The populations of *Pastinachus sephen* inhabit some parts of the eastern African coasts. The populations of the four other species are scattered along diverse coasts of the Indo-Pacific Ocean. Some were observed in brackish and freshwaters. They inhabit coastal and continental shelves.

Distribution map of Pastinachus sephen see: www.biodiversityexplorer.org

#### **Biological characteristics of the Family Pastinachidae**

All the individuals of the scattered populations of the generotype of this Family have five pairs of gill slits, a dasyatid-like body, no dorsal fins, caudal spines. They are ovoviviparous.

#### **Odontological characteristics of the Family Pastinachidae**

All the extant and extinct representatives of this Family possess teeth presenting a massive smooth crown overlapping the whole periphery of the top of their holaulacorhyzid root. Their dental root presents two massive vertical lateral root lobes. The base of their dental crown presents numerous short extern folds (Genus *Hypolophodon*) or none (Genus *Pastinachus* and Genus *Neotrygon*).

The teeth of the different species of the extant Genus *Pastinachus* form a dental plate with a symphyseal depression.

For image of the dentition of *Pastinachus sephen*: See: <u>www.sciences-de-la-terre.com</u>

For principal references and illustrations: See Bibliography-Systematics: Cappetta & Case 1975, Cappetta 2012: p.: 355, figs.: 344E to 344K, Müller & Henle, 1837 and Rüppel 1829.

# Spatio-temporal distribution of the Family Pastinachidae

#### Geological data

#### Genus Hypolophodon CAPPETTA, 1980

The type species of this Genus is *Hypolophodon sylvestris* (WHITE, 1931) based on isolated teeth discovered in the Blackheats Beds of lower Ypresian Age in the County of Kent (southern England). The four following taxa were successively attributed to this Genus: *H. ypresiensis* (CASIER, 1946), *H. farreri* (GURR, 1962), *H. dockeryi* (CASE, 1994) and *H. ovalis* UDOVICHENKO in NESSOV & UDOVICHENKO, 1984.

*H. ypresiensis* (CASIER, 1946) based on isolated teeth discovered in the Forest Sands Formation of Ypresian Age in the Brussels Regio (Belgium), *H. farreri* (GURR, 1962) based on isolated teeth discovered in the Woolwich Bottom Beds of Ypresian Age in the County of Kent (southern England), *H. dockeryi* (CASE, 1994) based on isolated teeth discovered in the Bachi Formation of Ypresian Age in Mississipi (U.S.A.) and *H. ovalis* UDOVICHENKO in NESSOV & UDOVICHENKO, 1984 based on isolated teeth discovered in a level of Thanethian Age in southern Kazakhstan (Central Asia).

Agreeing with Cappetta 2006 (p.: 82), the senior-author considers that *H. farreri* (GURR, 1962) is a synonym of *Hypolophodon sylvestris* but it represents maybe a population which lived in waters having a higher degree of hyalinity, such as its plausible ancestor *H. ovalis* UDOVICHENKO in NESSOV & UDOVICHENKO, 1984.

By lack of comparative material the senior-author is not sure that *H. dockeryi* (CASE, 1994) is a representative of the Euro-Asian Genus *Hypolophodon*.

For references and illustrations: See Bibliography-Systematics: White 1931: p.: 70, p.: 71, figs.: 94-108 and p.: 72, figs.: 109-115, Casier 1946, Gurr 1962 and Nessov & Udovichenko 1984.

The extinct Genus *Hypolophodon* CAPPETTA, 1980 regroups three taxa: *H. sylvestris* WHITE & FROST, 1931, *H. dockeryi* CASE, 1994 and *H. ovalis* UDOVISCHENKO *in* NESSOV & UDOVISCHENKO, 1984.

*H. sylvestris* is represented by numerous isolated teeth discovered in levels of Ypresian Age (Lower Eocene) in southern England and Ypresian Age (Lower Eocene) in northern France and in Belgium. *H. dockeryi* is represented by numerous isolated teeth discovered in a level of Ypresian Age (Lower Eocene) in Mississippi
(U.S.A.) and *H. ovalis* is represented by numerous isolated teeth discovered in levels of Thanetian Age (Upper Paleocene) in southern Kazakhstan (central Asia).

For references, see: Cappetta 2012: p.: 437 and 438: fig.: 431, Cappetta & Case 1975, Case 1994 and Udovitschenko 1984.

The oldest fossils of this Family are the teeth of the diverse species attributed to the Genus *Hypolophodon* CAPPETTA, 1980 which were inhabitants of estuarine waters of Western Europe, of coastal waters of central Europe and western Asia.

The extant representatives of their supposed relatives\* are presently inhabitants of some isolated zones of the Indian Ocean, of the western part, the north-western part and the central part of the Pacific Ocean. They were never mentioned more eastern than the Great Pacific Barrier.

\*The Genus Pastinachus.

Their present dispersal perfectly illustrates the influence of the Plate Tectonics on the dispersal of the diverse populations forming one benthic and coastal species.

For references, see: Cappetta 2012: p.: 421, Gosh 1959, Sahni & Merotra 1981 and Uyeno 1978.

#### Genus Pseudohypolophus CAPPETTA & CASE, 1975

The extinct Genus *Pseudohypolophus* CAPPETTA & CASE, 1975 is based on *H. sylvestris* WHITE & FROST, 1931 which is represented by numerous isolated teeth discovered in different levels of Thanetian (Upper Paleocene) and Ypresian Age (Lower Eocene) in southern England, northern France, central Belgium and in levels of Burdigalian Age (Lower Miocene) in western Africa.

In Europe, their teeth were signalized as teeth of *Platyhrhina ypresiensis* CASIER, 1946 and, in Africa, as teeth of *Platyhrhina malembeensis* DARTEVELLE & CASIER, 1959.

For references, see: Cappetta 2012: p.: 354, Casier 1946 and Dartevelle & Casier 1959.

#### Genus Pastinachus RÜPPEL, 1829

This Genus regroups the five following extant species: *P. sephen* (FORSSKAL, 1775), *P. atrus* McLEAY, 1883 *P. solocirostris* LAST, MANJAJI & YEARSLEY, 2005, *P. gracilicaudus* LAST, MANJAJI-MATSUMOTO, 2010 and *P. stellurostris* LAST, FAHMI & NAYLOR, 2010.

For distribution map of *Pastinachus sephen*: See: <u>www.discoverlife.org</u>

For references and illustrations: See Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt 1998 and Rüppel 1829.

#### Genus Neotrygon CASTELNAU, 1873

This Genus regroups the six following extant species which were, formerly considered as members of the Genus *Dasyatis: Neotrygon trigonoides* CASTELNAU, 1873, *Neotrygon kuhlii* (MÜLLER & HENLE, 1841), *Neotrygon annotata* (LAST, 1987), *Neotrygon leylandi* (LAST, 1987), *Neotrygon picta* LAST & WHITE, 2008, and *Neotrygon ningalooensis* LAST, WHITE & PUCKRIDGE, 2010.

Morphological studies and molecular analyses have recently\* allowed to revalidate this Genus and to regroup these six species, commonly called *Mask-rays*, in this Genus. \*For principal reference, see: Last & White 2008.

These six extant species are represented by numerous scattered populations that inhabit the shallow costal and continental shelves waters of the Indo-Pacific Ocean. None of them was signalized more eastern than the Great Pacific Barrier.

The morphology of their teeth is very close to this of the members of the Genus *Pastinachus*, but the placement of their teeth is slightly different.

The dentition of *Neotrygon kuhlii* (MÜLLER & HENLE, 1841) was illustrated by Herman, Hovestadt-Euler & Hovestadt in 1998.

For references and illustrations: See Bibliography-Systematics: Herman, Hovestadt-Euler & Hovestadt 1998 and Last & White 2008.

## **Possible ancestors of the Family Pastinachidae**

All the extinct and extant representatives of this Family have a massive, rounded and flat dental crown overlapping the whole periphery of their holaulacorhyzid dental root. Their teeth are placed in dense concentrations prefigured by the dental plates of the members of the Family Brachyrhyzodontidae HERMAN & VAN WAES 2012.

The Family Brachyrhyzodontidae was proposed for regrouping the three extinct Genera: Genus *Brachyrhyzodus* ROMER, 1842, Genus *Apocopodon* COPE, 1885 and Genus *Igdabatis* CAPPETTA, 1986.

The spatio-temporal distribution\* of the Family Brachyrhyzodontidae allows considering it as the phyletic origin of the Family Pastinachidae.

\*This Family has numerous North American representatives.

## Family Hexatrygonidae HEEMSTRA & SMITH, 1980

This Family is a mono-generic Family including only the Genus *Hexatrygon* which has a geological range from the Eocene to the Present Times.

#### Genus Hexatrygon HEEMSTRA & SMITH, 1980

This extant mono-specific Genus has for holotype *Hexatrygon bickelli* HEEMSTRA & SMITH, 1980 and includes a fossil taxon: *Hexatrygon senegasi* ADNET, 2006 based on isolated teeth discovered in a level of middle Lutetian Age (Middle Eocene) in the Aquitaine Basin (southwestern France).

#### Anatomical characteristics of the Genus Hexatrygon

All the individuals of this batoid Genus have six pairs of gill slits. Their jaws are greatly protruding, allowing it to capture embedded organisms. Their flesh is gelatinous and lacks dermal denticles.

Their mouth is wide and nearly straight. In each jaw, there are 44 to 102 rows of small, blunt teeth arranged in a quincunx pattern; the teeth are more numerous in adults. The moderately thick tail presents one or two serrated spines.

One recorded specimen had six gill slits on the left side and seven on the right side. The pelvic fins are rather large and rounded.

Mode of reproduction: aplacental viviparity.

#### Habitat of the Genus *Hexatrygon*

Its type species is represented by diverse benthic populations scattered in the Indo-Pacific Ocean from South Africa to Hawaii, usually found on upper continental slopes and around seamounts at depths of 500 to 1.200 metres. It was occasionally observed in shallower water feeding at a depth of 30 metres off southern Japan.

Distribution map of *Hexatrygon bickelli*: See on: <u>www.commons.wikimedia.org</u>

#### Odontological characteristics of the Genus Hexatrygon

The teeth of the additional individuals\*, of the diverse populations of this extant taxon, the senior-author has have the possibility to examine presented the same odontological characteristics as these mentioned in Herman, Hovestadt-Euler & Hovestadt 1998.

\*One male from India, two females from Japan and one male from Australia

Their teeth are wider than high. Their monocuspid dental crown overlaps all the margin of the top of their holaulacorhyrhid dental root which presents a very large median groove and two small root lobes.

Their dental crowns have an isosceles triangular morphology and their intern and extern sides are absolutely smooth.

Sexual dimorphism is quite imperceptible, but the cuspid of the dental crown of the anterior teeth of the males is lightly higher than the one of the females.

#### **Fossil representatives**

An Eocene representative was described as *Hexatrygon senegasi* ADNET, 2006. The teeth of this species, the oldest known attributed to this Genus, present an obvious sexual dimorphism.

If this generic attribution correct\* is, this taxon enhances the list of the genetic abnormal and traumatic taxa of marine vertebrates which appeared suddenly at the end of the Eocene Period, just before the Eocene-Oligocene Transition.

\*In absence of skeletal remains it is impossible to guarantee that *H. senegasi* was in possession of six pairs of gill slits or not.

In 2001, one individual of *Hexatrygon bickelli* presenting six gill slits on one side and seven on its other side caught off the south-west coast of India, was signaled by Babu, Kamachandran & Varghese.

For references and illustrations, see: Bibliography-Systematics: Adnet 2006, Babu, Kamachandran & Varghese 2001, Cappetta 2012: p.: 426, fig.: 417, Heemstra & Smith, 1980 and Herman, Hovestadt-Euler & Hovestadt 1998.

# **Order Rhiniformes HERMAN & VAN WAES, 2012**

This Order is based on the mono-generic Family Rhinidae MÜLLER & HENLE, 1837, based on the extant Genus *Rhina* BLOCH & SCHNEIDER, 1801, represented by a single species *Rhina ancyclostoma* BLOCH & SCHNEIDER, 1801, the sole species of the Batoidei being in possession of six pairs of gill slits.

For reference, see Bibliography-Systematics: Herman & Van Waes 2012.

# **Order Torpediniformes de BUEN**, 1926

This Order regroups the two extant Families: The Family Torpedinidae BONAPARTE, 1838, based on the extant Genus *Torpedo* HOUTTUYN, 1764 and the Family Narcinidae GILL, 1862, based on the extant Genus *Narcine* HENLE, 1834.

For description and illustration of the dentition of these two Genera, See Bibliography-Systematics: Herman, Hovestadt-Euler and Hovestadt 2002.

## Family Torpedinidae BONAPARTE, 1838

For reference, see Bibliography-Systematics: Bonaparte 1838, De BUEN, 1926, GIIL, 1862, Herman & Van Waes 2012: *Géominpal Belgica*. **2.**: p.: 76 and Houtthyn 1764.

## Family Narcinidae GILL, 1862

This Family is represented by the single extant Genus Narcine HENLE, 1834.

For references: See Bibliography-Systematics: Gill 1862 and Henle 1834.

# **Order Pristiformes nov.**

This Order is based on the extant Family Pristidae and its three Genera: *Propristis* DAMES, 1888 of uppermost Eocene Age, *Pristis* LINCK, 1790 of upper Paleocene to the Present Times and *Anoxypristis* WHITE & MOY-THOMAS, 1940 of Mio-Pliocene to the Present Times.

The diverse populations of the extant representatives of the Family Pristidae are inhabitants of marine waters, brackish or fresh waters. Their neonates and juveniles inhabit shallow coastal waters, but the adults may be encountered at a depth of 40 to 50 metres.

Some of their populations are encountered in rivers, far from the coast and one inhabits the Nicaragua Lake.

The rostral spines\* of the embryos remain flexible and are not indurated to protect the walls of the uterus of their mothers during their hatching process.

\*Spines, because these rostral teeth are principally bony structures.

The taxonomy, or in fact, the systematics, of the Family Pristidae remains, in 2014, only based on some visual characteristics.

The Genus Anoxypristis contains one species (A. cuspidata) and the Genus Pristis regroups four to six 'species'.

The Genus Pristis has been divided into two groups, commonly referred to as small-toothed and large-toothed.

The small-toothed ones regroup the three species *P. clavata* GARMAN, 1906, *P. pectinata* LATHAM, 1794 and *P. zijsron* BLEEKER, 1851 and the large-toothed ones regroup the three species *P. microdon* LATHAM, 1794, *P. perotteti* VALANCIENNES *in* MÜLLER & HENLE, 1841 and *P. pristis* (LINNAEUS, 1758).

Only genetics analyses could enable to specify which of these represent specific taxa and which of these represent only populations.

All the extant representatives of the three Genera included in this Family are ovoviviparous.

## **Obvious singularities**

The possession of an elongated rostrum with rostral teeth presenting no enameled capuchin and jaws presenting numerous minute elongated rhinobatoid oral teeth are the two first anatomical criteria that allow distinguishing this Order.

This Order is the third attempt of the post-Triassic Chondrichthyes to produce taxa disposing of an elongated rostrum: The Ganopristiformes (Upper Cretaceous), the Pristiophoriformes (Upper Cretaceous to the Present Times) and the Pristiformes (Paleocene to the Present Times).

## Other anatomical criteria of the Pristiformes

In addition to their rostrum, all the extant representatives of this Order possess five pairs of gill slits, two dorsal fins without fin spine, no anal fin and they are ovoviviparous.

### **Odontological criteria of the Pristiformes**

#### **General morphology**

Their minute teeth are twice high as wide.

#### **Dental root**

All the extant representatives of this Order are in possession of a holaulacorhyzid root, two elongated radicular lobes separated by a, more or less, elongated and wide lingula (intern extension of their crown).

The dental roots of all the extant representatives of the Family Pristidae are separated by a short and rectilinear lingula. Their root lobes are poorly developed. These of the members of the Family Rhinobatidae are widely extended.

#### Dental crown

All the extant representatives of this Order have smooth crowns with a rounded summit overlapping the top of their root.

For description and illustration of the oral and rostral teeth of the Genera *Pristis* and *Anoxypristis*: See Bibliography-Systematics: Herman, Hovestadt-Euler and Hovestadt 2002.

## **Spatio-temporal distribution of the Pristiformes**

#### For the extant representatives of this Order, see the following distribution maps:

 Pristis clavata on: www.environment.gov.au

 Pristis pectinata on: www.oceana.org

 Pristis zijsron on: www.artesdepesca.blogspot.com

 Pristis microdon on: www.biodiversity.explorer and www.artesdepesca.blogspot.com

 Pristis perotteti on: www.discoverlife.org

 Pristis pristis on: www.discoverlife.org

 Anoxypristis cuspidata on: www.boldsystems.org

#### Distribution of the extinct representatives

The extinct Genus *Propristis* DAMES, 1883 regroups two African species: Its type species *P. schweinfurthi* DAMES, 1883, based on rostral teeth discovered in the uppermost Eocene of the Fayum Depression (Egypt).

*P. mayumbensis* DARTEVELLE & CASIER, 1943 is based on reworked rostral teeth. They were discovered in a Burdigalian level (Miocene) in Cabinda (Angola) in which they were associated with some other Eocene reworked fossils.

These fossils demonstrate that the paleodistribution of the Genus *Propristis* included north African shallow waters as well as central African shallow waters.

## Remark

P. cheops DAMES, 1888 and P. reinachi (STROMER, 1905) are synonyms of P. schweinfurthi DAMES, 1883.

## Family Pristidae BONAPARTE, 1838

This Family regroups the two extant Genera: Genus *Pristis* LINCK, 1790 and Genus *Anoxypristis* WHITE & MOY-THOMAS, 1940 and the six extinct Genera: Genus *Amblypristis*\* DAMES, 1888, Genus *Eopristis*\* STROMER, 1905, Genus *Mesopristis*\*\* FARRES, 2003, Genus *Notopristis*\*\*\* AMEGHINO, 1906, Genus *Oxypristis*\*\* HOFFMAN, 1912 and Genus *Propristis* DAMES, 1883.

\*Amblypristis DAMES, 1888 and Eopristis STROMER, 1905 are synonyms of Propristis DAMES, 1883. \*\*Mesopristis FARRES, 2003 and Oxypristis HOFFMAN, 1912 are synonyms of Anoxypristis WHITE & MOY-THOMAS, 1940.

\*\*\* Notopristis AMEGHINO, 1906 is a synonym of Pristis LINCK, 1790.

# Super Order Myliobatomorphii HERMAN & VAN WAES, 2012

# **Order Myliobatiformes COMPAGNO, 1973**

This Order regroups the two extant Families: Family Myliobatidae BONAPARTE, 1838 and Family Rhinopteridae JORDAN & EVERMANN, 1896 and the two extinct Families: Family Rhombodontidae CAPPETTA, 1987 and Family Brachyryzodontidae HERMAN & VAN WAES, 2012.

A thorough re-examination\* of all the types of the extinct and extant representatives of this Order has demonstrated that all its extant taxa require genetic analysis.

\*See Bibliography-Systematics: Hovestadt and Hovestadt-Euler, 2013.

The upper and lower dental plates of the types of the four extant generic taxa are distinguishable, but the validity of all the extinct taxa based on isolated dental plates is more than dubious.

Only the Genus *Weissobatis* HOVESTADT & HOVESTADT-EULER, 1999, based on a skeleton with its dental plates remains a reliable taxon. But its relation with any other extinct or extant taxa remains purely speculative.

## Family Brachyrhizodontidae HERMAN & VAN WAES, 2012

This Family regroups the three extinct Genera: Genus *Brachyrhyzodus* ROMER, 1842, Genus *Apocopodon* COPE, 1885 and Genus *Igdabatis* CAPPETTA, 1986.

The Genus *Garabatis* CAPPETTA, 1986 from Campanian and Maastrichtian Ages from western Africa\*, Asia and Europe may be added to this list.

\*Thanks to J.-P. Prian (B.R.G.M.), the senior-author had the possibility to examine diverse specimens collected in prospective borings in Senegal in July 1983.

All the representatives of these four Genera are in possession of teeth presenting the first attempts to the formation of a poplyaulacorhyzid root structure.

The three Genera *Brachyrhyzodus*, *Apocopodon* and *Igdabatis* were previously included in the Family Myliobatidae\* BONAPARTE, 1838. \*See Cappetta 2006: pp.: 410-411 and Cappetta 2012: pp.: 447-449.

For references: See Bibliography-Systematics: Cappetta 1986, Cope 1885 and Romer 1842.

## Family Myliobatidae BONAPARTE, 1838 rev.

This Family regrouped *fide* Cappetta (2006: pp.: 410-411), the twenty following Genera: the five extant ones: Genus *Myliobatis* CUVIER, 1816, Genus *Aetobatus* de BLAINVILLE, 1816, Genus *Stoassodon*\* CANTOR, 1849, Genus *Aetomylaeus* GARMAN, 1908 and Genus *Pteromylaeus* GARMAN, 1913; and the five-teen extinct: Genus *Brachyrhyzodus* ROMER, 1842, Genus *Goniobatis*\* AGASSIZ, 1858, Genus *Apocopodon* COPE, 1885, Genus *Mesobatis*\*\* LEIDY, 1877, Genus *Promyliobatis*\*\* JAEKEL, 1894, Genus *Palaeomyliobatis*\*\* SILVA SANTOS & TRAVASSOS, 1960, Genus *Rhizochlatrus*\*\* SILVA SANTOS & TRAVASSOS, 1960, Genus *Rhizochlatrus*\*\* SILVA SANTOS & TRAVASSOS, 1960, Genus *Robert*, 1986, Genus *Lophobatis* CAPPETTA, 1986, Genus *Pseudoaetobatus* CAPPETTA, 1986, Genus *Eomobula* HERMAN, HOVESTADT-EULER & HOVESTADT, 1989, Genus *Garabatis* CAPPETTA, 1993, Genus *Aktaua* CASE, UDOVITCH, NESSOV, AVERIANOV & BORODIN, 1996 and the Genus *Weissobatis*\*\*\* HOVESTADT-EULER & HOVESTADT, 1999.

\*Stoassodon CANTOR, 1849 and Goniobatis AGASSIZ, 1858 are junior synonyms of Aetobatus de BLAINVILLE, 1816. \*\*Mesobatis LEIDY, 1877, Promyliobatis JAEKEL, 1894, Palaeomyliobatis SILVA SANTOS & TRAVASSOS, 1960, Rhizochlatrus SILVA SANTOS & TRAVASSOS, 1960 are junior synonyms of Myliobatis CUVIER, 1816, \*\*\*Weissobatis HOVESTADT-EULER & HOVESTADT, 1999 is based on a skeleton.

## Family Rhinopteridae JORDAN & EVERMANN, 1896

This Family regroups the three Genera: The extant Genus *Rhinoptera* CUVIER, 1829 and the two nominal extinct Genera: Genus *Zygobates* AGASSIZ, 1843 and Genus *Zygzabatis* MENDIOLA, 1895, both considered by Cappetta (2006: p.: 392) as synonyms of the Genus *Rhinoptera*.

The Genus *Rhinoptera* is represented by numerous extinct representatives. The oldest ones are of Paleocene Age; the more recent ones are of Holocene Age.

They have progressively colonised the central part of Western Europe, North and South Africa, the Near East and North and South Africa.

For references: See Bibliography-Systematics: Capetta 2012: p.: 454, Cuvier 1829 and Jordan & Evermann 1896.

## Family Rhombodontidae CAPPETTA, 1987

This extinct Family regroups the two extinct Genera: Genus *Rhombodus* DAMES, 1881 and Genus *Pucabatis* CAPPETTA, 1975.

Considering the morphology of the dental crown of its teeth, the extinct mono-specific Genus *Pucabatis* is presently separated from this Family and integrated in the Family Ptychotrygonidae HERMAN & VAN WAES, 2012, in which it is considered as an Upper Cretaceous link between the Middle and Upper Cretaceous Genus *Ptychotrygon* JAEKEL, 1894 and the extant mono-specific Genus *Rhina* BLOCH & SCHNEIDER, 1801.

#### For references: See Bibliography-Systematics: Cappetta 1975, Cappetta 1987, Cappetta 2012: pp.: 454-455, Dames 1881 and Jaekel 1894.

# **18.** Chondrichthyes' constant trials for domination of the Seas

## Generalities

Since their Devonian apparition, all the lineages, presently known, of the Chondrichthyes seem to have made the same continuous attempt to rise to the top of the marine vertebrates' ecological pyramid, which means a continuous increase of size and weight. It also required an increase of their predation capacities and of the efficacy of their single predation tools: their teeth.

Their teeth being constituted by a crown and a root, both these elements seem to have contributed to their success.

The various trials to ameliorate simultaneously the vascularisation and the innervation of their root were indeed efficient, but, when associated with a significant elongation\* of their root lobes, the fragility of their root drastically increased.

\*Indispensable to maintain the gravity centre of such teeth in the gravity centrum of the trihedra formed by the extremities of these root lobes and the tip of the crown.

That was the case for diverse extinct Genera such as the Genus Synechodus and the Genus Scapanorhynchus.

The formations of a lot of vertical ripples (or striations) on the intern (lingual) face of the tooth crown were not sufficient to resolve this physical problem.

The perfect physical solution to this problem, consisting of the integration in the same vertical plane of the crown and its moderately extended root lobes, was realized by only two lineages: The extinct lineage of *Megaselachus megalodon*, and the more recent lineage, which is represented by the extant taxon: *Carcharodon carcharias*.

# **19.** Convergent Evolution and Parallel Evolution

These two phenomena illustrate the extraordinary capacity of all the forms of Life inhabiting or having inhabited the Biosphere to occupy a vacant place in the successive ecosystems as quickly as possible.

Among the Chondrichthyes, the sudden apparition of the Genera *Pseudocetorhinus* DUFFIN, 1998 and *Pseudodalatias* SYKES, 1971, are two astonishing examples.

## **19.1.** Convergent Evolution

## Genus Pseudocetorhinus DUFFIN, 1998

This Triassic Genus is only represented by its holotype: Pseudocetorhinus pickfordi DUFFIN, 1998

#### *Pseudocetorhinus pickfordi* DUFFIN, 1998 (Sometimes erroneously mentioned as *P. pickfordi* DUFFIN & HERMAN, 1998)

#### Comments

As pointed out by its inventor himself, the histology of the teeth of this species differs considerably from this of *Cetorhinus parvus* LERICHE, 1912 and *Cetorhinus maximus* GUNNERUS, 1766, the two Cenozoic representatives of filtering Neoselachii.

The variation of the morphology of the teeth of this taxon corresponds perfectly with this of other small Triassic Hybodontiformes, such as the porosity of their root, which presents a primary anaulacorhyzid structure.

The base of the perfectly smooth dental crown of *C. parvus* overhangs the base of its dental root. The base of the dental crown of *Pseudocetorhinus pickfordi* is not smooth but presents some discrete *costulae* at the anterior extremity of its crown and its crown does not overhang the top of the massive and spongy root.

Contrarily to the teeth of *Cetorhinus parvus* or *Cetorhinus maximus*, no tooth of *Pseudocetorhinus pickfordi* presents a median foramen.

The largest Oligocene teeth of *Cetorhinus parvus* have a maximal length of 2.5 millimetres; the smallest of *Pseudocetorhinus pickfordi* have a length of 5 millimetres, which is enormous for a supposed ancestor.

Another important detail: the crystallite microstructure of the teeth of *Pseudocetorhinus pickfordi* differs significantly from that of the teeth of the Oligocene *Cetorhinus parvus* and of these of *Cetorhinus maximus*, the Miocene to Holocene extant filter-feeder Cetorhinidae (Neoselachii).

The supposed gill racket elements of *Pseudocetorhinus pickfordi* could in fact be modified *branchiospinae* of diverse primitive fishes.

*Pseudocetorhinus pickfordi* could be a case of evolution having for principal signification the filling of the gap of filter-feeding Euselachii.

For references, see Bibliography-Systematics: Duffin 1988.

#### Genus Pseudodalatias SYKES, 1971

#### Pseudodalatias barnstonensis SYKES, 1971

#### Comments

Another good example of convergent evolution is presented by the teeth of *Pseudodalatias barnstonensis* SYKES, 1971.

The extreme dignathic heterodontism presented by the teeth of the jaws of this species is absolutely comparable with the dignathic heterodontism of the extant Genus *Dalatias* RAFINESQUE, 1810.

It is only the structure of the enamel of the dental crowns of these two Genera that enforces the idea that these two generic taxa are not phylogenetically related.

Teeth of these species are rare in the British Rhaetic deposits, but relatively common in the Belgian Rhaetic deposits of Habay-la-Vieille (Luxembourg Province, Belgium).

For references, see Bibliography-Systematics: Sykes 1971.

#### **19.2.** Parallel Evolution

An elongated rostrum possessing rostral teeth, enameled or not, is a biological characteristic that all the representatives of the three different Orders of Neoselachii have in common: the Order Pristiophoriformes, the Order Ganopristiformes and the Order Pristiformes.

All the representatives of the extinct Order Ganopristiformes and the oldest representatives of the Order Pristiophoriformes were surely competitive Neoselachii during the Upper Cretaceous.

At the end of the Createous Period, the extinction of the last populations of the Ganopristiformes has favoured the smaller and more efficient predators, which were the primitive Pristiophoriformes.

The oldest representatives of the Order Pristiformes are of Paleocene Age and seem to have quickly occupied the ecological nests occupied by the last huge, heavy and slow Ganospritiformes of the Upper Cretaceous.

# 20. Hot vents and Origin of Life

## 20.1. Traditional conception of the Origin of Life

The traditional conception of the origin of terrestrial life supposes that life appeared in the upper parts of the Oceans were life conditions were ideal: optimal concentration of oxygen, sun-warmth, maximum of luminosity, maximal concentration of planktonic forms of life and maximal density of benthic invertebrates.

All together, these environmental conditions allow suggesting a progressive colonisation of the brackish zones, followed by the penetration into sweet waters and by the conquest of all the parts of Pangea, the primitive and unique Continent.

## **20.2.** Discovery of the hot vents and their biodiversity

The discovery of the hot vents (1949) was followed by the progressive discovery of their chemical differences and their extraordinary biodiversity (1960 to 2013).

Data known in 2012 signalize the existence of five hot vents in the western Pacific Ocean, one in the eastern Pacific Ocean and five in the northern Atlantic Ocean, presenting similar animal communities.

Off the North West coasts of Canada and Alaska three other hot vents present similar animal communities. In the central Pacific: eight hot vents present similar animal communities and in the North-West and North-East Atlantic, between Spain and Canada, there exist two other hot vents\*, also presenting very similar animal communities.

\*Near the Mid-Atlantic Ridge, and relatively recently (after the Eocene) separated.

These interesting biological facts enforce the hypothesis of Wegener (1929) and the proposal suggesting that in the oldest Paleozoic time only one primordial Ocean existed, with a common faunal stock, surrounding one primitive Continent, Pangea.

All the geological and paleontological discoveries, anterior or posterior to this date, have contributed to demonstrate the validity of this hypothesis.

For references, see Bibliography: Hot vents.

## 20.3. New suggestion and additional reflections

#### 1. Suggestion of Dr. Wächtershäuser

The hot vents environments are so similar to the geochemical environments supposed to have existed at the beginning of the Evolution that they could be the real origin of marine and terrestrial life.

Admitting this hypothesis, proposed in 1990, by Dr. Günther Wächterhäuser (München, Germany), Evolution could be considered as a slow and continuous process aimed at improving the conditions of all the forms of life\* growing and proliferating around these hot vents.

\*These forms of life include primitive Bacteria to evolved Teleostei, such as diverse generic taxa of the Family Macrouridae.

Dr. Wächtershäuser suggested that: An early form of metabolism\* predated genetics.

\*By metabolism, Dr. Wächtershäuser means a cycle of chemical reactions that release energy in a form that can be reutilized and transformed by other processes.

## 2. Suggestion of the senior-author

Additionally, the senior-author suggests that, in case of an accidental return to similar extreme conditions, all the forms of life having preserved the capacity to resist against such external aggressions, would still have a possibility to survive. One of the best examples is the biodiversity of the extant fauna of the Movile Cave (Romania).

For references, see Bibliography: Extreme environments.

#### **3. Additonal reflections**

## Paleoenvironment of the oldest fossil assemblages

#### 1. Generality

The oldest known fossil faunas presenting a high degree of biodiversity are the one from Ediacara Hill of Ediacarian Age, in southern Australia and the one from the Burgess Shales of the Middle Cambrian Era of British Columbia, Canada.

#### 2. Ediacara Hill and similar discoveries

The Ediacarian Age is of Precambrian Age, of 590 to 505 million years ago, according the Harland-Cox-Llewellyn-Picton-Smith-Walters Chart.

Other localities have fossils similar to these of Ediacara and also attributable to the Ediacaran Era, such as some localised in Newfoundland, along the Atlantic Ocean side.

But in these localities the fossils were discovered in volcanic sediments and relatively similar to hydrothermal formations and many of them are presently reconsidered as Mycelium-like structures\*.

\*See Bibliography: Peterson, Waggoner & Hagadorn 2013 and Xiao & Laflamme 2008.

#### 3. The faunal assemblage of the Burgess Shales

The paleoenvironment in which this primitive complex faunal community lived, including representatives of all the principal Phylla of invertebrate animals, is generally interpreted as a shallow water environment.

This means that the oldest known Cambrian marine fauna were not inhabitants of hot, or hydrothermal vents and that these forms of life have evolved in favourable conditions and were not extremophile animals\*.

\*See Bibliography: Narbonne 2005 and Narbonne & Gegling 2003.

#### 4. Morphology and nature of the Cambrian sea bottoms

These sea bottoms being anterior to the formation of the Oceanic trenches, they must also be anterior to the major hot vents always localised on the intense fracturation lines separating the present continental Plates.

## **20.4.** Settlement of the continents and return to a marine environment

#### 1. Generalities

During the final phase of the Evolution, all the marine vegetal or animal Phyllae, originated from hot spots or not, were confronted with two major problems: the preservation of their hydration and the acquisition of a new system to inhale oxygen.

The preservation of a sufficient hydratation will be resolved by a significant induration of the teguments.

The Arthropoda will resolve the problem of the inhalation of oxygen by the formation of numerous tracheids and, later the Pisces will resolve this problem by the transformation of their natatorial bladder into lungs, allowing the disappearance of their branchiae.

The possibility for the conquest of the emerged parts of the Earth was also open for different animal groups, such as the Amphibia, the Reptilia, the Aves and the Mammalia.

The fact that the majority of the mammal groups return so quickly\* to the sea remains difficult to explain without extern causes.

\*Geologically speaking, approximately sixty million years ago.

#### 2. A comeback to the marine environment

The Aves are the sole Class which will never return to a marine environment, but nearly all the diverse Classes of Reptilia and Mammalia will.

This strange and rapid comeback to marine waters is unexplainable without strong biological extern aggressions and remains a testimony of the extraordinary power of the influences of astrophysical Events on living forms.

Among the Mammalia, the Sirenia, the Pinipedia, the Odontoceta and the Mysticeta were the best illustrations of this phenomenon.

## **Data concerning the Mammalia**

#### First fossil records of Sirenia

The Sirenia, placental mammals, are the only extant marine mammals, exclusively herbivorous and without terrestrial representatives.

As far as known, their oldest fossils date from the early Eocene and the Sirenia are represented by some survivors regrouped in two monogeneric Families, the indo-Pacific Family Dugongidae and the Atlantic Family Trichechidae.

They were relatively diversified during the Oligocene and the Miocene Periods, but have declined since the end of the Miocene Periods. This progressive decline is a result of unfavourable combinations of climatic and oceanographic changes and finally of human\* activities.

\*Georg Wilhem Steller observed in the Sea of Behring the last living individuals of *Hydrodamalis gigas* (ZIMMERMANN, 1780) in the winter 1741-1742.

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#### First fossil records of Pinnipedia

The recent discovery of a femur of a primitive seal\* in a conglomeratic coastal deltaic level of northern Germany allows considering that the first Pinnipedia appeared in Europe during the Paleocene Period.

\*See: Diedrich 2011.

The discovery of this fragment of femur allows reconsidering the problem of the geographical appearance of the Pinnipedia, generally supposed localizable on the Eocene coastline of North America, and allows supposing that they originated along the subtropical to tropical coasts of central Europe.

This Publication did not explain how these tropical populations crossed the North Atlantic at this Period.

The abundance of teeth of large Elasmobranchii's predators of different lineages corresponding with the appearance of seals provides an argument that these Phocidae were already inhabitants of marine coastal environments.

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#### First fossil records of Odontaceta and Mysticeta

Recent evidence suggests that a gradual transition of early cetaceans from land to sea occurred in the early Eocene.

The Mysticeta seem to have diverged from the Odontoceta at the end of the Eocene Period and rapidly diversified during the Oligocene Period. The Odontoceta seem to have very rapidly diversified a little later.

During the Middle Miocene the still extant Families: Family Platanistidae, Family Physeteridae and Family Ziphiidae became distinct groups.

The appearance of the three extant Families: Family Monodontidae, Family Phocoenidae and Family Delphinidae occurred during the upper Miocene.

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#### Ancestors of the Cetacea

The Cetacea regroup the Archaeoceta, the Odontoceta and the Mysticeta. The Archaeoceta were in possession of teeth showing a similar differentiation as these of most extant land mammals. Their oldest remains were discovered in the earlier Eocene.

By the late Eocene, Archaeoceta whales had spread to many parts of the world. E.g.: *Basilosaurus* has also been found in Eocene rocks of Australia and Egypt.

The two modern lineages emerged from archaeocetan ancestors at the late Eocene.

Fossil remains of the majority of the extant Families of both Odontoceta and Mysticeta are commonly encountered since the late Miocene.

Adults Mysticeta completely lack teeth, although these are present in their embryos.

#### Discovery of a common ancestor of the Sirenia and the Cetacea

The most recent theory of the origins of the Hippopotamidae suggests that hippopotamids and Cetacea have a common semi-aquatic ancestor that branched off from other artiodactyls around 60 million years ago. This theory is based on the spectacular discovery of a nearly complete skeleton of *Pezosiren portelli*, from the lagoon deposits at Seven Rivers Jamaica by Dr. Domming in 2001.

The Seven Rivers' site is the oldest Western Indian site discovered so far, dating from late Early or early Middle Eocene.

This Formation was attributed to the late Early or early Middle Eocene by Dr. Robinson in 1988.

The other fossils discovered in the same locality were remains of aquatic vertebrates, fishes, crocodilians, turtles and one rhinocerotid species.

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### Last remarks

Sixty million years ago, the width of the North Atlantic is estimated to have been three fourths of its present width. The Archaeoceta were, presumably, able to cross such a distance but the Sirenia and the Pinnipedia were not.

The Pinnipedia had one possibility: to migrate along the North American coasts to join the European ones and later, the African coasts and the Antarctic coasts.

The sole logical phyletic possibility is that the Sirenia had an older ancestor than the earlier Eocene Jamaican Genus *Pezosiren* DOMMING, 2001, which means one lower or upper Paleocene ancestor still unknown.

As a paleontologist, the senior-author points out three principal phases in the evolution of the marine mammals. -Their sudden appearance, momentarily, supposed to have occurred during the earlier Eocene Period.

-The sudden appearance of the Mysticeta, estimated to have occurred during the later Eocene, simultaneously with the appearance of the chondrichthyan filter-feeding Family Cetorhinidae.

-The sudden diversification of the Odontoceta is estimated to have occurred during the earlier Miocene Period.

## Data concerning the Reptilia

The same observations are valid for three different lineages of Reptilia: The Plesiosauria, the Ichthyosauria and the Mosasauria. After a short period of continental evolution, dispersal and diversification, their ancestors turned suddenly back to marine environments. Being carnivorous, their sudden comeback to the seas, gave other Reptilia enormous feeding possibilities.

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# **21. Implications of the evolution of the Oceans and the Plate Tectonics**

## 1. Geographical definition of the extant Atlantic Ocean

The Atlantic Ocean is the second largest ocean of the Earth. Its waters cover a total area of more than 106 million square kilometres, which represents approximately 20 percent of the Earth's surface. This present surface is estimated to be 15 % to 20% more important than in extreme Glacial Periods.

The common designation *Atlantic Ocean* includes a lot of dependent Seas and Gulfs, such as the North Sea, the Mediterranean Sea, the Black Sea, the Irish Sea, the Labrador Sea, the Hudson Sea, the Gulf of Mexico and the Gulf of Gascogne.

## 2. Formation of the North Atlantic Ocean

During the middle part of the Jurassic Period\*, the Primitive Continent, called *Pangea*, was constituted by two principal entities: a northern one, called *Laurasia* and a southern one, called *Gondwana*.

\*According to Bless & Fernandez- Narvaiza, estimated at 152 to 148 million years ago.

Approximately along the present equatorial line, *Pangea* and *Gondwana* were separated by a very large and shallow Sea, called *Tethys*.

The *Tethys Sea* was prolonged in the eastern direction by a primitive Mediterranean Sea and the Indo-Pacific Ocean.

At the end of the Jurassic Period, the *Laurasia* began to be fractured into two parts: the North American Plate and the Eurasian Plate.

During the Middle Cretaceous\*, these two continental masses were separated by successive oceanic fractures of thousands of metres of depth.

\*Between 133 and 136 million years ago.

This means that, in the northern hemisphere, all the benthic populations of invertebrates or vertebrates were, as well as the continental ones, definitely isolated.

As long as South America and South Africa formed a single continental mass, all the benthic shallow water Chondrichthyes had the possibility to access the North American and North European coasts.

The constant eastern connection of the *Tethys* with the Indo-Pacific Oceans offered them another possibility, the colonization of more eastern coastal environments.

This eastern progression remained possible for them till the submersion of all the emerged areas of the eastern Pacific.

The junction of North America and South America, via Central America, is dated\* from the middle or the end of the Neogene Period.

\*According to the references' sources.

Principal reference(s): see Bibliography - Philosophy: Bless & Fernandez-Narvaiza 2000.

## **3.** Formation of the South Atlantic Ocean

During the upper part of the Cretaceous Period, the oceanic distance separating the western and eastern parts of *Gondwana* increased progressively forming the present South Atlantic Ocean.

Its western part constituted the original South American sub-Continent and its eastern part the African Continent.

## 4. Implications for the paleodistribution of all the benthic Chondrichthyes

At the end of the Jurassic Period, *Laurasia* began to be fractured into two parts: the North American Plate and the Eurasian Plate.

Before this Period, some taxa of diverse Orders having their ancestors in central Europe or in the Near-East had the possibility to colonize some parts of North America.

Since the end of the Jurassic Period, all the marine benthic populations of invertebrates or vertebrates, as well as the continental ones, were definitely isolated in the northern hemisphere.

But, the eastern connection with the Indo-Pacific Oceans offered them the possibility to occupy more eastern coastal environments and this remained possible for them till the submersion of all the emerged areas of the eastern Pacific.

## 5. Summary of the History of the formation of the Indo-Pacific Oceans

The History of these two Oceans is characterized by the continuous decrease of their surface. The Earth having presented a nearly constant\* volume and surface, the larger the Atlantic Ocean became, the more reduced these two ones were.

\*The volume of the Earth increases imperceptibly but continuously by absorption of sidereal ashes and meteorites.

## 6. Data concerning the Arctic Ocean

This Ocean, such as the Arctic Continent, remains the least known. Recent oceanographic expeditions have demonstrated that its circum currents associated with the northern circum polar currents are the most significant for the slow modifications of all the other oceanic currents.

An interglacial phase, dated of *circa* 15.000 BP\*, has provoked a temporary connection with the extremity of the southern part of the southern American Continent\*\*.

\*BP means: Before Present or before 1952, an International archaeologist and quaternarist Convention accepted in 1952. \*\*This terrestrial connection figures on the Piri'Reys maps of the beginning of the sixteenth century, copies based on documents of unknown age preserved in the small Library of Alexandria.

## 7. Impact of the Plate Tectonics on benthic coastal fauna

The Great Pacific Barrier is a good example to illustrate this impact. Some twenty-four million years ago, the Australian Plate began to glide under the eastern Pacific Plate. This tectonic event induced the formation of an abrupt vertical cliff on the eastern side but preserved the normal progressive increase of depth on the western side, which had been formed by the successive Glacial and Interglacial Periods.

This western topography gave a possibility to all the coastal benthic faunas to change their living zones during all the climatic changes without problems.

But the coastal benthic faunas inhabiting the eastern side were, by lack of glacial platforms, unable to follow these successive changes of water levels and they were definitely separated from their sister populations of the western side.

# 22. List and pagination of the new taxa and taxa revised (proposed in *Géominpal Belgica* 6)

## **New Super Orders**

Super Order Pristiophoromorphii nov.: p.: 134 Super Order Hybodontomorphii nov.: p.: 160 Super Order Hemiscylliomorphii nov.: p.: 172 Super Order Anacoracomorphii nov.: p.: 184 Super Order Isuromorphii nov.: p.: 186 Super Order Odontaspididomorphii nov.: p.: 192 Super Order Lamnomorphii nov.: p.: 194 Super Order Scapanorhynchomorphii nov.: p.: 196 Super Order Ganopristomorphii nov.: p.: 198

#### **New Orders**

Order Acrodontiformes nov.: p.: 160 Order Heptranchiformes nov.: p.: 170 Order Hemiscylliiformes nov.: p.: 173 Order Stegostomiformes nov.: p.: 175 Order Triakiformes nov.: p.: 179 Order Dasyatiformes nov.: p.: 211 Order Pristiformes nov.: p.: 219

#### **New Families**

Family Phorcynidae nov.: p.: 114 Family Pseudoechinorhinidae nov.: p.: 167 Family Orthechinorhinidae nov.: p.: 167 Family Pastinachidae nov.: p.: 214

## Taxa revised

Order Ptychodontiformes rev.: p.: 161 Order Orectolobiformes rev.:172 Family Odontaspididae rev.: p.: 192 Family Mitsukurinidae rev.: p.: 193 Family Lamnidae rev.: p.: 194 Super Order Carcharhinomorphii rev.: p.: 195 Order Ptychotrygoniformes rev.: p.: 196 Order Rhinobatiformes rev.: p.: 206 Family Rhinobatidae rev.: p.: 207 Family Myliobatidae rev.: p.: 221

## Taxa suppressed

Family Anotodontidae: p.: 186 Family Parodontidae: p.: 186

## Suggestions of new research orientation

## Attempt of virtual reconstitution of the transformation of one odontological morphotype into another one

Such researches will allow specifying the tempo of the morphological evolution of the teeth of all the Chondrichthyes, and ipso-facto the morphological evolution of their owners.

Once this tempo is known, paleontologists could point out when new morphotypes appeared and whether some transitional morphotypes have already been discovered in some strata.

## Intensification of the study of the development of the embryos extra or intra-uterus

Such studies will increase the knowledge concerning the development of the skeleton of all the extant specific taxa, and also the knowledge concerning the dental ontogeny of the Chondrichthyes and they will help to reconstitute their phylogenetic relationships.

## Social hierarchy in some populations of Chondrichthyes

Except for the numerous cases of group attacks of diverse taxa of the Genera *Isistius* GILL, 1865, *Carcharhinus* de BLAINVILLE, 1816 and *Sphyrna* RAFINESQUE, 1810, nothing allows supposing the existence of intentional group-movements in communities of Chondrichthyes.

Groups of *Isistius plutodus* GARRICK & SPRINGER, 1964 are able to kill adult individuals of huge Odontoceta such as *Orcinus orca* (LINNAEUS, 1758), but their attacks never seem to be coordinated by a leader.

This is also the case for the attacks of all the specific members of the two other Genera mentioned.

The sole indication of a territorial perception of the different extant species of the Genus *Heterodontus* de BLAINVILLE, 1816, is the fact that they systematically destroy the egg-capsules of other species laid on their territory

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## 24. Bibliography

## 24.1. Phylosophy, PlateTectonics and Radioactivity

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#### **Plate Tectonics**

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#### **24.7.** Locomotion of the marine vertebrates

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# **25. Plates**

### Motivation

These Plates are proposed as a response to the frequent questions concerning the meaning of the diverse odontological criteria utilized for the determination of the different systematic ranks of the Selachii and Batoidei proposed in the new Parasystematic published between 2010 and 2013.

These Plates are also proposed to illustrate the general morphology, the oology, the embryos, the neonates and the odontology of each generic taxon examined in this Publication.

The specific determination of all the specimens of extant taxa was assured by Dr. Mathias Stehmann (I.S. Hamburg, Germany. The authors are in possession of hundreds of additional SEM photographs which are available for all researchers revising extant taxa.



## Plate 1: Chondrichthyes: Odontology: Ilustration of some odontological criteria. 1.

**1a-1d**: Extern, radicular, occlusal and intern views of one lateral tooth of *Polyacrodus cloacinus* (QUENSTEDT, 1885). **2a-2d**: Extern, radicular, occlusal and intern views of one lateral tooth of *Squatina angeloides* VAN BENEDEN, 1873. **3a** and **3b**: Radicular and occlusal views of one central tooth of *Myliobatis dixoni* AGASSIZ, 1843. Photographs: Courtesy of Mr Pieter De Schutter (Aalst, Belgium). See comments.



## Plate 2: Chondrichthyes: Odontology: Ilustration of some odontological criteria. 2.

1a-1d: Occlusal, intern, radicular and extern views of a lateral tooth of *Nebrius thielensi* (WINKLER, 1874). 2a-2d: Lateral, extern, radicular and intern views of an anterior tooth of *Carcharodon carcharias* (LINNAEUS, 1758.
3a-3d: Occlusal, intern, radicular and extern views of a lateral tooth of *Rhombodus binkhorsti* DAMES, 1881. 4a-4b: Radicular and occlusal views of a lateral tooth of *Synechodus dubrisiensis* (MACKIE, 1863). Photographs 1a-3d: Courtesy of Mr Pieter De Schutter. Photographs 4a-4b: Courtesy of Mr Philippe Garot. See comments.



Plate 3: Living Neoselachii: Oology 1:

Order Scyliorhiniformes sensu HERMAN & VAN WAES, 2012: Family Scyliorhinidae GILL, 1862: 1: Genus Scyliorhinus de BLAINVILLE, 1816: Egg-capsules of Scyliorhinus cf. torazame (TANAKA, 1908). Order Heterodontifomes sensu HERMAN & VAN WAES, 2012: Family Heterodontidae GRAY, 1851: 2: Genus Heterodontus de BLAINVILLE, 1816: Egg-capsule of Heterodontus zebra (GRAY, 1831). Collection and photographs: Courtesy of Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments.



Plate 4: Living Chondrichthyes: Oology 2:

Super Ord. Heterodontomorphii: Genus Heterodontus de BLAINVILLE, 1816:
1: Lateral view of an egg-capsule of Heterodontus francisci (GIRARD, 1855).
2: Lateral view of a damaged egg-capsule of Heterodontus zebra (GRAY, 1831).
Super Ord. Scyliorhinomorphii: Genus Cephaloscyllium GILL, 1862:
3a - 3b: Lateral views of an egg-capsule of Cephaloscyllium laticeps (DUMERIL, 1853).
Collection and photographs Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments.



Plate 5: Living Chondrichthyes: Oology 3:
1: Egg-capsule of Scyliorhinus stellaris (LINNAEUS, 1758).
2: Egg-capsule of Scyliorhinus canicula (LINNAEUS, 1758).
3: Egg-capsule of Cephaloscyllium umbratile JORDAN & FOWLER, 1903.
4a-4b: Egg-capsule of Parascyllium variolatum (DUMERIL, 1853).
Collection and photographs Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments.



Plate 6: Living Chondrichthyes: Oology 4: Egg-capsules of diverse species.
1a-1b: Pseudoginglymostoma brevicaudatum (BONNATERRE, 1788).
2: Hemiscyllium trispeculare RICHARDSON, 1843. 3: Parascyllium variolatum (DUMERIL, 1853).
4a-4b: Hemiscyllium trispeculare RICHARDSON, 1843.
5: Schroederichthys bivius (MÜLLER & HENLE, 1838). 6: Cephaloscyllium umbratile (DUMERIL, 1853).
7: Cephaloscyllium laticeps (DUMERIL, 1853).
Photographs: Courtesy of Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments.



Plate 7: Eggs and juvenile of living Neoselachii
Super Order Scyliorhinomorphii HERMAN & VAN WAES, 2012:
1a-1b: Egg-capsule and neonate of *Cephaloscyllium umbratile* JORDAN & FOWLER, 1903.
2: Egg-capsules of *Scyliorhinus torazame* TANAKA, 1908.
3: Egg-capsules of *Scyliorhinus tokubee* SHIRAI, HAGIWARA & NAKAYA, 1992.
Photographs: Courtesy of Mr Chris Avila (Pisciculturist, Toronto, Canada).
See comments.



Plate 8: Living Chondrichthyes: Oology - Embryology: Order Hemiscylliiformes: Family Hemiscylliidae GILL, 1862: Genus Hemiscyllium MÜLLER & HENLE, 1838: 1 to 3: An egg-capsule and its embryo of Hemiscyllium trispeculare RICHARDSON, 1843 at two successive stages of growth. Collection and photographs: Courtesy of Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments.



Plate 9: Living Chondrichthyes: Morphology: Super Order Chlamydoselachomorphii nov.: Order Chlamydoselachiformes:

Family Chlamydoselachidae GARMAN, 1884: Genus Chlamydoselachus GARMAN, 1884:
Chlamydoselachus anguineus GARMAN, 1884: Male of 159 centimetres (t. l.), North-East Atlantic.
1a: Dorsal view of the complete individual, after two months in formaldehyde at 10%.
1b: Lateral view of the head of the same specimen.

Collection I.R.S.N.B., Brussels, Belgium. Photographs Jacques Herman. See comments.



Plate 10: Living Chondrichthyes: Morphology: Super Order Chlamydoselachomorphii nov.: Order Chlamydoselachiformes: Family Chlamydoselachidae GARMAN, 1884: Genus Chlamydoselachus GARMAN, 1884: Chlamydoselachus anguineus GARMAN, 1884: Female of 155 centimetres (t. l.), North-East Atlantic. 1a: Lateral view of the left side of its head. 1b: Ventral view of the anterior part of its body.

Collection I.R.S.N.B., Brussels, Belgium. Photographs Jacques Herman. See comments.



### Plate 11: Living Chondrichthyes: Odontology:

Super Order Chlamydoselachomorphii nov.: Order Chlamydoselachiformes:
Family Chlamydoselachidae GARMAN, 1884: Genus Chlamydoselachus GARMAN, 1884:
1a-1b: Upper and extern views of an anterior functional tooth. Linear magnification: x 5.
2a-2b: Upper and extern views of an anterior non-functional tooth. Linear magnification: x 5.
3a-3b: Upper and extern views of an anterior tooth in formation. Linear magnification: x 5.
SEM photographs Mr. Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 12: Living Chondrichthyes: Odontology:

Order Chlamydoselachiformes HERMAN & VAN WAES, 2012: Family Chlamydoselachidae GARMAN, 1884:
 Genus Chlamydoselachus GARMAN, 1884: Chlamydoselachus anguineus GARMAN, 1884:
 1a-1b: Intern and radicular views of an anterior functional tooth. Linear magnification: x 5.
 2a-2b: Intern and radicular views of an anterior non-functional tooth. Linear magnification: x 5.
 3a-3b: Intern and radicular views of an anterior tooth in formation. Linear magnification: x 5.
 SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 13: Living Chondrichthyes: Dermal denticles: Super Order Chlamydoselachomorphii nov.: Order Chlamydoselachiformes: Genus Chlamydoselachus GARMAN, 1884: Chlamydoselachus anguineus GARMAN, 1884:
1a to 1c: Lateral left, basal and upper views of a dermal denticle, near the lower left commissure: x 20.
2a to 2c: Lateral left, basal and upper views of a dermal denticle of the top of the head: x 10.
3a to 3c: Lateral left, basal and upper views of a dermal denticle of the side of the head: x 10.
SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 14: Living Chondrichthyes: Odontology: Super Order Echinorhinomorphii HERMAN & VAN WAES, 2012: Order Echinorhiniformes HERMAN & VAN WAES, 2012: Family Echinorhinidae GILL, 1862: Genus Echinorhinus de BLAINVILLE, 1816: Echinorhinus brucus (BONNATERRE, 1788): Female of 182 cm (t.l.). Indonesia. 1a: Lateral view of the right lower jaw. 1b: Lateral view of the right upper jaw. 1c: Detail of the lower symphyseal zone. Collection and Photographs Mr Dirk Hovestadt and Mrs Maria Hovestadt-Euler. See comments.



 

 Plate 15: Living Chondrichthyes: Odontology: Super Order Echinorhinomorphii HERMAN & VAN WAES, 2012:

 Order Echinorhiniformes HERMAN & VAN WAES, 2012: Family Echinorhinidae GILL, 1862: Genus Echinorhinus de BLAINVILLE, 1816: Echinorhinus brucus (BONNATERRE, 1788): Female 240 centimetres (t.l.). North Sea (1852). Linear magnification: x 8.

 1: Intern views of upper teeth. 2-3: Intern views of lower teeth. 4-5: Upper view of two dermal denticles. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 16: Living Chondrichthyes: Odontology:

Super Order Echinorhinomorphii HERMAN & VAN WAES, 2012: Order Echinorhiniformes HERMAN & VAN WAES, 2012: Family Echinorhinidae GILL, 1862: Genus Echinorhinus de BLAINVILLE, 1816: Echinorhinus cookei PIETSCHMANN, 1928: Female of 225 centimetres (t.l.). Indonesia.

1 to 3: Intern and extern views of lower teeth. 4-5: Intern and extern views of upper teeth. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 17: Living Chondrichthyes: Odontology: Super Order Heterodontomorphii HERMAN & VAN WAES, 2012: Order Heterodontiformes BERG, 1940: Family Heterodontidae GRAY, 1851: Genus Heterodontus de BLAINVILLE, 1816: Heterodontus portusjacksoni MEYER, 1793: Female. Australia: Port Jackson. No other data. Real size: 14.5 centimetres (t.l). 1: Original labelling. 2: View of the upper jaw. 3: View of the lower jaw. 4: Basal view of the skull. Collection I.R.S.N.B., Brussels, Belgium. Photographs Jacques Herman. See comments.



Plate 18: Living Chondrichthyes: Odontology:

Order Hemiscylliiformes nov. and Order Pristiophoriformes BERG, 1958 Comparison between the dentitions of the three *Genera Hemiscylliium* MÜLLER & HENLE, 1837, *Chiloscyllium* MÜLLER & HENLE, 1837 and *Pristiophorus* MÜLLER & HENLE, 1837. Read *C. punctatum* and *H. ocellatum* instead of: *C. punctatus* and *H. ocellata*. See comments. Collection and Photographs:

Courtesy of Mr Dirk Hovestadt and Mrs Maria Hovestadt-Euler (Terneuzen, the Netherlands).



Plate 19:Living Chondrichthyes: Morphology: Super Order Squatinomorphii rev.: Order Squatiniformes de BUEN, 1926: Family Squatinidae BONAPARTE, 1838: Genus Squatina DUMERIL, 1806: 1: Squatina japonica BLEEKER, 1858. Source: www.fr.wikipedia.org 2a and 2b: Squatina africana REGAN, 1908. See comments. 2: Photographs Courtesy Mr Frederik Mollen, Elasmobranch Research Belgium (E.R.B.).


Plate 20: Living Chondrichthyes: Odontology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Squatinidae BONAPARTE, 1838: Genus Squatina DUMERIL, 1806: Squatina Squatina (LINNAEUS, 1758): lower teeth of a male of 85 centimetres (t.l.) Origin: North Sea. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. Linear magnification: x4. See comments.



Plate 21: Living Chondrichthyes: Odontology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Squatinidae BONAPARTE, 1838: Genus Squatina DUMERIL, 1806: Squatina Squatina (LINNAEUS, 1758): upper teeth of a male of 85 centimetres (t.l.) Origin: North Sea. a: Anterior tooth. l: Lateral tooth. p: Posterior tooth. Linear magnification: x4. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 22: Living Chondrichthyes: Morphology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1896: Genus Orectolobus BONAPARTE, 1834: 1: Orectolobus maculatus: Source: www.commons.wikimedia.org 2: Orectolobus japonicus: Source: www.nl.wikipedia.org 3: Orectolobus maculatus: Source: www.commons.wikimedia.org See comments.



Plate 23: Living Chondrichthyes: Odontology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1896: Genus Orectolobus BONAPARTE, 1834: Orectolobus maculatus (BONNATERRE, 1788): Female of 74 centimetres (t.l.). Southern Australia. a: Anterior tooth. la: Latero-anterior tooth. lp: Latero-posterior tooth. Linear magnification: x4. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 24: Living Chondrichthyes: Odontology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1896: Genus Orectolobus BONAPARTE, 1834: Orectolobus maculatus (BONNATERRE, 1788): Female of 74 centimetres (t.l.). Southern Australia. a: Anterior tooth. l: Lateral tooth. lp: Latero-posterior tooth. c: Commissural tooth. Linear magnification: x 8. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 25: Living Chondrichthyes: Morphology Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1898: Genus Sutorectus WHITLEY, 1939: Sutorectus tentaculatus PETERS, 1864: 1a-1b: male of 73 centimetres (t. l.). Origin: Australia. 2a-2b: female of 14 centimetres (t. l.). Origin: Australia. Photographs Jacques Herman. See comments.



## Plate 26: Living Chondrichthyes: Odontology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1898: Genus Sutorectus WHITLEY, 1939: Sutorectus tentaculatus PETERS, 1864: Male of 73 centimetres (t. l.). Origin: Australia. a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x 8. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 27: Living Chondrichthyes: Odontology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1892: Genus Sutorectus WHITLEY, 1939: Sutorectus tentaculatus PETERS, 1864: Male of 73 centimetres (t.l.). Origin: Australia. a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x 8. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.











Plate 28: Living Chondrichthyes: Morphology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1896: Genus Eucrossorhinus: REGAN, 1908: Eucrossorhinus dasypogon (BLEEKER, 1887): Female of 87,5 centimetres (t.l.) Origin: Indonesia. 1: Dorsal view of this female. 1a: Frontal view of its head. 1b: View of the lower face of its head. Photographs Jacques Herman. See comments.

-296-



Plate 29: Living Chondrichthyes: Odontology: Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1896: Genus Eucrossorhinus REGAN, 1908: Eucrossorhinus dasypogon (BLEEKER, 1887): Female of 87,5 centimetres (t. l.). Indonesia. Intern and extern views of three upper and three lower teeth. a: Anterior tooth. l: Lateral tooth. c: Commissural tooth. Linear magnification: x8. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



## Plate 30: Living Chondrichthyes: Odontology:

Super Order Squatinomorphii rev.: Order Orectolobiformes rev.: Family Orectolobidae GILL, 1896: Genus Eucrossorhinus REGAN, 1908: Eucrossorhinus dasypogon (BLEEKER, 1887): Female of 87,5 centimetres (t. l.). Indonesia. a: Anterior tooth. l: Lateral tooth. c: Commissural tooth. Linear magnification: x8. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 31: Living Chondrichthyes: Morphology: Order Hemiscylliiformes nov.: 1: Family Hemiscylliidae GILL, 1862: Genus Chiloscyllium Müller & Henle, 1837: Chiloscyllium punctatum Müller & Henle, 1838. Source : www.nl.wikimedia.org See comments. Order Stegostomatiformes nov.: 2: Family Parascylliidae GILL, 1862: Genus Cirrhoscyllium SMITH & RADCLIFFE, 1913:

Cirrhoscyllium expolitum SMITH & RADCLIFFE, 1913. Source: www.en.wikipedia.org See comments.



Plate 32: Living Chondrichthyes: Morphology: Super Order Scyliorhinomorphii HERMAN & VAN WAES, 2012: Order Scyliorhiniformes *sensu* HERMAN & VAN WAES, 2012: Family Scyliorhinidae GILL, 1862: Genus *Cephaloscyllium* GILL, 1862: 1: Neonates of *Cephaloscyllium umbratile* JORDAN & FOWLER, 1903. 2: Neonate of the same species, two weeks later. Collection and photographs Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments.



Plate 33: Living Chondrichthyes: Morphology: 1: Family Hemiscylliidae GILL, 1862: Genus Chiloscyllium MÜLLER & HENLE, 1837: Chiloscyllium griseum MÜLLER & HENLE, 1838. Source : www.en.wikipedia.org 2-3:Family Parascylliidae GILL, 1862: 2: Heteroscyllium colcloughi (OGILBY, 1908). Source: www.nl.wikipedia.org 3: Parascyllium ferrugineum McCULLOCH, 1911. Source: www.commons.wikimedia.org

See comments.



Plate 34: Living Chondrichthyes: Morphology: Order Phorcyniformes nov.: Family Ginglymostomatidae GILL, 1862: Genus Ginglymostoma MÜLLER & HENLE, 1837: 1-2: Ginglymostoma cirratum (BONNATERRE, 1788): 1: Source: www.en.wikipedia.org 2: Source: www.ru.wikipedia.org See comments.



 Plate 35: Living Chondrichthyes: Odontology:

 Order Phorcyniformes nov.: Family Ginglymostomatidae GILL, 1862:

 Genus Ginglymostoma MÜLLER & HENLE, 1837: Ginglymostoma cirratum (BONNATERRE, 1788):

 Female of 232 centimetres (t.l.). Origin: Guinea-Bissau. 1983.

 1a: View of its right lower jaw. 1b: View of its lower symphyseal zone. 1c: View of its right upper jaw.

 Collection and Photographs Mr Frederik Mollen, Elasmobranch Research Belgium (E.R.B.).

 See comments.



## Plate 36: Living Chondrichthyes: Odontology:

Order Phorcyniformes nov.: Family Ginglymostomatidae GILL, 1862: Genus Ginglymostoma MÜLLER & HENLE, 1837: Ginglymostoma cirratum (BONNATERRE, 1788): Extern, radicular and intern views of some upper teeth of a female of 232 centimetres (t.l.). a: Anterior tooth. l: Lateral tooth. p: Posterior tooth. Linear magnification: x5. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 37: Living Chondrichthyes: Odontology:

lower teeth

Order Phorcyniformes nov.: Family Ginglymostomatidae GILL, 1862: Genus Ginglymostoma MÜLLER & HENLE, 1837: Ginglymostoma cirratum (BONNATERRE, 1788): Extern, radicular and intern views of some lower teeth of a female of 232 centimetres (t. l.). a: Anterior tooth. I: Lateral tooth. p: Posterior tooth. Linear magnification: x5. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 38: Living Chondrichthyes: Odontology:
Order Phorcyniformes nov.: Family Ginglymostomatidae GILL, 1862: Genus Nebrius RÜPPEL, 1837: Nebrius ferrugineus (LESSON, 1831): Diverse views of upper and lower teeth of two individuals from Indonesia.
a: Anterior tooth. I: Lateral tooth. p: Posterior tooth. Linear magnification: x2. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



1b



 Plate 39: Living Chondrichthyes: Morphology: Order Stegostomatiformes nov.:
 Family Stegostomatidae GILL, 1862: Genus Eostegostoma HERMAN, 1977: Eostegostoma fasciatum (MÜLLER & HENLE, 1837):
 1b: View of a lot of egg-capsules. Source: www.wikimedia.commons.org 1a: Oblique view of an adult individual. Source: www.en.wikipedia.org See comments.



Plate 40: Living Chondrichthyes: Odontology: Order Stegostomatiformes nov.: Family Stegostomatidae GILL, 1862: Genus *Eostegostoma* HERMAN, 1977: *Eostegostoma fasciatum* (MÜLLER & HENLE, 1837): Off the western coast of Ceylon. Intern, radicular and extern views of some superior teeth of a neonate of 28.5 centimetres (t.l.). a: Anterior tooth. l: Lateral tooth. c: Commissural tooth. Linear magnification: x4. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 41: Living Chondrichthyes: Odontology:

Order Stegostomatiformes nov.:

Family Stegostomatidae GILL, 1862: Genus Eostegostoma HERMAN, 1977: Eostegostoma fasciatum (MÜLLER & HENLE, 1837): Off the western coast of Ceylon.
Intern, radicular and extern views of some superior teeth of a neonate of 28.5 centimetres (t.l.).
a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x4. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 42: Living Chondrichthyes: Morphology: Order Stegostomatiformes nov.: 1: Family Stegostomatidae GILL, 1862: Genus Stegostoma GILL, 1862: Stegostoma fasciatum (HERMANN, 1783). Source: www.wikipedia.org See comments. Order Hemiscylliiformes nov.: 2: Family Hemiscylliidae GILL, 1862: Genus Chiloscyllium MÜLLER & HENLE, 1837: Chiloscyllium plagiosum (BENNET, 1830). Source: www.wikipedia.org See comments.



Plate 43: Living Chondrichthyes: Odontology: Order Hemiscylliiformes nov.: Family Hemiscylliidae GILL, 1862: Genus *Chiloscyllium* MÜLLER & HENLE, 1837: *Chiloscyllium plagiosum* (BENNET, 1830): Jaws of a Female of 22 centimetres (t.l). Origin: Off Luzon (The Philippines).1a: Lower jaw. 1b: Upper jaw. Linear magnification: x25. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



 Plate 44: Living Chondrichthyes: Odontology Order Hemiscylliiformes nov.:
 Family Hemiscylliidae GILL, 1862: Genus Chiloscyllium MüLLER & HENLE, 1837: Chiloscyllium plagiosum (BENNET, 1830): Female of 22 centimetres (t.l).
 1-2: Intern and radicular views of lower teeth. 3-4: Radicular and intern views of upper teeth. a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x40. SEM photographs Mr. Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



## Plate 45: Living Chondrichthyes: Morphology

1 and 2: Order Hemiscylliiformes nov.: Family Hemiscylliidae GILL, 1862:
 1: Lateral view of a juvenile of Hemiscyllium trispeculare RICHARDSON, 1843.
 2: Dorsal view of a juvenile of Chiloscyllium hasseltii BLEEKER, 1852.
 3 and 4: Order Stegostomatiformes nov.: Family Parascylliidae GILL, 1862:
 3 and 4: Dorsal views of neonates of Parascyllium collare RAMSAY & OGILBY, 1888.
 Photographs: Courtesy of Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments.



Plate 46: Living Chondrichthyes: Morphology: Order Hemiscylliiformes nov.: Family Hemiscylliidae GILL, 1862: Genus Hemiscyllium GILL, 1862: Hemiscyllium ocellatum (BONNATERRE, 1788): Group of juvenile individuals. Collection and Photograph: Courtesy of Mr Kyle McPheeters (Toronto, Canada). See comments.



Plate 47: Living Chondrichthyes: Morphology: Order Hemiscylliiformes nov.: Family Hemiscylliidae GILL, 1862: Genus *Hemiscyllium* MÜLLER & HENLE, 1838: *Hemiscyllium ocellatum* (BONNNATERRE, 1788): 1: Source: <u>www.nl.wikimedia.commons</u> 2: Source: <u>www.es.wikipedia.org.</u>

See comments.



Plate 48: Living Chondrichthyes: Morphology: Order Hemiscylliiformes nov.: Family Hemiscylliidae GILL, 1862: 1: Neonate of *Hemiscyllium ocellatum* (BONNATERRE, 1788). 2: Other view of the same specimen. Photographs: Courtesy of Mr Chris Avila (Pisciculturist, Toronto, Canada). See comments. upper teeth 6a 6p **6**1 **5**p 51 5a 4p **4**a 41 3a **3**p 31 21 **2**p 2a la **1p** 11 lower teeth

Plate 49: Living Chondrichthyes: Odontology: Order Hemiscylliiformes nov.: Family Hemiscylliidae GILL, 1862: Genus Hemiscyllium GILL, 1862: Hemiscyllium ocellatum (BONNATERRE, 1788): Male of 60 centimetres (t.l.). Southern Papua. a: Anterior tooth. l: Lateral tooth. p: Posterior tooth. Linear magnification: x45. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 50: Living Chondrichthyes: Odontology:

Order: Hemiscylliiformes nov.: Family Parascylliidae GILL, 1862: Genus Cirrhoscyllium SMITH & RADCLIFFE, 1913: Cirrhoscyllium expolitum SMITH & RADCLIFFE, 1913: 2a-2b: Intern and extern views and 3a-3b: Extern and Intern views of two lower anterior teeth: L. m.: x50. Order Stegostomiformes nov.: Family Stegostomidae GILL, 1862: 1: Comme Stepostomics Mill & EP, & Henker, 1827: Stepostomia family 1783): Unper Journ

1: Genus Stegostoma: MÜLLER & HENLE, 1837: Stegostoma fasciatum (HERMANN, 1783): Upper Jaw: L. m.: x5. 1-3: SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 51: Living Chondrichthyes: Odontology: Order Stegostomiformes nov.: Family Parascylliidae GILL, 1862: Genus Parascyllium GILL, 1862: Parascyllium variolatum (DUMERIL, 1853): Female of 30 centimetres (t.l.) from Tasmania. a: Anterior tooth. l: Lateral tooth. p: Posterior tooth. Linear magnification: x35. SEM photographs Mr. Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 52: Living Chondrichthyes: Odontology: Order Stegostomiformes nov.: Family Parascylliidae GILL, 1862: Genus Parascyllium GILL, 1862: Parascyllium variolatum (DUMERIL, 1853): Female of 30 centimetres (t.l.) from Tasmania. a: Anterior tooth. l: Lateral tooth. p: Posterior tooth. Linear magnification: x35. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 53: Living Chondrichthyes: Morphology: Order Stegostomatiformes nov.: Family Rhincodontidae GARMAN, 1913: Genus Rhincodon SMITH, 1829: Rhincodon typus SMITH, 1828: 1: Lateral view of an adult female. Source: www.commons.wikimedia.org 2: Anterior view of the same female. Source: http://www.aquariumofpacific.org/ 3: Ventral view of an adult female. Source: http://www.flickr.com/photos/dkeats/6147234019/ See comments.



Plate 54: Living Chondrichthyes: Odontology

Order Stegostomiformes nov.: Family Rhincodontidae MÜLLER & HENLE, 1839: Genus Rhincodon SMITH, 1829: Rhincodon typus SMITH, 1829: Male of 520 centimetres (t.l.). Off Ceylon. 1a to 2c: Lower teeth. 3a-3c: Upper Teeth. Linear magnification: x5. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 55: Living Chondrichthyes: Morphology: Order Triakiformes nov.: Family Triakidae GILL, 1896: Genus *Pseudotriakis* BRITO-CAPELLO, 1868: *Pseudotriakis microdon* BRITO-CAPELLO, 1868:

1a: Lateral view of an adult specimen of a male of 225 centimetres (t.l.). Off Northern Ireland, North Atlantic.1b: Magnification of its head.

Collection and Photographs Mr Dirk Hovestadt and Mrs Maria Hovestadt-Euler (Terneuzen, The Netherlands). See comments.


Plate 56: Living Chondrichthyes: Odontology: Order Triakiformes nov.: Family Triakidae GILL, 1896: Genus Pseudotriakis BRITO-CAPELLO, 1868: Pseudotriakis microdon BRITO-CAPELLO, 1868: Male of 225 centimetres (t.l.) Off Northern Ireland, North Atlantic. 1a: Detail of its lower symphyseal dentition. 1b: Its jaws. 1c: Detail of its upper symphyseal dentition. Photographs: Courtesy of Mr Dirk Hovestadt and Mrs Maria Hovestadt-Euler (Terneuzen, The Netherlands). See comments.



 Plate 57: Living Chondrichthyes: Odontology: Order Triakiformes nov.: Family Triakidae GILL, 1896:
 Genus Pseudotriakis BRITO-CAPELLO, 1868: Pseudotriakis microdon BRITO-CAPELLO, 1868: Female of 265 centimetres (t.l.). Off Northern Ireland, North Atlantic.
 1a to 3c: Extern, radicular and intern views of three lower teeth. Linear magnification: x35.
 4a to 5c: Radicular and extern views of three upper teeth. Linear magnification: x35. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 58: Living Chondrichthyes: Morphology:

 Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958:
 Family Pristiophoridae BLEEKER, 1859: Genus Pristiophorus MÜLLER & HENLE, 1837 Pristiophorus cirratus (LATHAM, 1794): Male of 68 centimetres (t.l.):
 1a: Dorso-lateral view of an adult female. 1b: Dorsal view of its rostrum.

**1c** and **1d**: Left and right proximal parts of its rostrum. See comments.

Collection I.R.S.N.B., Brussels, Belgium. Courtesy of Mr Georges Lenglet. Photographs Jacques Herman.



# Plate 59: Living Chondrichthyes: Embryology:

Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958: Family Pristiophoridae BLEEKER, 1859: Genus Pristiophorus MÜLLER & HENLE, 1837: Dorsal and ventral views of one Embryo of Pristiophorus cirratus (LATHAM, 1794). Photograph: Courtesy of Mr Kelvin Aitken: "marinethemes.com/Kelvin Aitken" See comments.



## Plate 60: Living Chondrichthyes: Odontology:

 Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958:
 Family Pristiophoridae BLEEKER, 1859: Genus Pristiophorus MÜLLER & HENLE, 1837
 Pristiophorus cirratus (LATHAM, 1794): Male of 95 centimetres (t.l.). Victoria (Australia). Occlusal, radicular and extern views of three upper teeth.
 a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x5. SEM photographs Mr. Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



### Plate 61: Living Chondrichthyes: Odontology:

 Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958:
 Family Pristiophoridae BLEEKER, 1859: Genus Pristiophorus MÜLLER & HENLE, 1837:
 Pristiophorus cirratus (LATHAM, 1794): Male of 95 centimetres (t.l.). Victoria (Australia). Extern, radicular and occlusal views of three lower teeth.
 a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x5. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



# Plate 62: Living Chondrichthyes: Odontology:

Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958: Family Pristiophoridae BLEEKER, 1859: Genus Pristiophorus MÜLLER & HENLE, 1837
1-3: Rostral teeth of Pristiophorus cirratus (LATHAM, 1794): Male of 95 centimetres (t.l.). Victoria (Australia).
2a: Magnification of the basal side of 2. Linear magnification of 1 to 3: x20 and of 2a: x40. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



### Plate 63: Living Chondrichthyes: Odontology

 Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958: Family Pliotrematidae BLEEKER, 1859: Genus Pliotrema REGAN, 1906: Pliotrema warreni REGAN, 1906: Female of 130 centimetres (t.l.). Off Zululand. Occlusal, radicular and extern views of three upper teeth.
 a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x5. SEM photographs Julien Mr Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



### Plate 64: Living Chondrichthyes: Odontology Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958: Family Pliotrematidae BLEEKER, 1859: Genus Pliotrema REGAN, 1906: Pliotrema warreni REGAN, 1906: Female of 130 centimetres (t.l.). Off Zululand. Extern, radicular and occlusal views of three lower teeth. Linear magnification: x5. a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



# Plate 65: Living Chondrichthyes: Odontology

 Super Order Pristiophoromorphii nov.: Order Pristiophoriformes BERG, 1958: Family Pliotrematidae BLEEKER, 1859: Genus Pliotrema REGAN, 1906:
 1 to 3: Rostral teeth of Pliotrema warreni REGAN, 1906: Female of 130 centimetres (t.l.). Off Zululand. Linear magnification: x20. 3b: Magnification of the base of 3. Linear magnification: x40. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 66: Fossil Chondrichthyes: Odontology:

 Super Order Pristophoromorphii nov.: Order Pristophoriformes BERG, 1958: Family Pristophoridae BLEEKER, 1859: Genus *Propristiophorus* WOODWARD, 1932:
 *Propristiophorus tumidens* WOODWARD, 1932: Specimen collected by our late friend, Louis Dubertret, in Summer 1960, in a level of Santonian Age (Upper Cretaceous) at Sahel-Alma in northern Lebanon.
 1a: Lower symphyseal zone. 1b: Proximal part of its rostrum. 1c: Median part of its rostrum. See comments. Photographs realized by Mr Daniel Serette (M.N.H.N. - C.N.R.S., Paris, France).



 Plate 67: Living Chondrichthyes - Batoidei: Morphology: Super Order Rajomorphii HERMAN & VAN WAES, 2012: Order Dasyatiformes nov.: Family Pastinachidae nov.: Genus Pastinachus RÜPPEL, 1829:
 1: Pastinachus sephen (FORSSKAL, 1775): Dorsal view of a female of 38.5 centimetres (width of the disk), caught off Mahé Island. Collection M.N.H.N., Paris, France. Photograph Dirk Hovestadt.
 2: Dorsal view of a female of 76 centimetres (width of the disk). See Website: www.es.wikipedia.org. See comments.



Plate 68: Living Chondrichthyes - Batoidei: Odontology: Super Order Rajomorphii HERMAN & VAN WAES, 2012: Order Dasyatiformes nov.: Family Pastinachidae nov.: Genus *Pastinachus* RÜPPEL, 1829: *Pastinachus sephen* (FORSSKAL, 1775): 1a and 1b: Extern and intern views of the jaws of a female of 84 centimetres (width of the disk), from off India. Courtesy of Mr Frederik Mollen, Elasmobranch Research Belgium (E.R.B.). See comments. 1c: Extern and intern views of the upper tooth set of a juvenile specimen of New Zealand. Photographs Jacques Herman. See comments.



Plate 69: Living Chondrichthyes: Odontology

Super Order Rajomorphii HERMAN & VAN WAES, 2012: Order Dasyatiformes nov.: Family Pastinachidae nov.: Genus *Pastinachus* RÜPPEL, 1829: *Pastinachus sephen* (FORSSKAL, 1775): Intern and occlusal views of two lower teeth of female of 101 centimetres (width of the disk). a: Anterior tooth. c: Commissural tooth. Linear magnification: x30. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 70: Living Chondrichthyes: Odontology:

Super Order Rajomorphii HERMAN & VAN WAES, 2012: Order Dasyatiformes nov.: Family Pastinachidae nov.: Genus *Pastinachus* RÜPPEL, 1829: *Pastinachus sephen* (FORSSKAL, 1775): Male of 38.5 centimetres (width of the disk). Diverse views of three upper and three lower teeth. a: Anterior tooth. I: Lateral tooth. c: Commissural tooth. Linear magnification: x60. SEM photographs Mr Julien Cillis, I.R.S.N.B., Brussels, Belgium. See comments.



Plate 71: Fossil Chondrichthyes:Neoselachii: Osteology 1. Super Order Ganopristomorphii nov.: Order Ganopristiformes HERMAN & VAN WAES, 2012: Family Ganopristidae HERMAN, 1977: Genus Libanopristis CAPPETTA, 1980. Dorsal view of the partial skeleton remains of an adult individual of Libanopristis hiram (HAY, 1903). Origin: Cenomanian (Upper Cretaceous) of Hadjula (northern Lebanon). Specimen collected by Prof. Louis Dubertret. Collection and photograph Mr Michel Crochard. See comments.



Plate 72: Fossil Chondrichthyes: Neoselachii: Osteology 2. Super Order Ganopristomorphii nov.: Order Ganopristiformes HERMAN & VAN WAES, 2012: Family Ganopristidae HERMAN, 1977: Genus Libanopristis CAPPETTA, 1980. Dorsal view of the skull of an adult individual of Libanopristis hiram (HAY, 1903). Origin: Cenomanian (Upper Cretaceous) of Hadjula (northern Lebanon). Specimen collected by Prof. Louis Dubertret. Collection and Photograph Mr Michel Crochard. See comments.



Plate 73: Fossil Chondrichthyes: Neoselachii: Osteology 3. Super Order Ganopristomorphii nov.: Order Ganopristiformes HERMAN & VAN WAES, 2012: Family Ganopristidae HERMAN, 1977: Genus Libanopristis CAPPETTA, 1980. Magnification of the right pectoral fin of an adult individual of Libanopristis hiram (HAY, 1903). Origin: Cenomanian (Upper Cretaceous) of Hadjula (northern Lebanon). Specimen collected by Prof. Louis Dubertret. Collection and Photograph Mr Michel Crochard. See comments.

Таб.Ш. 19 a 19.Ъ milita B Фильг. Hybodus parvus Rog Ф.з-5 Hybodus Kessleri Rog Фель Hybodus subulatus Rog Фильг. Hybodus dispar Reuss. Флз. is a Hybodus bidentatus. Rog. Фл418. Hybodus marginatus Rog. Флэ-20 a. Hybodus helophorus Rog. Ф 21-21 b. Hybodus marginalis Ag. Ф2222a. Hybodus carcinatus Ag. Ф2324. Notidanus serratissimus Ag. Ф2526. Notidanus microdon Ag. Ф22 Corax Kaupii Ag. Ф26-28 Corax falcatus Ag. Ф30 Corax. obliquus Reuss.

Plate 74: Fossil Chondrichthyes: Reproduction of Plate 3 of the Publication of Rogovich 1860: ROGOVICH, A., S. 1860: About fossil fishes of the District of Kiev. Vol. I: pls.: 1 to 9. Photograph: Courtesy of Dr. Evgeny Popov (Saratov Oblast, Russia). See comments.



# Plate 75: Past and Present:

 On the BYRON, September 1977: The senior-author taking notes concerning the results of the last trawling. Northern Hebridean Sector, North Atlantic. Photograph Captain Pierre Gueguen (Lorient, Brittany, France).
 A juvenile individual of *Hemiscyllium ocellatum* (BONNATERRE, 1788) caught by an Australian eagle, during its attempt to move from one intertidal water area to another one. Photograph Michael Fogg. Source: <u>www.vistaalmar.es</u> See comments.

# **26.** Comments to the Plates

### **Preliminary remarks**

The senior-author and his wife are particularly grateful to all their friends who helped them to collect all these photographs.

Other fossil teeth of diverse taxa concerned by this Publication are illustrated on the following Websites:

#### Pieter De Schutter: <u>http://www.somniosus.be/</u> Guy Van Den Eeckhaut: <u>http://www.belgiansharkteeth.be/</u> Philippe Garot: <u>http://www.requinsfossiles.be/</u>

#### **Comments to Plate 1 and Plate 2**

These two plates illustrate some radicular odontological criteria utilised for the differentiation of the higher taxa of the Elasmobranchii. They also illustrate diverse odontological criteria.

The extant Chlamydoselachiformes are the sole Elasmobranchii presenting teeth passing from a holaulacorhyzid step to a secondary anaulacorhyzid step during their growth and dental crowns presenting a distema between all their cuspids. The designation *chlamydoselachoryzid root-type* was proposed for this reason.

#### **Comments to Plate 1**

Figures **1a** to **1d** show a typical primary anaulacorhyzid tooth, but also a polycuspid tooth presenting a double, extern and intern striation of its dental crown.

Figures 2a to 2d show a typical hemiaulacorhyzid tooth, but also a dental crown with extern and intern smooth faces.

Figures **3a** to **3d** show a typical polyaulacorhyzid root, without particular ornamentation.

#### **Comments to Plate 2**

Figures **1a** to **1d** show a typical hemiaulacorhyzid tooth, but also a polycuspid tooth presenting an apron, a large medio-intern protuberance of its dental root and a serration on the two cutting edges of its crown.

Figures **2a** to **2d** show a typical secondary anaulacorhyzid tooth, but also a dental crown with extern and intern smooth faces and a powerful serration on the two cutting edges of its crown.

Figures **3a** to **3d** show a typical holaulacorhyzid tooth presenting vertical folds on its intern and extern sides.

Figures **4a** and **4b** show a typical polyhemiaulacorhyzid polycuspid tooth, presenting also a double, extern and intern striation of its dental crown.

### **Comments to Plate 3 to Plate 7**

These five plates illustrate the diversity of the morphology and the modes of the fixing of eggs of diverse oviparous Neoselachii. Oviparity is the most primitive mode of reproduction of the Vertebrates. It is interesting to remind that the most primitive Mammalia, the Monotremata are still oviparous.

This mode of reproduction presents an advantage and an inconvenience. The egg-capsules may be laid in diverse well-oxygenated places, but they represent easily accessible nutritional sources for diverse invertebrate or vertebrate predators.

Evolution will demonstrate that ovoviviparity and aplacental-viviparity will enhance the chances of survival of the young generations.

The Elasmobranchii are the sole group of Vertebrata to have acquired these three reproduction modes.

The spiralled egg-capsules of all the extant representatives of the Genus *Heterodontus* de BLAINVILLE, 1816, illustrated on the Plate 3 (fig.: 2) and on the Plate 4 (figs.: 1 and 2) have the most singular morphology. It evokes

the morphology of the rare egg-capsules of the Genus *Palaeoxyris* BRONGNIART, 1828 which were attributed to a hybodontoid-Euselachii taxon (See Cappetta 2012: p.: 31, fig.: 21) after long controversial discussions.

#### **Special References**

FISCHER, J. & KOGAN, I. 2008: Elasmobranch egg capsules *Palaeoxyris*, *Fayolia* and *Vetacapsula* as subject of palaeontological research – an annotated bibliography. Paläontologie, Stratigraphie, Fazies (16). Freiberger Forschungshefte C. 528: 75-91.

FISCHER, J., AXSMITH, B., J. & ASH, S., R. 2010: First unequivocal record of the hybodont shark egg capsule *Palaeoxyris* in the Mesozoic of North America. *Neues Jahrbuch für Geologie und Paläontologie. Ab.* **255(3)**: 327-344.

SCHIMPER, W., P. 1874: *Traité de paléontologie végétale ou la flore du monde primitif*. Paris, tome 1.: 740 pp., 56 pls., see: pp.: 95-110.

The extant representatives of the Super Order Scyliorhinomorphii present the largest diversity of morphology of egg-capsules.

This diversity is partially illustrated on Plates 3 to 7. The most singular egg-capsule's morphology is this of the species *Cephaloscyllium umbratile* JORDAN & FOWLER, 1903 which presents transversal ridges.

All the individuals of the diverse populations of the Genus *Cephaloscyllium* have also the possibility to inflate their body with air or air and water.

#### **Comments to Plate 8**

This plate illustrates the systematic importance of a future increase of the knowledge concerning the progressive anatomical transformation from the unicellular stage to the pre-hatching stage of the oviparous Chondrichthyes.

#### Comments to Plate 9 to Plate 65 and Plate 67 to Plate 70

As far as possible, for each revised generic taxon, colour photographs of living individuals are followed by macro-photographs of their neonates, photographs of their jaws, details of these photographs and SEM photographs of their upper and lower teeth as well as of their rostral teeth\*.

\*In case of possession of a rostrum.

#### **Comments to Plate 66**

This plate illustrates three parts of the second specimen known of *Propristiophorus tumidens* WOODWARD, 1892. Its dentition allows revalidating the Genus *Propristiophorus* WOODWARD, 1892. Sir Woodward had a far better knowledge of extant taxa than many of his followers.

#### **Comments to Plate 71 to Plate 73**

These three plates present a view of a well preserved individual of *Libanopristis hiram* (HAY, 1903) discovered by Jeanne Signeux in 1952, in a level of Cenomanian Age (Upper Cretaceous) at Hadjula (northern Lebanon) and magnifications of some parts of its skeleton.

#### **Comments to Plate 74**

This plate is the reproduction of one plate of a book nearly unobtainable in the majority of the western European Libraries.

#### Comments to Plate 75

This plate illustrates the risk which represents the conquest of a new environment. The majority of the extant representatives of the Genus *Hemiscyllium* are able to move, such as salamanders do, on hard substrates and to survive thirteen to fourteen hours out of the water, but they ignore the existence of the rapacious birds. This photograph is reproduced for its exceptional beauty and signification. Source: <u>www.vistaalmar.es</u> - Photograph Mr Michael Fogg. All the attempts to enter in contact with Mr Michael Fogg remained without answer.

# The original PDF was sent on 13 March 2014 to the Belgian Royal Library, Legal Electronic Depot Survey.

#### And to the following colleagues:

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#### And to

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