

# Géominpal Belgica

*Découvertes géologiques, minéralogiques et paléontologiques  
en Belgique.*

3

**Observations concerning the Evolution and the Parasytematic  
of all the living and fossil Heterodontiformes.**

By

Herman Jacques<sup>1</sup> & Hilde Van Waes<sup>1</sup>

2012

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**Lateral and occlusal views of one lateral tooth of *Heterodontus rugosus* (AGASSIZ, 1839)**

on its matrix: Uppermost phosphatic level (Cm1g) of the *Trivières Chalk* at Obourg, C.B.R. Quarry 4 (Province of Hainaut).

Collection Jacques Boel - Photos Pieter De Schutter

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## **Dedication**

**This work is dedicated to:**

**Dr. Marinus Boeseman (R.M.N.H. – Leiden, The Netherlands)**

**and**

**Dr. Cyril Alexander Walker (B.M.N.H. – London, England)**

**As a token of gratitude for**

**their scientific information**

**Respectfully,**

**at Beigem**

**15 November 2012**

*Jacques Herman*

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## Summary

Between Mid-June and Mid-July 2012, a Tetralogy concerning the largest part of the other Elasmobranchii\* was electronically published. This Publication has for proposal the completion of this Tetralogy.

\*References: HERMAN, J. & VAN WAES H. 2012: *Géominpal Belgica 2*, *Géominpal Belgica 2* (Supplement), *Géominpal Belgica 2* (End) and *Géominpal Belgica 2* (Erratum).

**Key-words:** Elasmobranchii, Systematic-Parasystematic, Heterodontomorphii, Paracestracioniformes, Heterodontiformes, Heterodontidae.

## Résumé

Entre la mi-juin et la mi-juillet 2012, fut publiée électroniquement une Tétralogie concernant la plupart des autres taxa d'Elasmobranchii\*. Cette Publication a pour but de compléter cette Tétralogie.

\*Références: HERMAN, J. & VAN WAES H. 2012: *Géominpal Belgica 2*, *Géominpal Belgica 2* (Supplément) .*Géominpal Belgica 2* (End) et *Géominpal Belgica 2* (Erratum).

**Mots-Clés:** Elasmobranchii, Systematic-Parasystematic, Heterodontomorphii, Paracestracioniformes, Heterodontiformes, Heterodontidae.

## Samenvatting

Tussen midden juni en midden juli, werd een Tetralogie betreffende het grootste deel van de andere Elasmobranchii\* elektronisch gepubliceerd. Deze Publicatie heeft als bedoeling deze Tetralogie te beëindigen.

\*Referenties: HERMAN, J. & VAN WAES H. 2012: *Géominpal Belgica 2*, *Géominpal Belgica 2* (Supplement), *Géominpal Belgica 2* (End) en *Géominpal Belgica 2* (Erratum).

**Sleutelwoorden:** Elasmobranchii, Systematiek-Parasystematiek, Heterodontomorphii, Paracestracioniformes, Heterodontiformes, Heterodontidae.

## Kurzfassung

Zwischen halb June und halb Julie, wurde eine Tetralogie betreffs der grösser Teil von der andren Elasmobranchii\* elektronisch herausgegeben. Heute Publikation hat für Ziel heute Tetralogie zu ergänzen.

\*Beziehungen: HERMAN, J. & VAN WAES H. 2012: *Géominpal Belgica 2*, *Géominpal Belgica 2* (Supplement), *Géominpal Belgica 2* (End) und *Géominpal Belgica 2* (Erratum).

**Schlüsselworten:** Elasmobranchii, Systematik-Parasystematik, Heterodontomorphii, Paracestracioniformes, Heterodontiformes, Heterodontidae.

## 2. Introduction

In July 2012, one, apparently, insignificant observation surprised the senior author of this Paper: all the living taxa of the Order Heterodontiformes are oviparous animals.

All the living Heterodontiformes have conserved another primitive characteristic: the possession of dorsal fin spines.

These spines have a real efficacy but only if their base is strongly anchored in a rigid part of their vertebral column and inserted at the front of a dorsal fin of which the base is sufficiently rigid.

All the primitive fossil taxa of the Order Heterodontiformes were in possession of fine and elongated anterior teeth, which suggests that they had supple and rapid moving ancestors.

The Super Order Heterodontomorphii, new taxon, allows regrouping all the fossil and living taxa. The species of this new taxon will preserve their dorsal spines, increase the thickness and the imbrication of the elements of their dermic protection, rigidify the anterior and central parts of their vertebral column and its *skull* will become the most massive of all the Elasmobranchii chondrocranium.

This new Super Order will regroup two Orders: the Order Heterodontiformes BERG, 1940 and the new Order Paracestrationiformes, regrouping their ancestors from the Triassic, the Jurassic and probably the Lower Cretaceous.

The Heterodontiformes of the Upper Mesozoic, the Cenozoic and the living forms were in possession of jaws with particularly massive lateral crushing teeth.

The mass of these lateral teeth seems\* to increase slowly, but continuously, from the Lower Cretaceous till the Holocene.

\*The senior-author has never observed any discontinuity in this process. This remark only concerns the (numerous) Belgian species discovered in these strata.

All these anatomical singularities, immediately observable by all neontologists, are sufficient\* to allow the elevation of this Order to the rank of Super Order.

\*The five fundamental criteria requested for the proposition of the creation of one new Super Order are biologically present (See Bibliography: HERMAN, J. & VAN WAES H. 2012).

The biologists of the nineteenth century were so persuaded of the originality of this Genus\* to propose this Genus as generotype of one monogeneric Family: The Family Heterodontidae GRAY, 1851.

\*In 1851, the Genus *Heterodontus* included only 3 species: *H. portusjacksoni* (de MEYER, 1793), *H. quoyi* (FREMINVILLE, 1840) and *H. zebra* (GRAY, 1851).

Berg was even more convinced of its originality, so that he turned the Family Heterodontidae into the type Family of the Order Heterodontiformes BERG, 1940, Order including only one Family regrouping one Genus and five species.

All the actual and fossil generic taxa of the Order Heterodontiformes are re-examined.

### 3. Introduction

En Juillet 2012, une observation, apparemment insignifiante, surprit le senior-auteur de cette Publication: Tous les taxa actuels des Heterodontiformes sont ovipares.

Toutes les espèces actuelles des Heterodontiformes ont conservé une autre caractéristique anatomique très primitive: La possession d'épines dorsales.

Ces épines dorsales ont une efficacité bien réelle, mais seulement si leur base est fermement ancrée dans une portion de colonne vertébrale rigide et qu'elles s'insèrent à l'avant de nageoires dorsales dont la base est, elle aussi, suffisamment rigide.

Toutes les espèces des ancêtres\* des Heterodontiformes actuels étaient en possession de dents antérieures fines et élancées, ce qui suggère que ces ancêtres étaient nettement plus souples et rapides que leurs descendants actuels.

\*Celles découvertes dans les couches du Trias et du Jurassique inférieur.

Les espèces de ce nouveau taxon conserveront leurs épines dorsales, accroîtront l'épaisseur et l'imbrication des éléments de leur protection dermique, rigidifieront les parties antérieure et centrale de leur colonne vertébrale et leur *crâne* deviendra le plus massif de tous les chondrocrânes d'Elasmobranchii.

Ce nouveau Super Ordre regroupe deux Ordres: L'Ordre des Heterodontiformes BERG, 1940 et le nouvel Ordre des Paracestrationiformes, incluant leurs ancêtres du Trias, du Jurassique et, vraisemblablement, ceux du Crétacé inférieur.

La masse de ces dents latérales broyeuses semble\* s'accroître lentement, mais continuellement depuis le Crétacé inférieur jusqu'à l'Holocène.

\*Le senior-auteur n'a pu observer la moindre discontinuité de ce processus. Remarque qui ne concerne toutefois que les dents des (nombreuses) espèces belges découvertes dans ces terrains.

Toutes ces singularités anatomiques, immédiatement contrôlables par tout néontologiste, forment une telle pluralité\* que les conditions de promouvoir cet Ordre au rang de Super Ordre se trouvent d'emblée réunies.

\*Les cinq critères fondamentaux requis pour la proposition de création d'un nouveau Super Ordre sont, biologiquement, réunis. (Voir Bibliographie: HERMAN, J. & VAN WAES H. 2012).

Les biologistes du dix-neuvième siècle furent à ce point conscients de l'originalité du Genre *Heterodontus*\* pour y voir le génotype d'une Famille monogénérique: La Famille des Heterodontidae GRAY, 1851.

\*A cette époque, le Genre *Heterodontus* ne comptait que 3 espèces: *H. portusjacksoni* (de MEYER, 1793), *H. quoyi* (FREMENVILLE, 1840) et *H. zebra* (GRAY, 1851).

Berg en sera d'autant plus convaincu qu'il fera de la Famille des Heterodontidae la Famille type de l'Ordre des Heterodontiformes BERG, 1940, Ordre fondé sur cette seule Famille ne regroupant encore qu'un Genre et cinq espèces.

Tous les taxa génériques actuels et fossiles de l'Ordre des Heterodontiformes sont ré-examinés.

## 4. Introductie

In juli 2012 werd de senior auteur van dit artikel verrast door een ogenschijnlijk onbelangrijke waarneming: alle levende taxa van de Orde Heterodontiformes zijn ovipare dieren.

Al de levende Heterodontiformes hebben een ander primitief kenmerk bewaard: het bezit van dorsale vin stekels. Deze stekels hebben een reële efficiëntie, maar slechts als hun basis stevig verankerd is in het harde deel van hun wervelkolom en vastzit aan de voorzijde van een dorsale vin waarvan de basis voldoende hard is.

Al de primitieve fossiele taxa\* van de Orde Heterodontiformes bezaten fijne en langwerpige voortanden, wat suggereert dat ze soepele en snel bewegende voorouders hadden.

\*Deze gevonden in de lagen van het Triassicum en het Onder Jurassicum.

De Super Orde Heterodontomorphii, nieuwe taxon, laat toe al de fossiele en levende taxa te hergroeperen. De soorten van dit nieuwe taxon zullen hun dorsale stekels behouden, de dikte en de overlapping van de elementen van hun huidprotectie verhogen, de voorste en centrale delen van hun wervelkolom verstevigen en hun *schedel* zal de massiefste van al de Elasmobranchii chondrocranium worden.

Deze nieuwe Super Orde zal twee Orden hergroeperen: de Orde Heterodontiformes BERG, 1940 en de nieuwe Orde Paracestrationiformes die hun voorouders van het Triassicum, het Jurassicum en waarschijnlijk die van het Onder Krijt omvat.

De Heterodontiformes van het Boven Mesozoïcum, het Cenozoïcum en de levende vormen waren in het bezit van kaken met bijzonder massieve laterale kraaktanden.

De massa van deze laterale tanden schijnt\* traag maar constant te verhogen vanaf het Lager Cretaceous tot het Holoceen.

\*De senior auteur heeft nooit een discontinuïteit vastgesteld in dit proces. Deze opmerking betreft alleen de (talrijke) Belgische soorten gevonden in deze strata.

Al deze anatomische eigenaardigheden, onmiddellijk waarneembaar door alle neontologen, zijn voldoende\* om deze Orde te mogen verheffen tot de rang van Super Orde.

\*De vijf fundamentele criteria vereist voor het voorstel van de creatie van een nieuwe Super Orde zijn aanwezig op biologisch vlak (Zie Bibliografie: HERMAN, J. & VAN WAES H. 2012).

De biologen uit de negentiende eeuw waren zo overtuigd van de originaliteit van deze Genus\* dat ze deze voorstelden als generotype van een mono generische Familie: de Familie Heterodontidae GRAY, 1851.

\*In 1851 omvatte de Genus *Heterodontus* slechts 3 soorten: *H. portusjacksoni* (de MEYER, 1793), *H. quoyi* (FREMENVILLE, 1840) en *H. zebra* (GRAY, 1851).

Berg was nog meer overtuigd van de originaliteit van de Familie Heterodontidae zodat hij ze omschiep tot het type Familie van de Orde Heterodontiformes BERG, 1940. Deze Orde bevatte zo slechts één Familie, één Genus en vijf gehergroepeerde soorten.

Al de levende en fossiele generische taxa van de Orde Heterodontiformes worden opnieuw onderzocht.

## 5. The formerly Heterodontiformes and the Heterodontomorphii nov. Sup. Ord.

### 5.1. The living Heterodontiformes

**General observations and conclusions:** All the living Heterodontomorphii have five branchial arches, are oviparous and have two dorsal fins with spines, three of the most primitive characteristics of the living Chondrichthyes.

**Their most important anatomical singularities are:** An extremely rigid vertebral column authorizing no snake-like movements, a massive polyhedral and heavy *neurocranium*, a very dense dermal protection constituted by heavy elements strongly imbricated\* and, such as their name indicates, a very strong monognatic heterodonty.

\*In Japan, their cutaneous protection was utilised for the ornamentation of the handle of the spades of the samurai since the 13<sup>th</sup> century.

The cutting edges of the dental crown of all the living or fossil species never present any kind of serrulation.

All the fossil skeletons attributed to the Heterodontiformes present dorsal fin prints with dorsal fin spines. Only their oviparity remains, of course, hypothetical.

Because of these characteristics, the Heterodontomorphii may be considered as cousins of the earliest Scyliorhinomorphii. Both remained at the most primitive reproduction step: the oviparity.



This new Super-Order may, easily, be subdivided into two Orders: The Order Heterodontiformes, based on the living Genus *Heterodontus* de BLAINVILLE, and the new Order Paracestrationiformes, based on the fossil Genus *Paracestration* KOKEN in ZITTEL, 1911.

**Odontological criteria added to justify this new conception:** For a palaeontologist, the existence of one *neurocranial crista* is undetectable on the base of isolated teeth. The last suggestions to establish a new Parasystematic classification for the other Order taxa were electronically published in the beginning of 2012\*

\*See the Bibliography: HERMAN, J. & VAN WAES, H. 2012, HERMAN, J. & VAN WAES, H. 2012 (Supplement), HERMAN, J. & VAN WAES, H. 2012 (End) and HERMAN, J. & VAN WAES, H. 2012 (Erratum).

Such as demonstrated in this Tetralogy, normally, five important odontological criteria must be detected to justify this revision.

Considering the fact that all the living species attributed to this new Super Order present the four following fundamental biological criteria: Oviparity, presence of dorsal fin spines, a very rigid vertebral column, heavy and strongly imbricated dermal denticles, one additional odontological argument should be sufficient to admit the proposal to turn this Order into a Super Order.

The following seven criteria are proposed: The very strong monognathic differentiation of their teeth, the overlapping of the outer side of their root crown by the outer side of their dental crown, the voluminous medio-intern protuberance of their root, the possession of one single principal cusp decreasing on the lateral teeth, the possession of only one pair of lateral cusps on their anterior teeth, an ornamentation restricted to the outer face of the crown of the anterior teeth and a reticulated ornamentation on the upper face of their lateral teeth. Additionally, the base of the dental root of the lateral teeth is nearly flat.

The Genus *Heterodontus* is the generotype and unique living Genus of the Family Heterodontidae which regroups only 9 surviving taxa.

These 9 species are the following: *Heterodontus galeatus* (GÜNTHER, 1870), *Heterodontus francisci* (GIRARD, 1855), *Heterodontus japonicus* MACLAY & MACLEAY, 1884, *Heterodontus portusjacksoni* (de MEYER, 1793), *Heterodontus mexicanus* TAYLOR & CASTRO-AGUIRRE 1972, *Heterodontus omanensis* BALDWIN 2005, *Heterodontus quoyi* FREMINVILLE 1840, *Heterodontus ramalheira* (SMITH 1949) and *Heterodontus zebra* (GRAY, 1831).

*Heterodontus portusjacksoni* is its type species. Paleontological records of the Genus extend from the Lower Cretaceous to the Holocene.

Their most primitive characteristics consist of the possession of one dorsal spine on the anterior side of their two dorsal fins and their reproduction stadium: oviparity.

Their chondrocranium is particularly massive, the anterior part of their vertebral column is singularly rigid and their dermal denticles closely imbricated.

Another singularity is that their mouth is located far from their nose and possesses anterior teeth, allowing them to catch small crustaceans, and lateral molar-like teeth making the crushing of their prey easier.

They are in possession of two largely spaced pro-eminent nostrils. They are relatively small species, only two species grow up to more than 160 centimetres. All the living species are endemic or have very restricted distribution areas.

They live in coastal and uppermost parts of continental slopes of tropical and sub-tropical waters.

### **Living materials**

See the lists of the jaws of the different species examined for the realisation of the Publication: HERMAN J., HOVESTADT-EULER M. & HOVESTADT D.C., 1993.

The examination of 98 other jaws, in diverse private Collections, of six living species has increased the general knowledge concerning the dentition of these species.

Thanks to Dr. Marinus Boeseman (Leiden, NL), important additional data concerning the distribution and the ecology of diverse Indo-Pacific species were accessible.

Dr. Boeseman offered to the senior-author, the possibility to read the personal *Acquisitie Nota* of Dr. Bleeker in Indonesia, dating from the nineteenth century.

Dr. Bleeker tried to obtain a maximum of specimens for the Leiden Museum Collections in retired and isolated little fishing harbours. In such little villages, the fishermen could navigate to a maximum of 15 km east from their village at night.

His very detailed notes concerning the invertebrates\* trapped in their nets give a very good idea of the places where the mothers deposited their eggs and of the living habitats of the juvenile *Heterodontus*.

\*Particularly some Genera of Echinoderma or Stellerida and, occasionally, some Crustacea or Mollusca.

The material examined allows us to guarantee that the percentage of the anterior, latero-anteral, lateral and commissural teeth rows is constant for babies, juveniles, adults and olds individuals.

Only the volume of the lateral (crushing) teeth increases obviously, and the height of the anterior (prehensile) teeth decreases progressively.

Consequently, the growth process of the teeth of the majority of the living species seems very regular.

## 5.2. The Fossil Taxa

### Cappetta 2006 (pp.: 397-398) cited, and commented, the 12 following fossil Genera:

*Bidentia* MUSPER, 1920 (Junior synonym of *Heterodontus*), *Bidentulus* WHITE & MOY-THOMAS, 1940 (Synonym of *Heterodontus*), *Drepanophorus* EGERTON, 1872 (Synonym of *Heterodontus*), *Gomphodus* REUSS, 1842 (Synonym of *Heterodontus*), *Heterodontobatis* LANDEMAINE, 1991 (Synonym of *Heterodontus*), *Heterodontus* de BLAINVILLE, 1816, *Paracestration*\* KOKEN, 1907, *Platyacrodus* AMEGHINO, 1935 (Synonym of *Heterodontus*), *Protoheterodontus* UNDERWOOD & WARD, 2004, *Pseudacrodus* AMEGHINO, 1906 (Synonym of *Heterodontus*), *Pseudoheterodontus* GLÜCKMAN & ZHELEZKO, 1971 (Synonym of *Heterodontus*) and *Selachidea* QUENSTDET, 1852.

He retained as valid taxa only the three following Genera: *Paracestration* KOKEN, 1907, *Protoheterodontus* UNDERWOOD & WARD, 2004 and *Selachidea* QUENSTDET, 1852.

### Genus *Heterodontus* de BLAINVILLE, 1816

#### Fossil materials examined

Numerous isolated teeth of *Heterodontus upnikensis* DALINKEVICIUS, 1935, *Heterodontus canaliculatus* EGERTON in DIXON, 1850, *Heterodontus lonzeensis* HERMAN, 1977, *Heterodontus maisierensis* HERMAN, 1977, *Heterodontus havreensis* HERMAN, 1977, *Heterodontus rugosus* (AGASSIZ, 1839), *Heterodontus* cf. *danicus* (ROZENKRANTZ, 1920), *Heterodontus* sp., *Heterodontus vincenti* LERICHE, 1905, and *Heterodontus* cf. *janefirdae* CASE, 1980.

Globally more than 5,000 isolated teeth were collected and examined by the senior-author and his field friends, between 1968 and 2010. These teeth were all collected *in situ*. The I.R.S.N.B. collections were only indispensable for the description of the taxon *Heterodontus lonzeensis* HERMAN, 1977, which is apparently endemic in this country and stratigraphically restricted to the Santonian.

*H. upnikensis*: 164 teeth from the Albian strata of the Der Pools (Aube Department, France), 46 teeth from Pargny, (Aube Department, France) and 16 teeth from Maurupt-le-Montois (Marne Department, France).

*H. canaliculatus*: 64 teeth from the *Actinocamax plenus* level, Bettrechies (France), 22 derived from the same Horizon, 18 at Autrepes (Belgium) and 4 at Chercq (Belgium), 166 teeth from the *Inoceramus labiatus* Horizon at Bettrechies (France) and 88 teeth from the *Terebratulina gracilis* Horizon at Bettrechies (France).

*H. lonzeensis*: 54 teeth in the I.R.S.N.B. Collections and 8 teeth in the Collection Coupatez, all from the Loncée Glaucony Formation (Santonian).

*H. maisierensis*: 16 teeth from the Maisières Chalk (Coniacian), 12 at Maisière and 4 at Casteaux (Province of Hainaut).

*H. havreensis*: more than 300 teeth from the Lower and Upper Belgian Campanian (Province of Liège and Province of Limburg).

*H. rugosus*: more than 200 teeth from all the classic Maastrichtian Belgian localities (Province of Liège and Province of Limburg).

*H. cf. danicus*: 16 teeth from the Tuffeau de Cibly, Lower Bryozoan level (Danian), at Cibly (Province of Hainaut).

*H. sp.*: 8 huge specimens from the Clay of Ghlin (Lowermost Ypresian) at Ghlin, Durieux-Guelton Clay pit (Province of Hainaut).

*H. wardenensis*: more than 1,000 teeth from the different Belgian Ypresian strata at Egem (Western Flanders), Forest and Evere (Brussels Regio).

*H. vincenti*: more than 2,500 teeth from all the classic Lutetian Belgian localities: Balegem and Oosterzele (Western Flanders), Meldert (Eastern Flanders), Zaventem, Mechelen and Diegem (Flemish Brabant) and Woluwe (Brussels Regio).

*H. cf. janefirdae*: 5 anterior teeth from the *Sint Niklaas Phosphorite Bed* (Lower Oligocene) at Belsele, SVK Clay Pit. (Eastern Flanders, Belgium).

Plate 3 of J. Herman 1977 PhD is the unique existing plate allowing a direct comparison between the extern faces of the anterior teeth of the five cretaceous Belgian species: *H. canaliculatus*, *H. lonzeensis*, *H. maisierensis*, *H. havreensis* and *H. rugosus*. Pitifully, the macrophotography facilities of the beginning of the 1970s were very limited.

In future editions of *Géominpal Belgica*, devoted to the cretaceous fauna of Belgium, the senior-author has planned to re-illustrate all these taxa.

The fossil material examined allows us to guarantee that the percentage of the anterior, latero-anteral, lateral and commissural teeth rows seems to have remained constant for babies, juveniles, adults and old individuals of all the Belgian and northern France Upper Cretaceous to Lower Oligocene species, as well as their growth process.

The lack of teeth with a height inferior to 2mm in these ancient collections falsifies the estimation of the number of the different teeth rows. These absences result, of course, from the too large sieving meshes used at these epochs.

### **Genus *Selachidea* QUENSTEDT, 1852**

This Genus is represented by only one species, its holotype: *Selachidea torulosi* QUENSTEDT, 1852 (Lower Aalenian, from the Bade-Wurtemberg (D)).

The Genus *Selachidea* QUENSTEDT, 1852 (type species: *Selachidea torulosi* QUENSTEDT, 1851), seems definitely to be rejected from the Heterodontiformes.

### **Genus *Protoheterodontus* UNDERWOOD & WARD, 2004**

The Genus *Protoheterodontus* includes three species: *P. sulcifer* (WAGNER, 1857), *P. bellis* UNDERWOOD & WARD, 2004 and *P. sylvestris* UNDERWOOD & WARD, 2004. Its type species is: *P. sylvestris* UNDERWOOD & WARD, 2004.

**Age and localities:** Bathonian: Watton Cliff\*: Forest Marble Formation, Kirtlington\*\*: Kirtlington Quarry and Woodeaton\*\*\*: Woodeaton Quarry: White limestone Formation (GB).

\*Teeth derived from an older Formation, \*\* Teeth *in situ*, \*\*\* Teeth *in situ*.

#### **Fossil materials examined**

72 isolated teeth collected at Eype-Mouth (Watton Cliffs, Dorsetshire) in the Forest Marble Formation in 1983, derived from the White limestone Formation, presently preserved in the *Collection Crochard*, Department of Palaeontology, Section Vertebrate Palaeontology, I.R.S.N.B. Brussels (Belgium).

12 isolated teeth in one private Belgian Collection, resulting from an exchange with one anonymous English collector.

14 isolated teeth collected, in 1985, by Georges Wouters (Kirtlington, Oxfordshire): Kirtlington Quarry: White limestone Formation, presently preserved in the *Collection Coupatez*, also stored in the Collections of the Department of Palaeontology, Section Vertebrate Palaeontology, I.R.S.N.B. Brussels (Belgium).

The Holotype, observed and examined by curiosity in 1974 and one other larger (56cm t.l.) specimen examined in a private German Collection. The access to this Collection was an exceptional favour of its owner. Photographs were not authorised. The specimen is quite complete, dorsal fin spines and lower teeth are present, but carry no crushing teeth.

### **Genus *Paracestration* KOKEN in ZITTEL, 1911**

The Genus *Paracestration* is represented by its type species: *P. falcifer* WAGNER, 1857 from the Lower Tithonic of Solnhofen, Bayern (D).

This Genus was really in possession of some last lateral dental rows of small low elongated crushing teeth (See CAPPETTA, 2012: J on fig. 139, p. 153 – BMNH N° P76072), which justify some considerations.

## **5.3. Taxonomic subdivisions of the Heterodontomorphii nov. Sup. Ord.**

This new Super-Order may, easily, be subdivided into two Orders: The Order Heterodontiformes, based on the living Genus *Heterodontus* de BLAINVILLE, 1816 and the Order Paracestrationiformes, based on the fossil Genus *Paracestration* KOKEN in ZITTEL, 1911.

### **Order Paracestrationiformes nov. Ord.**

**Composition:** This new Order is represented by one single Family: The Family Paracestrationidae nov. Fam.

**Anatomical Characteristics:** Skeletons\* with two dorsal fin spines, anterior and central parts of the vertebral column showing an increasing calcification, a progressive - from the Triassic taxa to the lower Jurassic taxa - augmentation of the volume of their chondrocranium and an apparently sudden apparition of crushing teeth.

\*When discovered.

## **Odontological characteristics of this new Family and Order**

Cappetta 2012 (p.152-153) precises that the isolated teeth attributed to the Genus *Paracestration* are narrow, slender and in possession of one principal cusp flanked by one, two or three pair(s) of acuminate but flat lateral cuspids.

Their roots are hemiaulacorhizid, with a well-developed central foramina. The medio-intern radicular protuberance is well developed.

Their large apron overlaps the upper face of the dental root. The extern face of their crown lacks any kind of ornamentation.

He cannot, of course, give any description of inexistent crushing teeth.

The total length of the Holotype of *Paracestration falcifer* WAGNER, 1857 is approximately 48cm. A re-figuration of this specimen is given by Cappetta (See Bibliography: CAPPETTA, 2012: p.: 152, fig. 138A).

The quality of this reproduction is relatively poor, but allows to observe that the volume of its chondrocranium is relatively normal and that the first dorsal fin spine is strongly anchored on the highly calcified anterior part of the vertebral column.

The second first dorsal fin spine is anchored on an obviously less calcified part of the vertebral column, the distinction between the anterior prehensile teeth and the lateral crushing teeth is completely realized.

This isolated taxon seems more evolved than the three species of the Genus *Protoheterodontus*.

Because of the lack of S.E.M. pictures of its anterior teeth, it is not sure that the isolated anterior teeth discovered in other strata and localities in England may be attributed to this Genus.

In 2004, UNDERWOOD and WARD considered, originally, their new species *bellis* as one *Protoheterodontus* species, but further in their work as a *Paracestration* species.

But if it is true that the dentition of *Paracestracion falcifer* WAGNER, 1857 has for principal characteristic, at least at the juvenile's stages, the lack of lateral crushing teeth, then it represents the ancestor of the Heterodontiformes.

In the Belgian Toarcian of Halanzy (Luxembourg Province, Belgium), the senior author has also only discovered non-crushing teeth.

In this locality, the quality of preservation of the Elasmobranchii teeth is too perfect to allow any reworking action or sedimentological segregation.

## **Order Heterodontiformes BERG, 1940 Ord. rev.**

### **Family Heterodontidae GRAY, 1851**

#### **Genus *Heterodontus* de BLAINVILLE, 1816**

#### **Fossil materials**

Thanks to Dr. Cyril Alexander Walker, during his PhD. Preparation, the senior-author had the opportunity to realize diverse observations and notes at the B.M.N.H. London and the Booth Museum at Brighton (East Sussex).

In 1971, the principal problem of the senior-author was to be sure that it was possible to differentiate upper cretaceous species on the base of lots of anterior isolated teeth which were relatively common in all the Belgian Upper Cretaceous strata that he had prospected for his PhD.

At this epoch, his attention was not particularly attracted by the anatomical data he had noted incidentally. But, actually, he remembers his astonishment concerning the extraordinary differences\* between the taphonomical and the sedimentological conditions existing between the fossiliferous strata of the Belgian Upper Cretaceous and the Upper Cretaceous of the North of France.

\*In Southern England Upper Cretaceous strata, complete skeletons, with their dorsal fin spines, their chondrocranium and their teeth are common fossils. In the fossiliferous strata of the Belgian Upper Cretaceous and the North of France, only isolated teeth and scarce dorsal fin spines were discovered.

The same observation is also valid for all the fossil species of the Order Synchodontiformes and the Order Ptychodontiformes.

Presently, re-consulting his ancient notes he discovered that he had collected some very important data, which are enumerated below:

The presence of two perfectly preserved dorsal fin spines strongly anchored on the vertebral column of specimens of *Heterodontus canaliculatus* EGERTON in DIXON, 1850 was observable on the specimens B.M.N.H. N°: PV-P49734 and Booth Museum N°: BMB 008555.

The massive constitution of the chondrocranium of one specimen of *Heterodontus canaliculatus* EGERTON in DIXON, 1850 was observable on Booth Museum specimen N°: BMB 007329.

The possession of massive lateral crushing teeth of *Heterodontus canaliculatus* EGERTON in DIXON, 1850 was obvious on B.M.N.H. N°: PV-P20123, B.M.N.H. N°: PV-P38550, B.M.N.H. N°: PV-P49079, B.M.N.H. N°: PV-P49735, B.M.N.H. N°: PV-P49079, B.M.N.H. N°: PV-P39061 and Booth Museum specimen N°: 007329.

The heavy dermal protection of *Heterodontus canaliculatus* EGERTON in DIXON, 1850 was observable on B.M.N.H. specimens N°: PV-P20123 and N°: PVP-P49735.

All these data present, in the context of this Paper, considerable implications and request future taphonomical interpretations.

## **6. List of the new taxa proposed and list of the revised taxa in this volume**

In this Publication, only two new taxa are proposed: One Super Order: The Heterodontomorphii and one Order: The Order Paracestrationiformes.

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