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A Late Cretaceous Aporrhaidae-dominated gastropod assemblage from the Gosau Group of the Pletzsch Alm near Kramsach (Tyrol, Austria).

With an appendix on the taxonomy of Mesozoic Aporrhaidae and their position in the superfamily Stromboidea.

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(With 6 figures and 2 plates)

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Abstract

A gastropod assemblage from the Late Cretaceous Lower Gosau Group of the Pletzsch Alm, near Kramsach (Tyrol, Austria) is characterized by diverse Aporrhaidae. The fauna contains the Aporrhainae species *Quadrinervus carinatus* (DELPEY) and *Biculteriala gratti* nov. gen. nov. spec., the Anchurinae *Pletzschia furcata* nov. gen. nov. spec., and the Harpagodinae *Harpodactylus marolti* nov. gen. nov. spec., and *Rhombovomeria passer* (ZEKELI). Additionally, the assemblage contains representatives of the Trochoidea, Turbinidae, Cassiopidae, Gyrodidae, Ampullinida, Diozoptyxidae and Acteonellidae and characterizes distal inner shelf areas.

By applying morphological criteria of the teleoconch, the Mesozoic representatives of the Aporrhaidae are subdivided into the subfamilies: Spinigerinae KOROTKOV, Aporrhainae GRAY (1850), Pterocerellinae BANDEL (2007), Harpagodinae PCHELINTSEV (1963), Pugnellinae KIEL & BANDEL (1999), Anchurinae nov. subfam., Arrhoginae POPENOE (1983), Dimorphosominae nov. subfam., and Struthiopterinae ZINSMEISTER & GRIFFIN (1995). In a first pulse, the Aporrhainae, Pterocerellinae, Harpagodinae and Dimorphosominae evolved from the Spinigerinae in the middle Jurassic. In a second pulse during the Albian (late Lower Cretaceous) the Dimorphosominae gave rise to the Anchurinae, Arrhoginae and Pugnellinae. From the Arrhoginae, two lineages lead to the Paleogene Stromboidea.

Keywords: Gastropoda, Aporrhaidae, Late Cretaceous, Gosau Group, Austria, taxonomy

Zusammenfassung

Aus oberkretazischen Ablagerungen der oberkretazischen Unteren Gosau Gruppe der Pletzsch Alm, nahe Kramsach (Tirol, Österreich) wird eine Gastropoden-Vergesellschaftung beschrieben. Diese ist durch eine diverse Fauna von Aporrhaidae gekennzeichnet. Die Fauna enthält die Aporrhainae *Quadrinervus* cf. *subtilis* (ZEKELI) und *Biculteriala gratti* nov. gen. nov. spec., die Anchurinae *Pletzschia trifurcata* nov. gen. nov. spec., sowie die Harpagodinae *Harpodactylus marolti* nov. gen. nov. spec., und *Rhombovomeria passer* (ZEKELI). Die Vergesellschaftung umfasst außerdem Vertreter der Trochidae, Turbinidae, Cassiopidae, Gyrodidae, Ampullinidae, Diozoptyxidae und Acteonellidae und stammt aus dem distalen inneren Schelfbereich.

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Mit Hilfe der Morphologie des Teleoconchs (Umgänge und Mündungsflügel) werden die mesozoischen Aporrhaidae in sieben, teilweise neue, Unterfamilien untergliedert.: Die Spirigerinae KOROTKOV, Aporrhaidae GRAY, Pterocerellinae BANDEL (2007), Harpagodinae PCHELINTSEV (1963), Pugnellinae KIEL & BANDEL (1999), Anchurinae nov. subfam., Arrhoginae POPENOE (1983), Dimorphosominae nov. subfam. und Struthiopterinae ZINSMEISTER & GRIFFIN (1995). Ausgehend von den Spirigerinae kommt es im mittleren Jura zu einer ersten Ausbreitung mit dem Erstauftreten der Aporrhaidae, Pterocerellinae, Harpagodinae und Dimorphosominae. Die zweite Entwicklungsphase der Aporrhaidae findet im Albium (höhere Unterkreide) statt. Bei dieser gehen aus den Dimorphosominae die Anchurinae, Arrhoginae und Pugnellinae hervor. Aus den Arrhoginae entwickeln sich im Maastrichtium in unterschiedlichen Faunenprovinzen die Hippochrenidae und die Calyptraphoridae, die zu den Paläogenen Stromboidea überleiten.

Schlüsselworte: Gastropoda, Aporrhaidae, Ober-Kreide, Gosau Gruppe, Österreich, Taxonomie

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1. Introduction

The fossiliferous Upper Cretaceous Gosau Group of the Pletzsch Alm in the Sonnbjerg mountain range (North Tyrol, Austria) is known since the second half of the 19th century. Fossil lists have been published by MÜNSTER in GOLDFUSS (1844), PICHLER (1869, 1871), LECHLEITNER (1886), KLIPSTEIN (1885), SCHLOSSER (1895), but the fauna has never been formally described. The present contribution deals with the gastropod assemblage which has been collected by Herbert GRATT and Alexander MAROLT. Most remarkable are new taxa of Aporrhaidae. Although the outer shell layers are incomplete, they provide sufficient evidence for the scientific description.

All holotypes and figured specimens are kept in the collection of the Natural History Museum Vienna, Department of Geology and Palaeontology.

2. Earlier contributions to the Cretaceous gastropod assemblages of the Pletzsch Alm

According to SCHLOSSER (1895), Cretaceous taxa described by MÜNSTER in GOLDFUSS (1844) from the Tyrolian Alps ("e montibus Tyroliae") had their origin on the Pletzsch

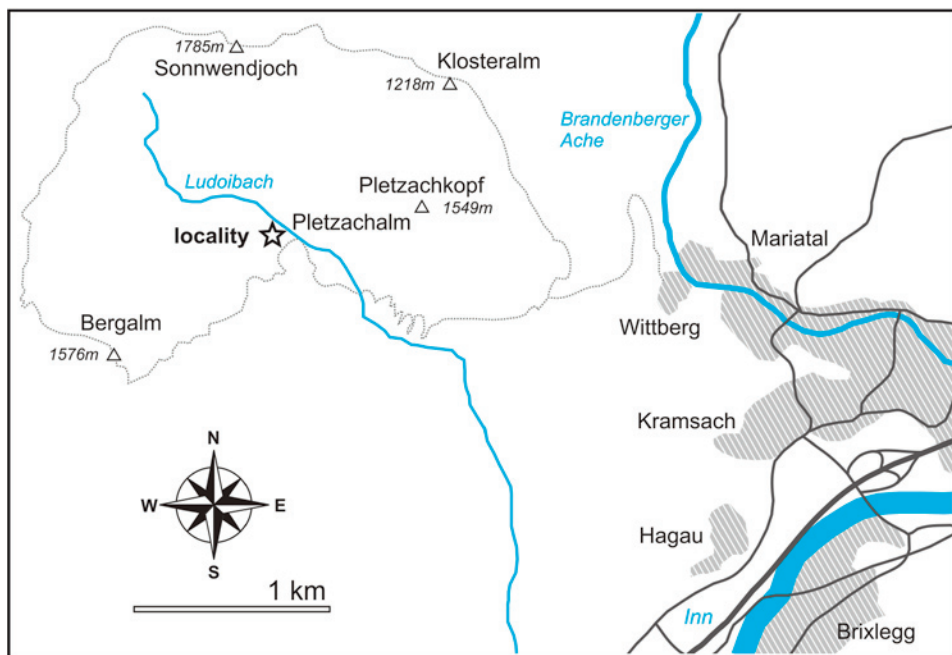


Fig. 1. Position of the fossil locality

Alm. Two taxa (*Cerithium millegranum* MÜNSTER, *Trochus plicatogranulosus* MÜNSTER) were first described from this locality. Under the locality name Sonnwendjoch, PICHLER (1869) gave a short list of fossils from the same area. Among others, an *Acteonella* cf. *renauxiana* ZEKELI (recte *Trochactaeon*), several *Cerithioidea*, and a small *Nerineoidea* taxon were listed by PICHLER. The gastropods had been determined by K. ZITTEL. As there is no reference to the revisions of gastropods from the Gosau Group by REUSS (1853) and STOLICZKA (1865) the monograph by ZEKELI (1852) has obviously served exclusively for the determinations. In a short note, PICHLER (1871) mentions a *Pileolus tirolensis* from the “Ladoi am Sonnwendjoch”. This species has never been formally described.

For a more detailed description of the geological situation of the “Ladoialpe” (Ludoi Alm of the current topographical map of Austria, scale 1:50.000) we owe KLIPSTEIN (1885). He recorded about 60 taxa, mainly gastropods and anthozoans. KLIPSTEIN pointed out that the fossils were in a secondary position.

LECHLEITNER (1886) rectified KLIPSTEIN’s locality name into Pletzach Alm. He further contradicted Klipstein concerning the rareness of *Trochactaeon* and the total lack of “*Cerithium*” *fenestratum* and *C. haidingeri* in this locality.

SCHLOSSER (1895) gave a more concise description of the geology and fauna of the Pletzach Alm. With *Pterocera haueri* ZEKELI (1852) and *Pt. passer* ZEKELI two Harpagodinae taxa were included in the list. Three other species of Aporrhaidae mentioned in the list do not occur at our locality.

LEIS (1988) quoted *Trochactaeon*, *Nerinea* and other taxa from shales of approximately 80 cm thickness. The gastropod fauna is accompanied by corals, and bivalves (rudists and ostreids). The composition of the assemblage is therefore different from that described here.

3. Locality and Stratigraphy

Pletzsch Alm close to Kramsach, Tyrol (Alm is the terminus for an alpine pasture). The topographic position is shown in Figure 1. The GPS Coordinates determined by H. GRATT are: 11°79' 58" East, 47°27' 09" North.

The deposits of the Pletzsch Alm belong to the Late Cretaceous Lower Gosau Group. The exact biostratigraphic position is unknown.

4. Abbreviations

The morphological terminology used in the systematic part follows in general POPENOE (1983). The following abbreviations are used:

| | |
|----|--------------------------|
| H | Total height of shell |
| B | Maximum breadth of shell |
| LW | Height of last whorl |
| AA | Apical angle |

5. Description of taxa

Superfamily Trochoidea RAFINESQUE, 1815

Family Trochidae RAFINESQUE, 1815

Subfamily Trochinae RAFINESQUE, 1815

Genus *Discotectus* FAVRE, 1913

***Discotectus plicatogranulosus* (MÜNSTER in GOLDFUSS, 1842)**
(pl. 1, fig. 4)

- 1842 *Trochus plicato-granulosus* MÜNSTER in GOLDFUSS, p. 60, pl. 182, fig. 3
- 1852 *Trochus plicato-granulosus* MÜNSTER – ZEKELI, p. 50, pl. 9, fig. 2
- 1852 *Trochus coarctatus* ZEKELI, p. 50, pl. 9, fig. 3
- 1852 *Trochus triqueter* ZEKELI, p. 49, pl. 4, fig. 16, pl. 1, fig. 31
- 1969 *Trochus coarctatus* ZEKELI – SCHENK, p. 16, pl. 1, fig. 3

Material: NHMW 2008z0015/0014

Type: The species was first described by MÜNSTER in GOLDFUSS (1842) from the “Tyrolian Mountains”. According to SCHLOSSER (1895), the actual locality is the Pletzsch Alm. A type has not been determined.

Description: Small, high trochiform shells. Whorls imbricating, sculpture consisting of 3 spiral ribs and 4 on last whorl. Periphery of last whorl angular.

Remarks: *Trochus triqueter* ZEKELI, 1852, is synonymous with *T. plicatogranulosus* MÜNSTER. The imbrication of the whorls is systematically not relevant. Specimens of the same species in which the external shell layer was not preserved were named *T. coarctatus* by ZEKELI (1852).

The umbilical pouch which is typical for *Discotectus* is not preserved but the angulate periphery and the concave base leave no doubt about the generic assignment.

Localities: In addition to the Pletzsch Alm, ZEKELI (1852) recorded *D. plicatogranulosus* from the Santonian Hochmoos Formation of the Wegscheidgraben of Gosau (Upper Austria) and from the Nefgraben close to Russbach, Salzburg, both in the basin of Gosau.

Family Turbinidae RAFINESQUE, 1815

Subfamily Angariinae GRAY, 1857

Genus *Angaria* RÖDING, 1789

***Angaria pelossei* (ROMAN & MAZERAN, 1920)**

(pl. 1, figs 1-3)

1920 *Delphinula pelossei* ROMAN & MAZERAN, p. 33, pl. 5, fig. 3,

1964 *Angaria* (*Angaria*) *aculeata* (ZEKELI) – BENKÖ-CZABALAY, p.159, pl.1, fig. 1–3

Material: NHMW 2008z0015/0013

Description: Shells small, almost discoidal, with flat spire. Upper whorl face with 3 to 4 spiral rows of hollow nodes; periphery high on whorl, angular, with coarse spines. Base deeply convex, with 6 closely spaced rows of nodes. Umbilicus moderately broad, delimited by rounded shoulder, bearing some widely spaced rows of nodes.

Remarks: *Delphinula pelossei* is allocated to *Angaria* because of the radial position of its aperture. *Nummogaultina* KOLLMANN, 2005, has a similar sculpture. It differs from *Angaria* by its strongly oblique aperture and belongs therefore to the *Astraeinae* DAVIES, 1933. Among living taxa of *Angaria* RÖDING the outline of the shells varies considerably (see HICKMAN & MCLEAN 1990).

While small specimens are almost disk-shaped, the height of the base and the spire increase with ontogeny. Large specimens reach dimensions like in *Delphinula pelossei* ROMAN & MAZERAN, 1920, from Uchaux, France. *Angaria aculeata* BENKÖ-CZABALAY, 1964, non ZEKELI, 1852, from Sümeg, Hungary, falls within the variability of *Angaria pelossei*. *Delphinula muricata* ZEKELI, 1852, and the synonymous *D. aculeata* ZEKELI

(see STOLICZKA 1865), possess broad shells with low bases and spires of medium height.

L o c a l i t i e s : Late Turonian deposits of Uchaux, France.

Superfamily Cerithioidea FLEMING, 1822

Family Cassiopidae BEURLIN, 1962

Genus *Cassiope* COQUAND, 1862

***Cassiope suffarcinata* (MÜNSTER in GOLDFUSS, 1844)**

(pl. 1, fig. 6)

1844 *Cerithium suffarcinatum* MÜNSTER in GOLDFUSS, p. 36, pl. 174, fig. 10

1984 *Hexaglauconia lanzingensis* MENNESSIER, p. 41, pl. 9, fig. 3-6

1988 *Cassiope suffarcinata* CLEEVELY & MORRIS, p. 242, fig. 2

M a t e r i a l : NHMW 2008z0015/0016

D e s c r i p t i o n : Shell coniform. Whorls flat sided, sculpture of 3-4 coarsely noded spiral ribs.

R e m a r k s : The taxonomy of the *Cassiopidae of the Alpine Cretaceous* and especially that of *C. suffarcinata* MÜNSTER, 1844, has been discussed by CLEEVELY & MORRIS (1988). Additionally to the synonymies given by these authors, *Hexaglauconia lanzingense* MENNESSIER, 1984, falls within the variability of *Cassiope suffarcinata*.

L o c a l i t i e s : Lower Gosau Group (Turonian) of Gams bei Hieflau (Styria, Austria) and Lanzing (Lower Austria).

Superfamily Stromboidea RAFINESQUE, 1815

Family Aporrhaidae GRAY, 1850

R e m a r k s : The taxonomic subdivision of Mesozoic Aporrhaidae which is applied here will be discussed in the appendix.

Subfamily Aporrhainae GRAY, 1850

Genus *Quadrinervus* COSSMANN, 1904

***Quadrinervus carinatus* (DELPEY, 1939)**

(figs 2.1, 2.2)

1939 *Chenopus carinatus* DELPEY, p. 99, textfig. 12

M a t e r i a l : NHMW 2008z0015/0004 - 0005

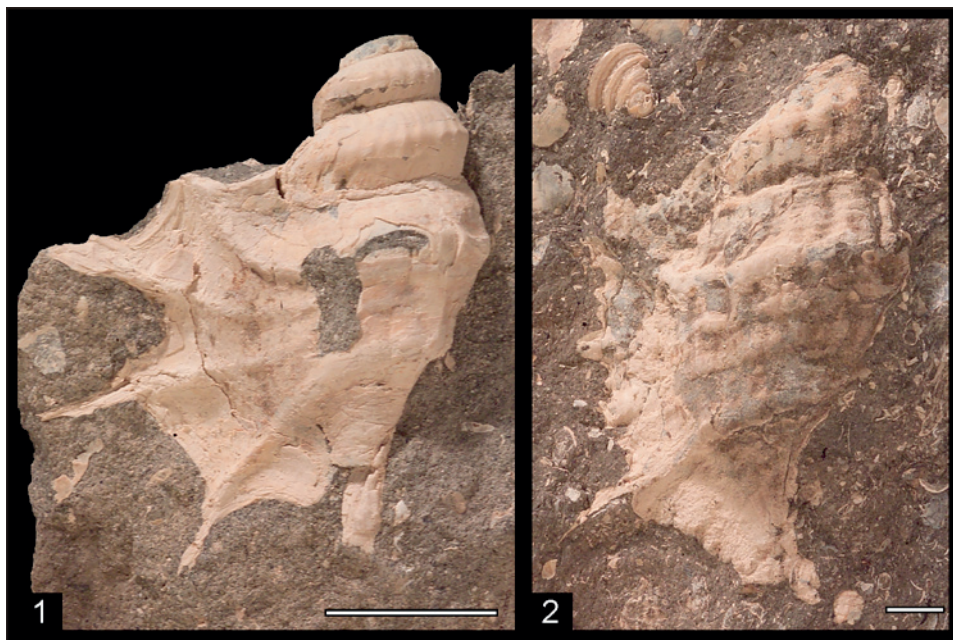


Fig. 2. *Quadrinervus carinatus* (DELPEY). 2.1. Almost complete small specimen, NHMW 2008z0015/0004; 2.2. Large internal mould with shell remains; wing not preserved, NHMW 2008z0015/0005. Scale bars equal 10 mm

Description: The spire is broadly turriculate and its whorls are distinctly angulate with broad, inclined subsutural ramps. The abapical whorl face tapers slightly towards the shell axis. The sculpture consists of moderately opisthocline collabral ribs. They are most prominent on the ramp and form elongate nodes on the angulation.

The last whorl is high and the subsutural ramp steep and slightly concave. In both specimens the ramp is terminated by a distinct angulation. Another angulation limits the base which is low and slightly concave. In the large internal mould (Figure 2.2) broad collabral ribs and four delicate spiral ribs are preserved on the ramp. The angulations bear strong spiral ribs, two more are developed on the whorl face between them. The labral wing is broad. The two angulations and two of the ribs in between extend to wing's external margin where they end in moderately long spines. The proximal digitation is rather short and not attached

Measurements (in mm)

| H | B, including wing | B, without wing |
|----|-------------------|-----------------|
| 55 | 23 | 17 |

Records: *Quadrinervus carinatus* (DELPEY, 1939) has been recorded from Late Turonian deposits of the Charente (France).

Remarks: *Quadrinervus subtilis* (ZEKELI, 1852) from the Gosau Group (see also REUSS 1853), is closely related to *Quadrinervus carinatus* DELPEY, 1939. It differs by

its labral wing which surpasses the height of the spire and having one acute rib between the angulations of the last whorl while *Qu. carinatus* possesses two.

Genus *Biculteriala* nov. gen.

N a m e : *Bi* = two; *culter* = knife (lat.); *ala* = wing (lat.)

T y p e s p e c i e s : *Biculteriala gratti* nov. gen, nov. spec.

D i a g n o s i s : High turruculate spire, whorls angulate, with collabral ribs. Last whorl high, with two angulations extending to the labral wing. Wing broad, with two rather narrow digitations bent in adapical direction. Rostrum long, bent.

R e m a r k s : The new genus was hitherto only represented by its type species. It is considered as an *Aporrhinae* genus because of the angulated whorls, the two digitations of the labral wing and the bent rostrum. It differs from *Aporrhais* by its longer rostrum and the digitations which are bent adapically. The incision between the digitations is deep, its margins form a right angle.

***Biculteriala gratti* nov. spec.**

(figs 3.1-3.3)

N a m e : After Herbert GRATT who has collected the fossil material in the field and made it available to scientific investigations.

H o l o t y p e : NHMW 2008z0015/0006,

P a r a t y p e s : NHMW 2008z0015/0007-0008

D i a g n o s i s : See generic diagnosis.

D e s c r i p t i o n : The whorls possess a broad, strongly inclined subsutural shoulder which is delimited by an angulation. On the shoulder, the collabral ribs are slightly prosocyr and more accentuated than on the abapical whorl face. They form nodes on the angulation.

The last whorl is more than half of the total height. Its subsutural shoulder is broad. Abapically, the whorl face is convave and delimited towards the base by a second angulation. The rostrum is long and strongly bent.

The labral wing is broad and possesses two blade-shaped digitations which both point in an adapical direction. The surface of the wing shows a sculpture of indistinct spiral ribs and growth lines. The adapical angulation extends to the upper digitation and the abapical angulation to the lower. The margin of the wing is deeply incised between the digitations, the sides of the incisions form an acute to right angle.

M e a s u r e m e n t s (in mm):

| H | B, including wing | B, without wing | LW | AA |
|----|-------------------|-----------------|----|-----|
| 77 | 52 | 23 | 66 | 30° |

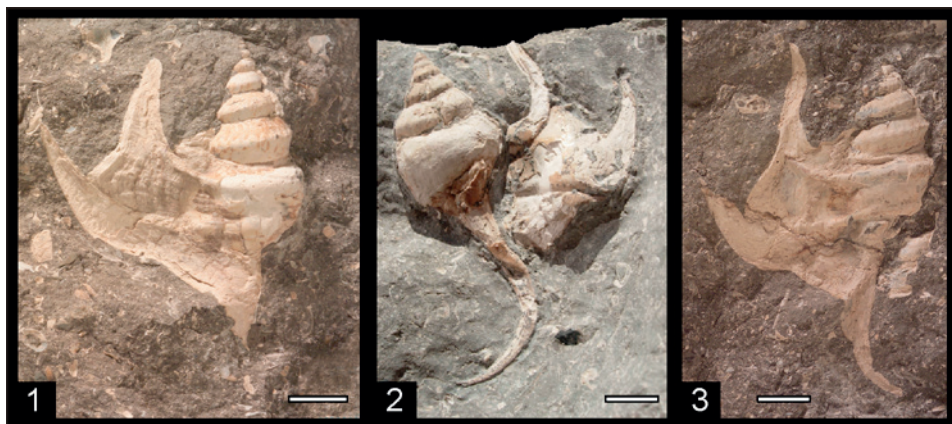


Fig. 3. *Biculteriala gratti* nov. gen. nov. spec. 3.1. Holotype, NHMW 2008z0015/6 ; 3.2. Paratype, showing a complete rostrum, NHMW2008z0015/0007; 3.3. Paratype NHMW 2008z0015/0008. Scale bars equal 10 mm

R e m a r k s : There are only fragments of the outer shell layer preserved on the last whorl. An eventual spiral sculpture like on the earlier whorls is not discernable.

Family Anchurinae nov. subfam.

Genus *Pletzachia* nov. gen.

D i a g n o s i s : Large Anchurinae genus, wing not attached to the spire, externally rounded, with two large digitations pointing in adapical direction.

T y p e s p e c i e s : *Pletzachia furcata* nov. gen. nov. spec.

R e m a r k s : The proximal digitation is prominent and not attached to the spire. The two distal digitations point upwards. Between them and the proximal digitation an additional thorn-like extension is developed.

Anchura CONRAD, 1860, differs from *Pletzachia* nov. gen. by its narrow and bipartite labral wing.

***Pletzachia furcata* nov. gen. nov. spec.**
(figs 4.1-4.3)

M a t e r i a l : 3 specimens, all incomplete

H o l o t y p e : NHMW 2008z0015/0009

P a r a t y p e s : NHMW 2008z0015/0010-0011

N a m e : *Furca* = Fork (lat.), after the shape of the labral wing.



Fig. 4. *Pletzachia furcata* nov. gen. nov. spec. 4.1. Holotype, NHMW 2008z0015/0009; 4.2. Paratype with broad shell, NHMMW 2008z0015/0010; 4.3. Paratype showing the proximal digitation, NHMW 2008z0015/0011. Scale bars equal 10 mm

D i a g n o s i s : Shell large, shoulder of last whorl passing into keel of the wing and extending farther into the prominent distal digitation. Proximal digitation very long and narrow, almost parallel to shell axis. Small thorn between digitations.

D e s c r i p t i o n : The shell is large and high turriculate, the apical angle approximately 30° . The whorls are convex with a narrow sutural neck and a sculpture of strong, prosocline collabral ribs which are rounded on top. A spiral sculpture is not discernable.

The last whorl possesses a broad, rounded shoulder. The labral wing is smooth. A strong keel escaping from the margin of the shoulder extends into the distal digitation. The proximal digitation is long, delicate and almost parallel to shell axis. Its posterior angulation is generated on the wing above the angulation. Between these digitations a small but broad thorn is located. The external margin of the labral wing is incomplete in any of the specimens but seems to be broadly rounded. In one specimen (Figure 4.2.) a short rostrum is preserved.

M e a s u r e m e n t s (in mm):

| H | B, including wing | B, without wing |
|----|-------------------|-----------------|
| 56 | 2 | 54 |

R e m a r k s : The basal part is not preserved in any of the specimens. The convex whorls and the keel of the proximal digitation escaping above the main keel of the wing resemble an equally insufficiently preserved specimen from the Late Santonian of the Gosau Group which has been determined as *Cuphosolenus* sp. by KOLLMANN (1980). *Chenopus olisiponensis* CHOFFAT, 1886, from Alcantra, Portugal, agrees by its sculpture and the accentuated rib bending adapically from the shoulder of the last whorl. Also in this specimen the larger part of the wing is not preserved and the relationship with *Pletzachia furcata* nov. gen. nov. spec. is uncertain.

Subfamily Harpagodinae PCHELINTSEV, 1963

Genus: *Harpodactylus* nov. gen.Name: After *harpa* = sword (lat.) and *dactylus* = finger (lat.)Type species: *Harpodactylus marolti* nov. spec.

Diagnosis: Large shells with angular whorls; last whorl cylindrical, with two strong angulations and a sculpture of spiral ribs. Ribs and angulations proceed onto the broadly expanded wing where they end in acute digitations. The rostrum is strongly circularly bent apexward.

Other species belonging to *Harpodactylus* nov. gen.: *Rostellaria pinnipenna* ZEKELI, 1852, from the Blahberg, close to Windischgarsten, Austria; *Rostellaria ovata* MÜNSTER in GOLDFUSS, 1844, from the Campanian of Haldem, Westfalen, Germany.

Remarks: *Harpodactylus* nov. gen. differs from other genera of the Harpagodinae PCHELINTSEV by the strongly angular whorls of the spire and the almost cylindrical last whorl. *Phyllocheilus* differs by its convex whorl and the labral wing which is broadly attached to the spire.

***Harpodactylus marolti* nov. gen. nov. spec.**

(figs 5.1-5.3)

Name: After Alexander MAROLT, who has also provided material from the Pletzsch Alm.

Holotype: NHMW 2008z0015/0001

Paratypes: NHMW 2008z0015/0002-0003

Diagnosis: *Harpodactylus* with broad, concave subsutural ramp and concave lower whorl face bearing a strong ribbon in the middle.

Description: The shells are large and the spire broadly turriculate. The whorls possess a broad, inclined subsutural ramp which is delimited by an acute angulation. The abapical whorl face is slightly oblique towards the shell axis. The sculpture consists of spiral threads and irregular fold-like opisthocline collabral ribs which form irregular nodes at the angulation.

The last whorl is about 2/3 of the total height. The abapical whorl face is concave. The angulations towards the subsutural ramp and the concave base bear strong ribbons. A third ribbon is located in the middle of the abapical whorl face. There are also traces of spiral threads preserved. The rostrum is strongly bent.

The ribbons extend to the broadly expanded wing where the middle one splits into two or three. These and the ribbons emerging from the angulations extend into spines at the margin of the wing.

Remarks: The subdivision of the middle ribbon is different in various specimens and lies obviously within the variability of the species. All other morphological characters are constant.



Fig. 5. *Harpodactylus marolti* nov. gen. nov. spec. 5.1. Holotypus, NHMW 2008z0015/0001; 5.2. Paratype showing sculpture of spire whorls, NHMW 2008z0015/0002 (specimen coated with ammonium chloride); 5.3. Paratype showing sculpture of last whorl, NHMW 2008z0015/0003. Scale bars equal 10 mm

There is a close relationship with *Rostellaria pinnipenna* ZEKELI, 1852, from the Blahberg (Windischgarsten, Upper Austria). Its type specimen, kept in the collection of the Austrian Geological Survey, is an internal mould with impressions of the wing (fig. 6.1) Similar to *H. marolti*, it possesses a broad spire and angular whorls. The abapical whorl face is higher and bears delicate spiral ribs. The labral wing is more expanded than in *H. marolti*. The digitations shown by ZEKELI (1852, plate 12, fig. 5) do actually not exist and the rostrum is less bent.

Genus *Rhombovomeria* nov. gen.

Type species: *Rostellaria passer* ZEKELI, 1852, p. 68, pl. 12, fig. 6

Name: *Rhombus* = the rhombic outline of the wing; *vomer* = ploughshare (lat.), because of the shape of the wing.

Diagnosis: High-spired shell; last whorl high, bi-angulate, with more or less well-developed shoulder; sculpture of ribbons on and between angulations; labral wing narrow, with rounded processes at the end of the ribbons.

Remarks: This new genus is part of the Harpagodinae PCHELINTSEV, 1963. From the angular body whorl, ribbons extend to the margin of the labral wing where they form spines. The sculpture of the wing is similar to that of *Harpodactylus* but not as broadly expanded and the spines are more delicate.

Rhombovomeria passer (ZEKELI, 1852) (figs 6.2)

1852 *Rostellaria passer* ZEKELI, p.68, pl. 12, fig. 6

1853 *Rostellaria passer* ZEKELI – REUSS, p. 906



Fig. 6. 6.1 *Harpodactylus pinnipenna* (ZEKELI, 1852), Holotype, Blahberg (Windischgarsten, Upper Austria), Geologische Bundesanstalt Vienna. Specimen coated with natrium chloride ; 6.2. *Rhombovermeria passer* (ZEKELI, 1852), figured specimen, NHMW 2008z0015/0012 . Scale bars equal 10 mm

Material: NHMW 2008z0015/0012

Description: The shell is large and the spire high. The whorls are strongly convex and show traces of collabral ribs and spiral threads. The last whorl is high, the strongly inclined subsutural ramp is terminated abapically by an indistinct angulation. The sculpture is clathrate and consists of widely spaced collabral ribs and almost equally strong spiral ribs. The labral wing is massive, triangular in outline and attached to the penultimate whorl. Adapically, it extends into a broad, lanceolate digitation. The external margin shows irregular, rounded processes with narrow incisions. The rostrum is not preserved.

In the internal mould, the angulation terminating the ramp abapically is more accentuated. Another angulation is developed towards the base. The whole whorl including the base is covered by weak spiral ribs. Each angulation bears a ribbon, two additional ribbons are located on the whorl face between them. The ribbons extend to the margin of the labral wing where they form short spines.

Measurements of the holotype (in millimetres):

| H | B, including wing | B, without wing | AA |
|----|-------------------|-----------------|-----|
| 52 | 16 | 40 | 35° |

Remarks: The whorl morphology and the sculpture of the internal mould agree with the figure given by ZEKELI (1852). In the internal mould, the whorls are more rounded but agree by their sculpture. ZEKELI figures a thin, bent rostrum. According to STOLICZKA (1865) it is actually shorter and the inner lip is broadly expanded.

Superfamily Ampullinoidea LOZOUET, LESPORT & RENARD, 2001

Family Gyrodidae WENZ, 1941

Genus *Gyrodes* CONRAD, 1860

***Gyrodes amplissima* (M. HÖRNES, 1856)**

(pl. 1, fig. 10)

1856 *Natica amplissima* M. HÖRNES, p. 178, pl. 2, fig. 2

1865 *Natica amplissima* M. HÖRNES – STOLICZKA, p. 149

Type locality: Lower Gosau Group; Eisenau near Gmunden, Upper Austria

Material: NHMW 2008z0015/0020

Description: Shells very large, globular, whorls moderately convex, converging in adapical direction; subsutural ramp broad, concave.

Remarks: The two specimens are distorted and their outer shell layers are missing. The large size, the shell outline and the broad subsutural ramp agree with *Natica amplissima* M. HÖRNES, 1856. Because of the preservation, the prosocline growth lines and the sculpture of broad ribbons of the original cannot be observed. The base is covered by matrix. The original possesses a moderately broad umbilicus with a small, acute umbilical fold.

POPENOE, SAUL & TAKEO SUSUKI (1987) have subdivided *Gyrodes* into 4 subgenera. All of them are smaller in size, the outline of the shell is not as broad as that of *G. amplissima* and no ribbons are developed. Although the species is not typical for *Gyrodes*, it fits into this genus by its broad subsutural ramp, the prosocline growth lines and the umbilicus. The original shows a distinct “sheath” which determines the systematic position within the Ampullinoidea (KASE & ISHIKAWA 2003).

Family Ampullinidae COSSMANN, 1919

Genus *Pseudamaura* P. FISCHER, 1885

***Pseudamaura brevissima* (REUSS, 1852)**

1852 *Natica angulata* Sowerby – ZEKELI, p. 46, pl. 8, fig. 4

1853 *Natica brevissima* REUSS, p. 150

1865 *Natica bulbiformis* SOWERBY – STOLICZKA, p. 146 (pars)

Material: NHMW 2008z0015/0015

Type locality: Gams bei Hieflau, Styria, Lower Gosau Group, Schönleiten Formation, Late Turonian

Description: Shell globular, anomphalous, with moderately inflated whorls and a flat subsutural ramp. Inductura strongly inflated.

Remarks: *Pseudamaura brevissima* differs from the widely distributed *A. bulbiformis* by its low last whorl. The sutural ramp is flat but not impressed. The inductura is thick forming a well-rounded deposit over inner and basal lip.

ZEKELI (1852) assigned the taxon to *Natica angulata* SOWERBY, 1832, a species that is much smaller, anomphalous, and does not possess a distinct subsutural ramp.

Superfamily Campaniloidea DOUVILLÉ, 1904

Family Diozoptyxidae PCHELINTSEV, 1965

Genus *Armenocerithium* EGOYAN, 1955

***Armenocerithium haidingeri* (ZEKELI, 1852)**

(pl. 1, figs 7-9)

1852 *Cerithium Haidingeri* ZEKELI, p. 115, pl. 24, fig. 3 - 5

1852 *Cerithium fenestratum* ZEKELI, p. 117, pl. 24, fig. 8

1865 *Cerithium* (?*Vibex*) *Haidingeri* ZEKELI – STOLICZKA, p. 214

Material: NHMW 2008z0015/0017-0019

Type locality: Lower Gosau Group, Eisenau near Gmunden, Upper Austria

Material: 2 specimens, apertures covered by matrix.

Description: Shells very large and high turriculate; whorls flat, with sculpture of regular, slightly prosocline to orthocline collabral ribs of low profile; sutures linear; periphery angulate, base moderately convex; aperture with short, broad siphonal canal.

Remarks: The large size, the flat whorls and a sculpture of broad but flat collabral ribs qualifies the species as *Armenocerithium* EGOJAN, 1955. The genus is assigned to the Campaniloidea because of the large and solid turriiform shell and the internal plication.

The common occurrence of *Cerithium fenestratum* ZEKELI, 1852, and *C. haidingeri* in the Eisenau and at the Pletzsch Alm suggests a dimorphism. STOLICZKA, loc. cit., has already pointed out the possibility of a synonymy between *Cerithium haidingeri* and *C. matheronii* d'ORBIGNY, 1843. In the latter, the ribs are slightly opisthocline, not as broad and more numerous than in *A. haidingeri* (see KOLLMANN 2005). *Cerithium sanctiarromani* PERON, 1889, has comparable dimensions but the ribs are slightly bent. ALBANESI & BUSSON (1974) show the existence of a parietal plait which develops inside the shell.

6. Discussion of the assemblage

PICHLER (1869), LECHLEITNER (1886) and LEIS (1988) have mentioned the abundance of *Trochactaeon* (“*Actaeonella*”) in the assemblages. This genus is widely distributed in the Lower Gosau Group but the present assemblage contains only a single fragment of a high-spined species (? *T. lamarcki* J.de C. SOWERBY (1832). HERM (1977), SANDERS & al. (1997) and KOLLMANN (2005a) have shown that *Trochactaeon* inhabited the proximal inner shelf, where it formed mostly monospecific assemblages. In contrast to this environment, the Aporrhaidae were restricted to the distal inner shelf and to the proximal outer shelf. This is supported by (indeterminable) specimens of Turritellidae which, according to ALLMON (1988), prefer soft substrates. The environments did not overlap. The irregular positions of the gastropods in the sediment and the displacement of bivalve shells indicate a temporary disturbance of the environment by storm waves.

7. On the taxonomy of Mesozoic Aporrhaidae

Following in general the taxonomic concept of COSSMANN (1904), WENZ (1940) considers the distinction between the Strombidae and the Aporrhaidae as arbitrary. Accordingly, he did not establish new taxonomic categories between the family and the generic level. The assemblage described here represents hitherto unknown taxa of Aporrhaidae. This required more closely examining the systematic position and the relationship between the Aporrhaidae and the Strombidae.

In the last decades, various families and subfamilies of Aporrhaidae have been introduced by PCHELINTSEV (1963), KOROTKOV (1992), KIEL & BANDEL (1999) and BANDEL (2007). KOROTKOV (1992) introduced the order Strombiformes and replaced the Aporrhaidae of other authors with four families: the Aporrhaidae, Dicrolomidae, Perissopteridae and Spinigeridae. No higher-ranking taxon for the Aporrhaidae in the common sense is retained. BOUCHET & ROCROI (2005) treat KOROTKOV’s families as subfamilies of the Aporrhaidae. Independent of the rank, KOROTKOV’s subdivision of the Aporrhaidae into families is not consistent. The same applies to DEKKERS (2008), who considers the Harpagodidae, the Pugnellidae and the Aporrhaidae as separate families of the superfamily Stromboidea.

Like KOROTKOV, l.c. and DEKKERS, l.c., BANDEL (2007) does not retain a higher-ranking taxon to embrace the Aporrhaidae of other authors. He divides them into 5 families which he positions in the Stromboidea RAFINESQUE, 1815: The “Alariidae, KOKEN, 1889”, Spinigeridae KOROTKOV, 1992, Aporrhaidae GRAY, 1850, Pterocerellidae BANDEL, 2007 and the Pugnellidae KIEL & BANDEL, 1999, with two subfamilies: the Pugnellinae s.s. and the new subfamily Tundorinae BANDEL, 2007.

Of these taxa, especially the Alariidae require some comments. The genus *Alaria* was introduced by MORRIS & LYCETT (1854). The generic name *Alaria* is invalid as it has been applied before to a butterfly and a worm (BOUCHET & ROCROI 2005). Concerning the family name Alariidae, BOUCHET & ROCROI (2005) and BANDEL (2007) refer to KOKEN (1889). This is a mystification because KOKEN’s paper does not mention a family Alariidae (and indeed could not because it deals with Cambrian to Triassic gastropods!).

The family name Alariidae is invalid from a nomenclatorial standpoint because of the invalidity of the generic name *Alaria* MORRIS & LYCETT, 1854. BANDEL's argumentation that it is restricted to Jurassic taxa is certainly correct in itself, but does not change the fact that it is a younger homonym.

BANDEL, l.c., defines the "Alariidae" as follows (original quotation): "The spire of the shell is conical and ornamented by axial spiral elements, have no varices with the exception of *Diarthema* with varices on the body whorl. The fully grown shell has the outer lip expanded. Its margin extends into one to several spines with groove on their inner side. The siphon (rostrum) is also a spine-like canal that may be straight or curved to the left or right. The protoconch is conical with rounded whorls of the morphology as found in modern *Aporrhais*."

The seven genera allocated by BANDEL, l. c. to the "Alariidae" are diverse. They comprise taxa with convex or angulated whorls and labral wings which vary between a simple, sword-like digitation (*Cuphotifer*), two digitations (*Dicroloma*) and broadly expanded wings (for example *Phyllocheilus*). The flaring labral wing and the median keel of the whorls, which according to BANDEL are characteristic for the Aporrhaidae, may be equally observed in "Alariidae" genera like *Cuphosolenus*. On the other hand some of the taxa assigned by BANDEL to the Aporrhaidae do not show this combination of characters, as for example *Arrhoges* GABB.

Like KOROTKOV's (1992) systematic concept of the Aporrhaidae, the concept of Bandel seems to be inconsistent, at least as far as the teleoconchs are concerned. The concept of the Mesozoic Aporrhaidae presented here is based on the following morphological characters (see outline drawings on pl. 2):

1. The whorl profile (angular, multi-angular or evenly convex) and the sculpture of the whorls (collabral ribs, spiral ribs or clathrate sculpture; sculpture of the last whorl).
2. The general outline of the labral wing. YONGE (1937) and SAVAZZI (1991) have demonstrated in *Aporrhais pespelicani* (LINNÉ) that the shape of the wing is closely related to the mode of life. Among the Aporrhaidae subfamilies distinguished below, three types of labral wings occur:

- A broadly expanded wing with an abapical sinus (Aporrhainae, Pugnellinae, Arrhaginae, Struthiopterinae). It corresponds with the wing of Recent *Aporrhais*. YONGE (1937) has shown the function of the wing in entering the sediment at a low angle to the surface and establishing a chamber for separating the inhalant and the exhalant currents (see also POPENOE 1983; SAVAZZI 1991). It further supports the animal on the substrate and the landing after a leap.

- A prolongation into spines, including a pseudo-canal Spinigerinae, Harpagodinae, Pterocerinae) which has to be interpreted as "snowshoe" adaption (SAVAZZI 1991). In the Harpagodinae an apical sinus is developed additionally; it probably served to direct the exhalant current.

- A plough-shaped wing (Dimorphosominae, Anchurinae). The blade-shaped wing was probably used for entering the sediment at a low angle to the surface.

8. Aporrhaidae taxa above the generic level

Superfamily Stromboidea RAFINESQUE, 1815

Family Aporrhaidae GRAY, 1850

Subfamily Spinigerinae KOROTKOV, 1991

D i a g n o s i s : High turriculate taxa; whorls strongly angulate, smooth or with sculpture of strong collabral and weak spiral ribs; *Spinigera* with spines at right angle to shell axis; sculpture of final whorls sometimes reduced, with straight or slightly bent labral spine (pl. 2, fig. 1).

T y p e g e n u s : *Spinigera* d'ORBIGNY (1850)

N o m e n c l a t o r i a l r e m a r k : There is a peculiar discrepancy concerning the year of publication of *Spinigera* d'ORBIGNY. In the first volume of the Prodrôme, d'ORBIGNY (1850) refers to "d'Orb., 1847". The same year has also been quoted by PIETTE (1891) for the first description of the genus. COSSMANN (1904) who has retained this date refers on the other hand to the above-mentioned volume of the Prodrôme which was published in 1850. There is in fact no publication by d'Orbigny in 1847 in which *Spinigera* could have been described (BARTA-CALMUS 2002).

R e m a r k s on the subfamily. *Spinigera huddlestoni* WILSON, 1887, of Sinemurian (Lower Liassic) age is the oldest known Aporrhaidae species. In early whorls of the teleoconch, collabral ribs are crossed by spiral threads. The penultimate and last whorls are weakly angulate, their sculpture consists exclusively of spiral threads. On the last whorl, digitations are developed opposite to the aperture and at the aperture.

According to figures by HUDLESTON (1887) the shell morphology of *Spinigera* taxa is quite variable. Besides species with convex whorls and weak spiral ribs like *Spiniger longispinus* DESLONGCHAMPS, others with angulated whorls (*Spinigera recurva* HUDLESTON) or two angulations (*Sp. rollieri* de LORIO, 1901) exist. In some species, collabral ribs are developed on the early teleoconchs. *Pietteia* COSSMANN, 1904, a broad spine may be developed opposite of the aperture. In contrast to BANDEL (2007) who has assigned this genus to the "Alariidae" it is positioned here in the Dimorphosinae nov. subfam. (see there).

BANDEL (2007) distinguishes the Spinigeridae from other taxa mainly by their regular pattern of varices carrying hollow thorns. Besides *Spinigera* d'ORBIGNY, 1850, he includes *Diempteris* PIETTE, 1876, which possesses strong spines opposite of the aperture in this family. This genus (type species: *Diempteris lonqueuanus* PIETTE, 1876) has a rather broad shell, angular whorls, two short digitations and a short rostrum. Despite its two spines opposite of the aperture, the shell outline of *Diempteris* is that of an Aporrhainae genus (see there). The same is the case with specimens from Albian deposits of Cosne (Nièvre), which de LORIO (1882) has incorrectly assigned to *Fusus dupinianus* d'ORBIGNY, 1843, and positioned in *Spinigera* d'ORBIGNY, 1850 (for the actual systematic position see KOLLMANN 2005). The shell outline and labral wing, which are different from *Spinigera* d'ORBIGNY, 1850, demonstrate that the varices with hollow spines are not restricted to the Spinigerinae but appear later also in the Aporrhainae.

Subfamily Aporrhainae Gray, 1850

D i a g n o s i s : Spire high, consisting of angular whorls; labral wing with broad adapical and abapical sinuses; 2 digitations in continuation of the noded angulations of the last whorl, proximal digitations, if present, variably attached to spire; rostrum relatively short (pl. 2, fig. 2)

T y p e g e n u s : *Aporrhais* da COSTA, 1778

O t h e r g e n e r a : *Diemterus* PIETTE, 1876, *Monocuphus* PIETTE, 1876, *Dicroloma* GABB, 1868, *Trilemna* BLAGOVETSHENSKIY & SHUMILKIN, 2006, *Biculteriala* nov. gen.

R e m a r k s : The labral wing is almost symmetrical. The anterior and posterior sinuses serve as onsets of sand tubes to maintain a current in the mantle cavity (YONGE 1937).

In contrast to KOROTKOV (1992), *Phyllocheilus* and *Tessarolax* are not included in the Aporrhainae. *Phyllocheilus* is allocated to the Harpagodinae and *Tessarolax* to the Pugnellinae (see there).

From Bathonian deposits, SW of the Ardennes, France, FISCHER (1969) describes *Monocuphus camelus* PIETTE, 1876, *M. vespa* J.A.EUDES-DESLONGCHAMPS, 1843, as well as *Diarthema paradoxum* J.A.EUDES-DESLONGCHAMPS, 1843. *Monocuphus* differs from *Diarthema* only by its expanded labral lip, while the shell outline and the sculpture are virtually the same. *Diarthema* may therefore be the juvenile of a *Monocuphus* species.

BANDEL (2007) defines the Aporrhainae (given family rank by him) by their median keel, flat adapical and abapical whorl faces and additional spiral ribs on the last whorl in some genera. However, in the detailed description, BANDEL, l.c. includes genera which do not conform to these diagnostic characters but possess evenly convex whorls. Among the Mesozoic taxa, *Perissoptera* TATE, 1865, *Latiala* SOHL, 1960, *Graciliala* SOHL, 1960, and *Mexopus* KIEL & PERRILLIAT, 2001, are here assigned to the Arrhaginae POPENOE, 1983. Based on their whorl and labral morphology, *Anchura* CONRAD, 1860, *Helicaulax* GABB, 1868, and *Drepanocheilus* MEEK, 1864, are positioned in the Anchurinae nov. subfam.

BANDEL (2007) included *Dicroloma* GABB, 1868, and *Cuphosolenus* PIETTE, 1882, into the “Alariidae”. In *Dicroloma* GABB, which replaces *Alaria* MORRIS & LYCETT, 1854, for the above-described nomenclatorial reasons, the two angulations of the last whorl extend into digitations. This genus is therefore allocated to the Aporrhainae. In *Cuphosolenus* PIETTE, l. c. the digitations are thin and long and the rostrum is strongly bent. It is allocated to the Pterocerellinae BANDEL but has an intermediate position between the Aporrhainae and this subfamily.

Subfamily Harpagodinae PCHELINTSEV, 1963

D i a g n o s i s : Globular to moderately high-spined large shells with narrow basal and broad subsutural notch; whorls convex to strongly angular, with dominant spiral sculpture; last whorl bearing at least 5 spiral ribs or ribbons extending to broadly expanded labral wing, where they end in spines; strongly bent and sometimes bipartite rostra (pl. 2, fig. 3,4).

T y p e g e n u s : *Harpagodes* GILL, 1870

Other genera: *Phyllocheilus* GABB, 1868, *Harpospira* NEAGU & PANA, 1995, *Harpodactylus* nov. gen., *Quadrinervus* COSSMANN, 1904, *Kaunhowenia* ABDEL-GAWAD, 1986.

Remarks: PCHELINTSEV (1963) has established the family Harpagodesidae (recte Harpagodidae). It comprises almost globular to strongly angular shells and is therefore very diverse. Common features are the small basal notch and the broadly expanded labral wing on which the ribs end in spines.

Because of a basal notch, KOLLMANN (2005) has allocated the Harpagodinae to the Strombidae. This assignment remains doubtful as no other relationship to any Strombidae taxon can be proved (see below). It is therefore assumed that the basal notch occurs also in the Aporrhaidae. The Harpagodinae are therefore considered here as a subfamily of this family BOUCHET & ROCROI (2005) have proposed. BANDEL (2007) allocates all genera of Harpagodinae PCHELINTSEV, 1963, to the “Alariidae” KOKEN. Members of the Harpagodinae possess at least four strong ribbons. They extend into the ribs, which support a broadly expanded labrum, while the Aporrhaidae possess two digitations. *Kaunhowenia* ABDEL-GAWAD, 1986, belongs to this subfamily because of its widely expanded labral wing and the basal notch.

NEAGU & PANA (1995) have subdivided *Harpagodes* into three subgenera (*Jaccardites*, *Bancilites* and *Desorites*). They have further established the new genera *Derventiella* and *Harpospira*. The type species of *Harpospira* is *Pterocera polycera* d’ORBIGNY, 1843. The holotype of this species is an internal mould (KOLLMANN 2005). Of the labral wing, only an impression is preserved. It shows a large number of delicate ribs. The genus remains doubtful because of the unfavourable preservation of the type. KOLLMANN (2005) has assigned it tentatively to *Phyllocheilus* GABB. However, *Pterocera subtilis* ZEKELI, 1852, possesses a sculpture of strong nodes and a labral wing of almost semi-circular outline and seems to be closely related. Although doubtful, *Harpospira* NEAGU & PANA is therefore added to the list of genera.

In *Pterodonta inflata* d’ORBIGNY (1843), which NEAGU & PANA, 1995, assign to *Harpospira*, the original material is preserved as internal moulds (KOLLMANN 2005). The thickness of the shell diminishes towards the labrum. The internal moulds therefore give the impression of an expanded outer lip, which actually is not the case.

Another doubtful species based solely on internal moulds is *Rostellaria arenosa* REUSS, 1844, from the Bohemian Cretaceous. It was first figured by REUSS (1845). The figured specimen is large and high turriculate. The assignment of specimens from the Late Cretaceous of Braunschweig, Germany, to this species by MÜLLER (1898) is doubtful. Early whorls of these specimens possess a spiral ornamentation. The last whorl is only rudimentarily preserved. It exhibits two rounded angulations. The adapical one is slightly prolonged, but the shape of a labral wing is not discernable.

Subfamily Pterocerellinae BANDEL, 2007

Diagnosis: Stout shells with moderately high spires, whorls angulated, with spiral sculpture; last whorl biangulate, high, angulations extending into long and delicate digitations; rostrum long, strongly bent and bipartite in some genera (pl. 2, fig. 5).

Type genus: *Pterocerella* MEEK, 1864

Other genera: *Ceratosiphon* GILL, 1870, *Tridactylus* GARDNER, 1875, *Cuphosolenus* PIETTE, 1882.

Remarks: This subfamily differs from the Aporrhainae by its stout shells, the long and delicate digitation and the extremely long, bent rostrum.

In the type genus and in *Tridactylus* GARDNER, the digitations bear broad appendages and the rostrum is split into three branches as in the Harpagodinae. In *Ceratosiphon* GILL, 1870, a proximal digitation is developed which emanates from the adapical angulation of the last whorl. It is attached to the spire and surpasses it considerably in height. The generic name *Ornithopus* GARDNER, 1875 is invalid because it is pre-occupied.

COSSMANN (1904) considers *Ceratosiphon* GILL, 1870, as a younger synonym of *Tessarolax* GABB, 1868. He “supports” this opinion by adding the description of *Rostellaria retusa* J.de C. SOWERBY in FITTON, 1836, which actually is the type species of *Ceratosiphon*. COSSMANN, l. c. was followed by WENZ (1940), KIEL (2006) and BANDEL (2007), while KOLLMANN (2005) considered *Ceratosiphon* GILL as a valid genus. The shell is broader than in *Tessarolax*, the inductura does not cover the whole spire, and the digitations are delicate and long. The rostrum may branch, but this is not even consistent on the species level (KASE & MAEDA 1980).

Unfortunately, the type species of *Tessarolax distorta* GABB, 1868, is not well preserved. The rostrum is missing and has been added in the figure. The adapical digitation of the labrum is obviously rather broad, the adapical one is incomplete. In the text GABB, l. c. states: “the greater part or the whole of the spire and body whorl covered by an extension of the inner lip in the adult”. This morphological feature is well visible in GABB’s specimen, which STEWART (1926) has re-figured. It supports a systematic position of *Tessarolax* in the Pugnellinae.

Ceratosiphon GILL and *Tessarolax* GABB belong therefore to different genera. *Ceratosiphon* is a valid genus and not a junior synonym of *Tessarolax*.

Subfamily Dimorphosominae nov. subfam.

Diagnosis: Spire high; whorls convex or angular, with collabral sculpture or nodes; last whorl bi-angulate, sometimes tri-angulate, sculpture reduced; adapical angulation passing into sharp dorsal crest of single digitation which is lanceolate and more or less bent upwards; rostrum of short to medium length (pl. 2, fig. 8).

Type genus: *Dimorphosoma* GARDNER, 1887.

Other genera: *Pietteia* COSSMANN, 1904; *Cuphotifer* PIETTE, 1891.

Remarks: COSSMANN (1904) and WENZ (1940) consider *Dimorphosoma* GARDNER, 1875 (type species: *D. calcarata*), as synonymous with *Drepanocheilus* MEEK, 1864. This is not the case. In the type species of *Drepanocheilus*, *D. evansi* COSSMANN, 1904, the whorls are convex and the wing is shorter than in *Dimorphosoma*, triangular and obliquely truncated.

BANDEL (2007) has assigned *Pietteia* COSSMANN, 1904, and *Cuphotifer* PIETTE, 1891, to the “Alariidae KOKEN”. Because of the angular whorls and the undivided labral wing, they are positioned here in the Dimorphosominae nov. subfam.

The type species of *Pietteia*, *P. hamus* DESLONGCHAMPS, possesses a distinct basal angulation. KAIM (2004) demonstrates this morphologic feature also on *P. subbicarinata* (MÜNSTER in GOLDFUSS, 1844) and *P. pellati* (PIETTE). In contrast, *Cuphotifer hamulus* (EUDÉS-DESLONGCHAMPS), which is the type species of this genus, lacks this feature (see FISCHER 1969) and can therefore not be considered as a younger synonym of *Cuphotifer* PIETTE, 1891, as KAIM (2004) and BANDEL (2007) have proposed.

Subfamily Pugnellinae KIEL & BANDEL, 1999

D i a g n o s i s (after KIEL & BANDEL 1999, and BANDEL 2007) : Spire low, outer lip large and reinforced, often with horn-like extension. Callus commonly spread over large parts of the shell (pl. 2, figs. 6, 7).

T y p e g e n u s : *Pugnellus* CONRAD, 1860

O t h e r g e n e r a : *Pyktes* POPENOE, 1983, *Gymnarus* GABB, 1868, *Tephlon* POPENOE, 1983, *Perustrombus* OLSSON, 1934, *Torgnellus* OLSSON, 1934, *Bizarrus* KIEL & BANDEL, 1999, *Lispodesthes* WHITE, 1877, *Tessarolax* GABB, 1868, *Tundora* STEPHENSON, 1941.

R e m a r k s : KRONENBERG & BURGER (2002), consider the definition of the Pugnellidae by KIEL & BANDEL, loc. cit., as too widely conceived because it would also comprise some Recent genus-level taxa of Strombidae. BANDEL (2007) has therefore given additional data on this taxon. The rather stout shell, the bent siphonal canal and the angular whorls, which are obscured by the callus, are added here as morphological characters.

Because of a “double sinus” abapically of the labral wing in “*Pugnellus*” *hamulus* GABB – which actually belongs to *Pyktes* POPENOE, 1983, – COSSMANN (1904), DELPEY (1939), WENZ (1940) and SOHL (1960) have positioned *Pugnellus* in the Strombidae. POPENOE, loc. cit., points out that “stripped of their calcareous surcoats” the Aporrhaid morphology of *Pugnellus* taxa becomes evident. This view was confirmed by DOCKERY (1993) and KIEL & BANDEL (1999), who have established the Pugnellinae on the family level. The expanded callus and the reduced digitations distinguish the Pugnellinae from other Aporrhainae. Tentatively, KIEL & BANDEL, loc. cit., have added *Lispodesthes* WHITE and *Tessarolax* GABB to the Pugnellinae.

BANDEL (2007) has introduced two subfamilies: the Pugnellinae and the Tundorinae. The Pugnellinae comprise forms around *Pugnellus* CONRAD, 1860. Although obscured by the callus spreading over the whole shell, an extremely variable morphology and sculpture may be observed (see for example STANTON 1893; STEPHENSON 1941; SOHL 1960). *Lispodesthes* WHITE, 1877, which possesses two small labral digitations, is closely related to *Pugnellus* and not to *Tundora* STEPHENSON, 1941, as BANDEL (2007) suggests.

Tundora STEPHENSON possesses a sculpture of strong nodes. The whorls are convex (STEPHENSON 1941; SOHL 1964) to indistinct bi-angular (DOCKERY 1993). It is closely related or identical with *Tessarolax* GABB, 1868.

Subfamily Anchurinae nov. subfam.

D i a g n o s i s : Whorls convex with well-developed sculpture of nodes at intersections of strong collabral and weak spiral ribs; last whorl low, with angulation or shoulder

passing into keel of labral wing; rostrum long, straight to slightly bent. Wing proximally constricted but distally with “ears”, bifurcations or additional digitations (pl. 2, figs. 11, 12).

Type genus: *Anchura* CONRAD, 1860

Other genera: *Alarimella* SAUL, 1998, *Drepanocheilus* MEEK, 1864, *Helicaulax* GABB, 1868, *Pugioptera* PCHELINTSEV, 1953, *Pseudanchura* KOLLMANN, 2005, *Pletzchia* nov. gen.

Remarks: The Anchurinae are distinguished from other Aporrhaidae subfamilies by their heavy sculpture, their low, angulated or shouldered last whorl, the proximally narrow and externally elaborate wing, and a broad abapical sinus. The genera are distinguished by additional proximal and distal digitations, which sometimes give it a hammer-like outline. DOCKERY (1993) has demonstrated that the diversity is high even on the species level. Posterior digitations vary even intraspecifically (see HOLZAPFEL 1888). *Dicroloma* is considered as an Aporrhainae genus (see there).

BANDEL (2007) has allocated the genera assigned here to the Anchurinae nov. subfam. to the Aporrhaidae. They may be distinguished from members of this subfamily by the strong ornamentation, the low last whorl and the labral wing consisting of one broad digitation with elaborate appendices.

Subfamily Arrhoginae POPENOE, 1983

Diagnosis: Whorls convex, collabral sculpture dominant; last whorl evenly rounded; Labral wing externally rounded to ploughshare-shaped or bipartite; rostrum short to moderately long (pl. 2, figs. 9, 10).

Type genus: *Arrhoges* GABB, 1868

Other genera: *Perissoptera* TATE, 1867, *Latiala* SOHL, 1960, *Graciliala* SOHL, 1960, *Auriala* AKOPJAN, 1976, *Mexopus* KIEL & PERRILLIAT, 2001.

Remarks: *Arrhoges* GABB, 1868, has been established on the Recent *Arrhoges occidentalis* (BECK). Besides *Arrhoges*, POPENOE, 1983, has included *Pugnellus* CONRAD, 1860, and *Drepanocheilus* MEEK, 1864, in the Arrhoginae. *Pugnellus* has been allocated to the Pugnellinae KIEL & BANDEL, 1999, and *Drepanocheilus* in the original sense of MEEK, 1864, to the Anchurinae nov. subfam. (see there).

SOHL (1960) pointed out that Cretaceous taxa formerly assigned to *Arrhoges* are not typical for this genus. He has established the subgenera *Latiala* and *Graciliala* which are considered here as independent genera. These and other Mesozoic taxa allocated to the Arrhoginae differ from the type species mainly by the presence of an abapical notch of the labral wing. On the other hand, there is a high correspondence of the other morphological characters (whorl outline and sculpture, shape of the labral wing) which let suggest a position in the same subfamily.

With *Perissoptera* TATE as type genus, KOROTKOV (1992) has erected the family Perisopteratidae. Because of the convex whorls, the collabral ribs and transitions between the ploughshare, and the bipartite form of the wing (see SAUL 1998) *Perissoptera* is assigned to the subfamily Arrhoginae POPENOE, 1983.

COSSMANN (1904) and WENZ (1940) consider *Perisoptera* as a subgenus of *Anchura*. SOHL (1960) has pointed out that the evenly convex whorls and the broad labral wing identify *Perisoptera* as a distinct genus. In *Mexopus* KIEL & PERILLIAT, 2001, the wing is not known. The collabral sculpture is weak but similar to that of *Arrhoges* GABB, 1868.

According to KOROTKOV, 1992, *Perisoptera* and *Anchura* evolve from *Pietteia*. This genus has a lanceolate wing and is therefore included in the Dimorphosominae nov. subfam.

BANDEL (2007) has includes *Arrhoges* and related genera into the Aporrhidae although they clearly differ from *Aporrhais* and related forms by their convex whorls, including the last one, and the broad labral wing.

Subfamily Struthiopterinae ZINSMEISTER & GRIFFIN, 1995

D i a g n o s i s (after ZINSMEISTER & GRIFFIN 1995): Wing subrectangular with prominent posterior digitations; anterior digitation bluntly developed; wing inclination varies from parallel to 30 degrees to the axis of coiling; posterior digitations may be strongly dorsally curved; two well-developed spiral carinae with posterior carina more strongly developed on body whorls (pl. 2, fig. 13).

Type genus: *Struthioptera* FINLAY & MARWICK, 1937.

Other genera: *Hemichenopus* STEINMANN & WILCKENS, 1908, *Austroaporrhais* ZINSMEISTER & GRIFFIN, 1995, *Strutiochenopus* ZINSMEISTER & GRIFFIN, 1995.

Remarks: According to ZINSMEISTER & GRIFFIN 1995 this subfamily is restricted to the southern hemisphere (Antarctic regions, southern South America and New Zealand). It embraces high-spined taxa. In the Late Cretaceous (Maastrichtian) *Struthioptera* the whorls are high, angulate to subangulate and possess a subsutural neck. The sculpture consists of irregular, strongly oblique opisthocline elongate nodes. The last whorl has two keels. The growth lines are opisthocline in the adapical part and curve abruptly backwards at the abapical angulation. The labral wing is trapezoid and adapically prolonged to form an acute tip. The siphonal neck is short. In *Austroaporrhais* ZINSMEISTER & GRIFFIN, 1995, the labral wing is bipartite. The digitations are short.

9. Evolutionary phases of the Mesozoic Aporrhidae

A review of some of the major Mesozoic Aporrhidae faunas shows the following evolutionary steps:

The stratigraphically earliest known Aporrhidae belong to the subfamily Spinigerinae KOROTKOV, 1992. The high diversity suggests that *Spinigera* as it is conceived now embraces in fact a larger number of genera which gave rise to different Aporrhidae subfamilies. The earliest known representative is *Spinigera huddlestonei* WILSON, 1887, from the Sinemurian (Lower Liassic). According to PIETTE (1891), and de LORIOI (1901), *Spinigera* ranges stratigraphically into the Oxfordian (Late Jurassic).

The diversity of Aporrhidae increases in the Middle Jurassic. Bajocian/Bathonian. Besides the Spinigerinae, the Dimorphosinae are represented by *Pietteia* (see: HUDLE-

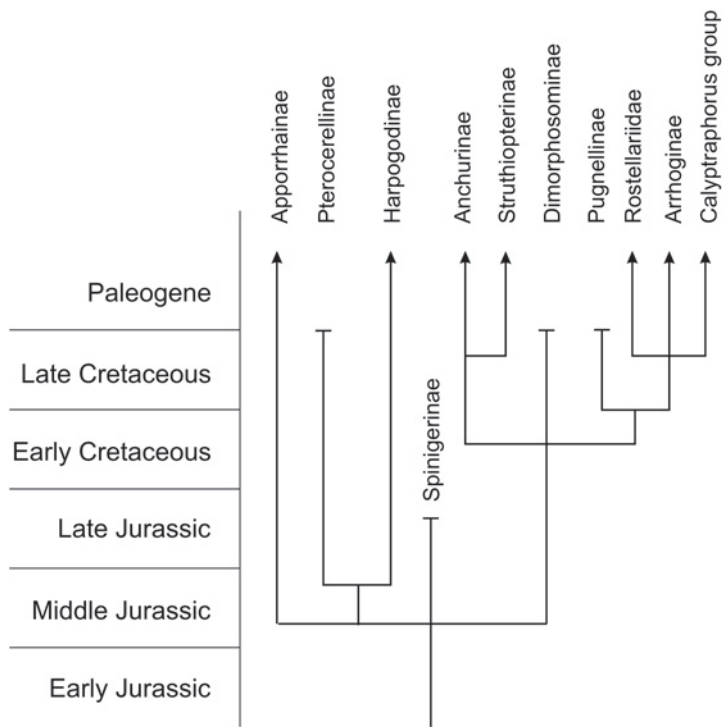


Fig. 7. Relationship between the Mesozoic Aporrhaidae subfamilies and possible origin of the Stromboidea family Rostellariidae and the *Calyptraphorus* group. Arrows symbolize a distribution beyond the Cretaceous/Paleogene boundary.

STON 1887, PCHELINTSEV 1963), the Aporrhainae by *Dicroloma* and the Harpagodinae by *Phyllocheilus*. Together with indeterminable Aporrhaidae, SCHRÖDER (1995) has recorded *Dicroloma* from the Lower Middle Jurassic (Aalenian) Opalinum shale of North Germany). From the same deposits, SCHRÖDER, l.c. described *Mesostrombus* and concluded a Jurassic origin of the Strombidae. He was followed by BANDEL (1993). Without stating it explicitly, BANDEL (2007) has allocated *Mesostrombus* to *Cuphotifer* and has abandoned this concept of a parallel development of the Aporrhaidae and the Strombidae since the early Jurassic.

The Bathonian of the Ardennes (FISCHER 1969) shows again an increased diversity of the Aporrhaidae. *Cuphotifer* of the subfamily Dimorphosominae, *Quadrinervus* of the Harpagodinae, and the Aporrhainae genera *Dicroloma* and *Monocuphus* have their first appearance. GRÜNDEL (2003) has recorded a comparable diversity from Bajocian/Bathonian deposits of south Germany. *Pietteia* has further been recorded from the Bajocian limestones of the Bakony Mountains in Hungaria (SZABO 1983).

The increase in diversity from the Lower to the Middle Jurassic represents a major evolutionary step of the Aporrhaidae (see also ROY 1994). With *Cuphosolenus*, the earliest Pterocerellinae BANDEL, have been recorded in the Upper Jurassic but may have developed already in the middle Jurassic together with the Harpagodinae. *Cuphosolenus* has an intermediate position between the Aporrhainae and the Pterocerellinae. The Pterocerellinae share with the Harpagodinae the long, strongly bent rostrum and the broadly expanded labral wing. Although there is no evidence in the middle Jurassic,

they have probably evolved from the same Aporrhainae taxon. The Pterocerellinae are widely distributed in Lower Cretaceous low-energy environments and have been recorded from many parts of the world: From North Germany (KOLLMANN 1982), the Jura mountains in Switzerland (PICTET & CAMPICHE 1864) and the London-Paris Basin (GARDNER 1875; d'ORBIGNY 1843, 1850) in Europe; from the Albian of Madagascar (*Tessarolax retusa* J.de C. SOWERBY after KIEL 2006); from Barremian deposits of Japan (KASE 1984). A further typical representative of *Ceratosiphon* GILL is "*Pterocera*" sp. indet. JELETZKI (1976) from Barremian deposits of Vancouver Island, British Columbia (own observation on JELETZKI's undescribed material). *Aporrhais* ? *kentensis* STANTON, 1947, from the Washita Group of Texas, agrees by its general outline but is only known from unfavourably preserved internal moulds (see also KOLLMANN, DECKER & LEMONE 2002). The Arrhoginae, which had their first appearance in the Barremian (KASE 1984), are derived from the Dimosphosominae.

In his cladogram, BANDEL (2007) indicates a connection between *Harpagodes* GILL and the Tylostomatidae STOLICZKA, 1868. The Tylostomatidae comprise the genera *Tylostoma* SHARPE, 1849, and *Pterodonta* d'ORBIGNY, 1843. The shells are globular to oviform. In contrast to the Aporrhaidae, the Tylostomatidae lack a rostrum. The aperture and the whorl portion opposite the aperture are constricted by varices or teeth. Internal moulds – which are the general mode of preservation – give the impression of a flaring labrum, which actually does not exist. The genus has been allocated to the Stromboidea because of the varicose aperture. At least currently, a connection with the Aporrhaidae cannot be proved.

The Albian transgression (HANCOCK 1975) has established a multitude of low-energy soft-bottom marine facies. This has led to a high diversity of Aporrhaidae (see the high diversity in the Gault facies described by GARDNER 1875). In this stage, the Anchurinae and the Pugnellinae KIEL & BANDEL have evolved from the Dimosphosominae. The Pugnellinae evolved in the Americas (POPENOE 1983). The earliest recordings of Pugnellinae genera (*P. cypraeformis*) are in the middle to late Albian of Peru (OLSSON 1934). POPENOE (1983) has derived the Pugnellinae from *Arrhodes* but the long bent rostrum contradicts this opinion. The Anchurinae form a separate lineage characterized by a heavy sculpture and a low, angular last whorl.

Following the Albian diversification, the Aporrhaidae experienced peak radiation in the Cenomanian (ROY 1994). This is partly due to the increase of genera of the Pugnellinae KIEL & BANDEL (1999). They spread through the gradually opening South Atlantic to East Africa and the Indian and Pacific provinces (STOLICZKA 1868; KIEL & BANDEL 1999) but not into the Theian realm (KOLLMANN 2002). Like *Pugnellus*, the shells of *Lispodesthes* and *Tessarolax* are covered by a thick callus. The digitations are rudimentary developed in *Lispodesthes*. In *Pyktes* POPENOE the adapical digitation is reduced; in *Gymnarus* GABB, *Teflon* POPENOE, *Pugnellus* CONRAD and *Perustrombus* OLSSON and *Bizarrus* KIEL & BANDEL, it is not developed.

The Struthiopterinae appeared first in the Campanian of the Antarctic Peninsula and New Zealand ZINSMEISTER & GRIFFIN (1995). They are endemic in the Late Cretaceous/Palaeogene Weddellian Province (ZINSMEISTER 1979). The sculpture and the labral wing morphology indicate an ancestry among the North American/East African/Indian Anchurinae stock represented by *Anchura* and *Drepanocheilus*.

10. Late Cretaceous Strombidae

Earliest recordings of *Hippochrenes* MONTFORT, 1810, are of late Cretaceous age. KRONENBERG & BURGER (2002) refer to *Hippochrenes nuda* BINKHORST, 1861, from the Maastrichtian of the Netherlands. Additionally, *Hippochrenes subtilis* PETHÖ, 1906, and *Hippochrenes* sp. indet. by the same author, both from the Fruska Gora mountain range (Serbia), and *Hippochrenes kussi* KIEL & BANDEL, 2002, from Maastrichtian deposits of Egypt have to be included into this subfamily (see BANDEL 2007). Representatives of this family possess almost flat whorls, a sculpture of weak, orthocline collabral ribs and a broadly expanded labral wing. Its margin forms a regular arc from the base to the adapical portion of the spire.

In Cretaceous taxa hitherto allocated to *Calyptrophorus* CONRAD, 1857, the callus conceals the ventral side of the shells completely and the dorsal side marginally. The new genus *Eocalyptrophorus* BANDEL, 2007, is applicable exclusively to the type species, *E. binodiferus* PERRILLIAT & VEGA, 1997, from lower Maastrichtian deposits of Mexico (see KIEL & PERRILLIAT 2001). In contrast to other taxa it possesses a rather low last whorl with heavy, irregular nodes. The spiral whorls have a sculpture of delicate collabral ribs and spiral threads. This type of sculpture is also developed in *C. hopkinsi* OLSSON, 1934, from the late Cretaceous Monte Grande formation of Peru, in which the last whorl is only moderately inflated. In *C. palliata* (FORBES) from the Campanian-Maastrichtian of India and Madagascar (KRONENBERG & BURGER, loc.cit., STOLICZKA 1868), the whorls are moderately concave. They show densely spaced growth lines but no other sculpture. *C. africana* COX, 1952, from Campanian deposits of Ghana needs closer examination because of its oblique columella.

Hippochrenes as well as the *Calyptrophorus* group have moderately convex whorls, a sculpture of collabral ribs and a short to medium-size rostrum. It may have evolved from *Latiala* SOHL, 1960, from which it differs by the labral wing, which is elongated in adapical direction.

Besides the callous cover, the *Calyptrophorus* group differs from *Hippochrenes* by a notch on the basal lip. This feature first appeared in the Campanian-Maastrichtian in the Arrhaginae genus *Graciliala* SOHL, 1960, which is therefore considered here as the stem of the *Calyptrophorus* group. SAUL (1998), in contrast, derived *Calyptrophorus* from *Alarimella* SAUL. This taxon, which is here assigned to the Anchurinae, lacks the basal notch.

We may conclude that the two earliest undisputed non-aporrhaid Stromboidea taxa descend in the Late Cretaceous from two closely related genera of the Arrhaginae POPE-NOE. Of these, early *Hippochrenes* is restricted to the Theian realm (wrongly Tethyan realm, see KOLLMANN 2002), whereas the *Calyptrophorus* group spread into the North American and from there through the Proto-Atlantic into the Indopacific realm.

From the *Calyptrophorus* group, *Rimella* and related forms have derived; their basal notches are even more pronounced.

Hippochrenes forms the base of the Rostellariidae GABB, 1868, which lack a basal notch (KRONENBERG & BURGER 2002). *Tibia* RÖDING, 1798, and related taxa have probably evolved from *Hippochrenes* in the Paleogene. KOLLMANN & PEEL (1983) have allocated

tentatively fragments of shells from Paleocene deposits of Greenland to this genus. There is no proof that *Rimella* has developed in the Maastrichtian as was suggested by BANDEL (2007). *Rimella mexcala* KIEL & PERRILLIAT, 2001, appears to be the fragment of an Anchurinae specimen. It has strongly convex whorls and, attached to the spire, is an equally fragmentary proximal finger of the labral wing reminiscent of *Helicaulax* GABB, 1868. Also the Maastrichtian *Rostellaria laevis* ALTH, 1849, originally described from Lwow, Poland, and allocated to Tibia by ABDEL-GAWAD (1986), is not adequately preserved to allow a reliable determination.

11. Conclusions

While describing a Late Cretaceous gastropod assemblage with hitherto unknown Aporrhaidae taxa, it became evident that little is known about the taxonomy and phylogeny of this group. One reason is that only unsatisfactory attempts at a subdivision of this gastropod group into higher taxonomic categories have been made. Even BANDEL's (2007) monograph on the Stromboidea, which has appeared in the final stages of preparation of this paper, offered little help in this respect. The main reason was the author's concept of the "Alariidae" and Aporrhaidae. They comprise genera of extremely diverse morphologies, which hardly allow the delineation of phylogenetic relationships.

The taxonomic concept presented here is based on a small number of morphological characters of the teleconch which allow a differentiation of taxa above the generic level. Independently from a taxonomic subdivision, the distribution of these characters in geological times provides the frame for the phylogenetic analysis of the group as presented in the cladogram.

Mesozoic families like the Tylostomatidae STOLICZKA, 1868, and the Colombellinidae P. FISCHER, 1884, have been allocated to the Stromboidea mainly based on their reinforced outer lips (COSSMANN 1904; WENZ 1940; KOLLMANN 2005; BOUCHET & ROCROI 2005; BANDEL 2007). The origin of these families is not known and their connection with modern Stromboidea is not evident. According to the detailed morphological analysis, earliest undisputed non-aporrhaid Stromboidea taxa *Hippochrenes* MONTFORT and the *Calyptrophorus* group, which was not further subdivided in this study, evolved in the Late Cretaceous in different marine provinces from different stems of the Arrhoginae POPENOE. The Calyptrophorinae BANDEL possess a basal notch. They may have given rise to the Rimellinae and perhaps other Stromboidea with a basal notch, while the Rostellariidae, which generally lack a notch, have evolved from *Hippochrenes* MONTFORT.

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Plate 1

Figs 1-3. *Angaria pelossei* (ROMAN & MAZERAN, 1920), NHMW 2008z0015/0013

Fig. 4. *Discotectus plicatogranulosus* (MÜNSTER in GOLDFUSS, 1844). NHMW 2008z0015/0014

Fig. 5. *Amauropsis brevissima* (REUSS, 1854). NHMW 2008z0015/0015

Fig. 6. *Cassiope suffarcinata* (MÜNSTER in GOLDFUSS, 1844). NHMW 2008z0015/0016

Figs 7-9. *Armenocerithium haidingeri* (ZEKELI, 1852). NHMW 2008z0015/0017-0019

Fig. 10. *Gyrodes amplissima* (M. HOERNES, 1856). NHMW 2008z0015/0020

Scale bars equal 5 mm.

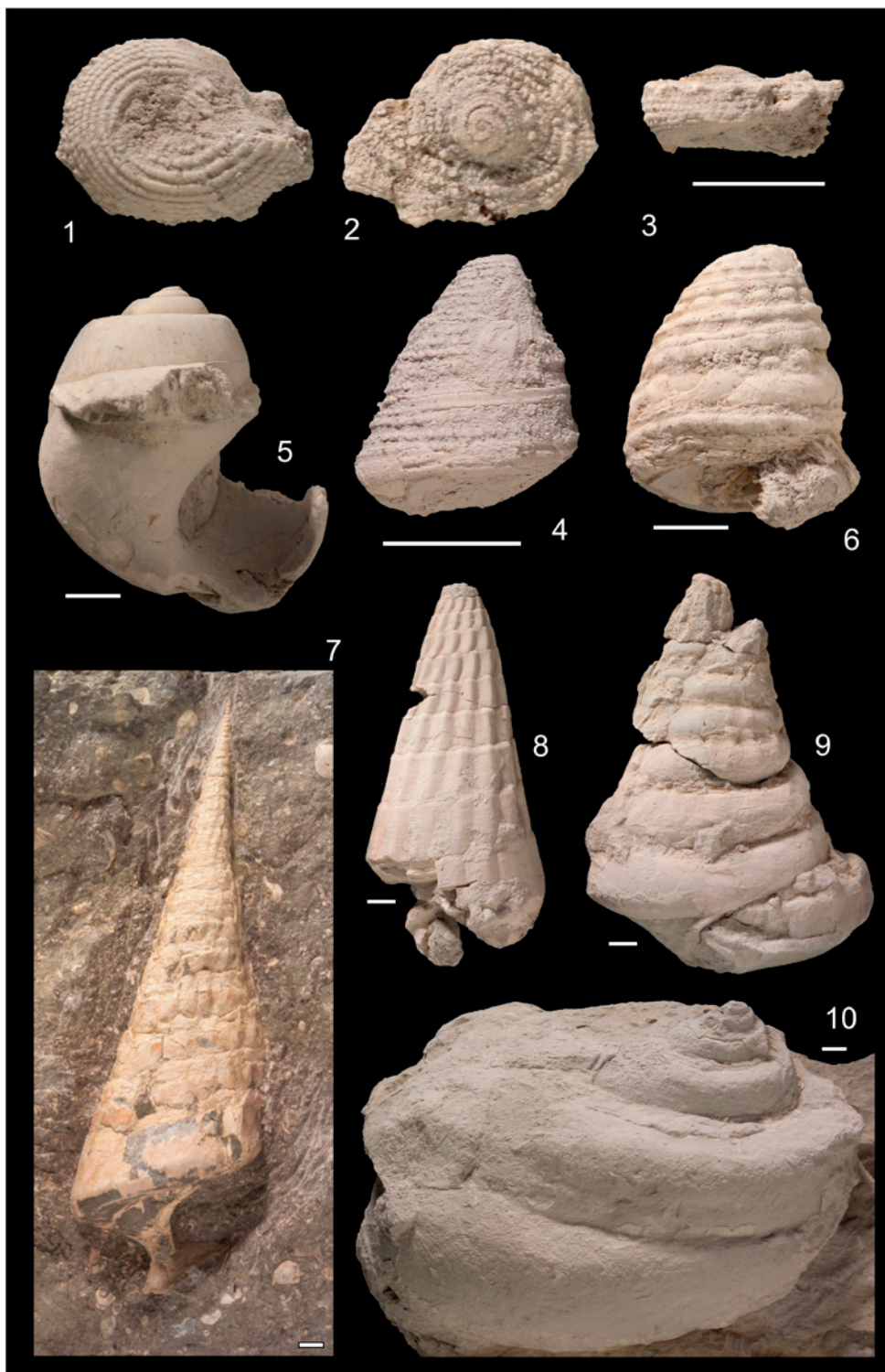
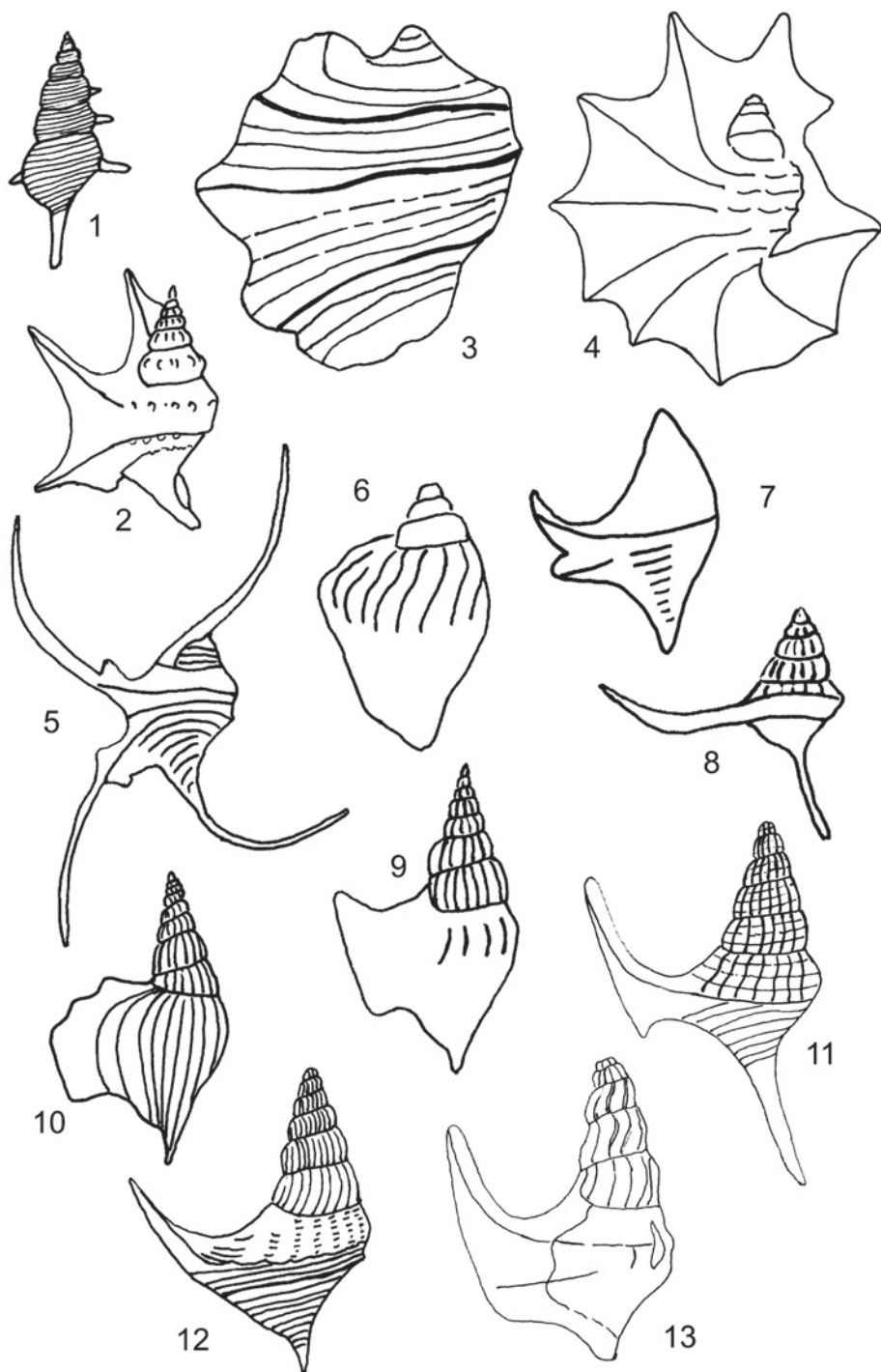


Plate 2

Representative taxa of the Aporrhaidae subfamilies.

- Fig. 1. Spinigeridae: *Spinigera longispina* (DESLONGCHAMPS) (after HUDLESTON 1887)
- Fig. 2. Aporrhainae: *Aporrhais pespelicani* LINNÉ (after WENZ 1940)
- Fig. 3. Harpagodinae: *Harpagodes beaumontiana* (d'ORBIGNY) (after KOLLMANN 2005)
- Fig. 4. Harpagodinae: *Phyllocheilus ponti* BRONGNIART (after WENZ 1940)
- Fig. 5. Pterocerellidae: *Ceratosiphon fittoni* (FORBES) (after GARDNER 1875)
- Fig. 6. Pugnellidae: *Pugnellus densatus* CONRAD (after SOHL 1960)
- Fig. 7. Pugnellidae: *Lispodesthes patula* STEPHENSON (after STEPHENSON 1952)
- Fig. 8. Dimorphosominae nov. subfam.: *Dimorphosoma doratochila* GARDNER (after GARDNER 1875)
- Fig. 9. Arrhaginae: *Arrhoges (Latiala) lobata* WADE (after SOHL 1960)
- Fig. 10. Arrhaginae: *Perissoptera schlotheimi* (ROEMER) (after COSSMANN 1904)
- Fig. 11. Anchurinae nov. subfam.: *Anchura abrupta* CONRAD (after SOHL 1960)
- Fig. 12. Anchurinae nov. subfam.: *Drepanocheilus evansi* COSSMANN (after SAUL 1998)
- Fig. 13. Struthiopterinae: *Struthioptera camachoi* ZINSMEISTER (after ZINSMEISTER & GRIFFIN 1995)



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