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About some aporrhaid and strombid gastropods from the Late Cretaceous

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with 5 figures

Abstract: Sixteen species of the Stromboidea (Gastropoda) from the Late Cretaceous are described in this study. One species belongs to the Strombidae, the others to eight genera and subgenera of the Aporrhaidae. Eight species are new. They have been found in the Cenomanian of Kassenberg in western Germany, the Coniacian of the Mungo River in Cameroon, the Santonian of the Eastern Cape Province of South Africa, the Santonian/Campanian of the Ariyalur area in southern India, the Campanian of northern Spain, and the Maastrichtian of the Western Desert in Egypt.

Two species of *Drepanocheilus* from South Africa are considered stem-group representatives of the aporrhaids which inhabited the Weddellian Province in the early Tertiary. One new species of the strombid genus *Hippocrenes* is regarded as an early species of the evolutionary lineage leading to the Seraphsidae. The new species are *Latiala? ponsi*, *Drepanocheilus herberti*, *Drepanocheilus triliratus*, *Drepanocheilus* (*Tulochilus*) *jouberti*, *Graciliala quaasi*, *Kaunhowenia catalanica*, *Kaunhowenia punctata* and *Hippocrenes kussi*.

Keywords: Late Cretaceous, Gastropoda, Aporrhaidae, Strombidae, phylogeny

Kurzfassung: Sechzehn Arten oberkretazischer Stromboidea (Gastropoda) werden beschrieben, eine davon wird den Strombidae zugeordnet, die anderen werden zu acht Gattungen und Untergattungen der Aporrhaidae gestellt. Acht Arten sind neu. Das Material stammt aus dem Cenoman des Steinbruches Kassenberg bei Mülheim a.d. Ruhr, dem Coniac der Mungokreide von Kamerun, dem Santon der Trichinopoli Formation im Gebiet von Ariyalur in Tamil Nadu, Südindien, dem Santon/Campan der Umzamba Formation an der Ostküste Südafrikas, dem Campan von Nordspanien im Becken von Tremp und dem Maastricht der Ammonitenberge in der westlichen Wüste von Ägypten.

Zwei neue Arten der Gattung *Drepanocheilus* aus Südafrika werden als Stammgruppenvertreter einiger Aporrhaidae angesehen, die im frühen Tertiär in der Weddell Provinz dominierten. Eine neue Art von *Hippocrenes* (Strombidae) wird als ältester Vertreter einer zu den Seraphsidae führenden, evolutionären Linie gedeutet. Die neuen Arten sind: *Latiala? ponsi*, *Drepanocheilus herberti*, *Drepanocheilus triliratus*, *Drepanocheilus* (*Tulochilus*) *jouberti*, *Graciliala quaasi*, *Kaunhowenia catalanica*, *Kaunhowenia punctata* und *Hippocrenes kussi*.

Schlüsselwörter: Oberkreide, Gastropoda, Aporrhaidae, Strombidae, Phylogenie

Introduction

From their appearance in the mid-Jurassic to the K/T mass extinction, the Aporrhaidae MÖRCH, 1852 have seemingly formed the dominant stromboidean family. They comprise species characterised by an extended outer lip which can be lobe-like or digitate in shape. Species are abundant in marine deposits and have been commonly described. The last major revisions of the group have been carried out by GABB (1868) and COSSMANN (1906), and the evolutionary patterns of the Aporrhaidae are still poorly understood.

KOROTKOV (1992) introduced four new families based mainly on the number of digits on the outer lip of the adult shell. He allotted the genera *Anchura* CONRAD, 1860 and *Helicaulax* GABB, 1868 to different families even though they are only distinguished by the length of their posterior spur and rostrum. *Helicaulax* and *Gymnarus* GABB, 1868, in contrast, where assigned to the same family, despite the fact that they differ in several more morphological features than only the shape of the outer lip. A taxonomy based on such minute differences appears to be of little use. Similar to KOROTKOV's (1992) attempt, also ROY (1994) used the number of digits on the outer lip to introduce two artificial aporrhaid "morphogroups". ELDER & SAUL (1996) and SAUL (1998) showed that these groups are polyphyletic. ROY's (1994) phylogenetic analysis concerned only genera gathered from the literature, without an evaluation of their validity. Furthermore, no mid- or Late Cretaceous genera were involved, so that this analysis appears to be of little value.

BANDEL (1991) suggested some Triassic and Carboniferous precursors of the Stromboidea RAFINESQUE, 1815 based on similarities regarding protoconch morphology. But these taxa lack an extended outer lip and their relationships to the Stromboidea remain tentative. The oldest aporrhaids with the typical extended outer lip and the large, convex-conical larval shell are known from the Middle Jurassic (MORRIS & LYCETT 1854; LORIOL &

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PELLAT 1874; PIETTE 1891; BRÖSAMLEN 1909; GRÜNDEL 1993, 1998). Relationships of the Jurassic genera to those of the Late Cretaceous concerned herein are still unclear. The *Pugnellus*-like genera were considered Strombidae (WENZ 1938-44; SOHL 1960), but POPENOE (1983) referred them to the Aporrhaidae, due to differences in the function of the basal sinuses of pugnellids and strombids. DOCKERY (1993) accepted this opinion based on similarities in the juvenile sculpture found in *Pugnellus* CONRAD, 1858 and modern *Aporrhais* DACOSTA, 1778. KIEL & BANDEL (1999) excluded them from the Aporrhaidae and united them in a new family, the Pugnellidae KIEL & BANDEL, 1999.

Cretaceous Strombidae are only known from Campanian and Maastrichtian strata, comprising *Calyptraphorus* CONRAD, 1857 (PERRILLIAT & VEGA 1997), *Rimella* AGASSIZ, 1840 (KIEL & PERRILLIAT 2001), and *Hippocrenes* MONTFORT, 1810 (KAUNHOWEN 1897; PETHÖ 1906, and herein). ELDER (1990) introduced *Tibiaporrhais* as a possible link between aporrhaids and the strombid genus *Tibia* RÖDING, 1798. SAUL (1998) proposed *Alarimella* SAUL, 1998 as an intermediate genus between *Aporrhais* and *Rimella*. Contrary to the opinions of ELDER (1990) and SAUL (1998), KIEL & PERRILLIAT (2001) indicated, that only the posterior canal which extends from the aperture to the spire and bends downwards near the apex, can be used to distinguish early strombids from the Aporrhaidae.

After the K/T mass extinction most aporrhaids had vanished and the rise of the Strombidae RAFINSEQUE, 1815 and Seraphsidae JUNG, 1974 began (WENZ 1938-44; JUNG 1974). During the Paleogene, the Aporrhaidae were still relatively abundant in the Antarctic Realm (ZINSMEISTER 1977; ZINSMEISTER & GRIFFIN 1995), but later they were replaced by the Struthiolariidae FISCHER, 1887.

The scope of this study is to describe some new stromboidean species from the Late Cretaceous and to investigate the phylogenetic relationships of the groups to which they belong.

Material

The fossils from the Umzamba Formation were collected by us in summer 1995. This locality was described in detail by KLINGER & KENNEDY (1980), who determined its age as Santonian and early Campanian. The fossils were collected in the exposures right next to the mouth of the Umzamba river.

The Indian fossils were collected in 1994 by K. BANDEL and D. KORTUM, in the vicinity of Ariyalur in the Tiruchirapalli District of Tamil Nadu in south-eastern India. The gastropods of the Trichinopoli group described herein were found near the villages Garudamangalam and Anandapura and near Kutthur and Sirinattam, especially in the lower portion of the upper Trichinopoli group (BANDEL 2000). They are thus of Santonian age (GOVINDAN & RAVINDRAN 1996).

The Egyptian fossils from the Ammonite Hills (Dakhla Formation) in the western desert are exposed in channels between the huge dunes of the Sand Sea. They were gathered by K.W. BARTHEL and W. HERRMANN-DEGEN, who also described the locality in detail (BARTHEL & HERRMANN-DEGEN 1981) and determined its age as Maastrichtian.

From the Late Cretaceous deposits of Cameroon the types described by RIEDEL (1932) were made available to us from the Museum für Naturkunde in Stuttgart. The two species concerned in this study were discovered in the locality "Bombe". A visit at that locality in 1998 by K. BANDEL and T. KOWALKE failed to locate fossil bearing outcrops which could have provided these well-preserved specimens. The age of this locality is problematic since only two ammonites have been found. RIEDEL (1932) assumed that its age ranges from Emscher (= Coniacian) to Maastrichtian. According to REYMENT (1954) the ammonites are of Coniacian age.

Fossils from the Puimanyons Olisthostrome around Torallola, near Pobla de Segur in the Tremp basin of northern Spain, were collected by the authors, students and colleagues from Hamburg University during several field trips since 1989. According to ROSELL et al. (1972), these fossil-rich, grey marls are of Campanian age.

The fossils from the Kassenberg quarry near Mülheim in the Ruhr Area of Germany are of Cenomanian age and represent the oldest species described here. The material belongs to the collection of the Ruhrland-Museum in Essen.

We compared our material with species from the Ripley Formation and its Coon Creek and Coffee Sand members of Mississippi and Tennessee. These are largely from D.T. DOCKERY III's collection and from collecting jointly with him.

Abbrevations: RME: Ruhrland-Museum in Essen, Germany; SNMS: Museum für Naturkunde in Stuttgart, Germany; TUB: Technische Universität Berlin, Germany; GPI: Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Germany; SAM: South African Museum in Cape Town, South Africa.

Systematic paleontology

Class Gastropoda CUVIER, 1797
Subclass Caenogastropoda COX, 1959
Superfamily Stromboidea RAFINESQUE, 1815
Family Aporrhaidae MÖRCH, 1852

Genus *Latiala* SOHL, 1960

Type species: *Anchura lobata* WADE, 1926 from the Ripley Formation, Maastrichtian.

Description: The medium sized, high spired shell has a broad, thick outer lip that is thickened and bilobed at the terminus with one lobe directed upward and a second blunter lobe directed downward. The interior of the outer lip is not grooved and the inner lip is only slightly callused.

Differences: The wing of *Perissoptera* TATE, 1865 is formed by an upward directed horn and a blunt lobe below, separated by a more or less developed sinus. The wing of *Graciliala* SOHL, 1960 is keeled and not smooth as in *Latiala*.

Latiala papilionacea (GOLDFUSS, 1844)
Fig. 1A-E

*1844 *Rostellaria papilionacea* n. sp. GOLDFUSS: 18, pl. 170 fig. 8.
1868 *Alaria papilionacea* GOLDFUSS. – STOLICZKA: 31, pl. 2 figs. 9, 10.
1906 *Perissoptera* sp. – WOODS: 319, pl. 28 fig. 14.
1930 *Dicroloma* (*Perissoptera*) *bailyi* n. sp. RENNIE: 217, pl. 25 figs. 11-15.

Material: One damaged specimen from Kulakalnattam (GPI 3782), Trichinopoli Formation, Southern India and five incomplete specimens from the Umzamba Formation, South Africa (SAM PCP 12894-5).

Description: The moderately large shell consists of nine convex whorls. The first four whorls are smooth, the later ones show 12-16 ribs which are slightly turned to the left on the base. In addition, there are fine spiral lirae and occasional varices. On the body whorl the ribs become more knob-like and appear only in the upper third. The wing is ornamented only by growth lines. It is thickened at its outer margin were it forms a small downward, and a big upward lobe. The rostrum is slightly turned towards the wing, and the inner lip is callus covered, especially in its lower part. The specimens from the Umzamba locality are 23 mm high (Fig. 1A, B) and 18 mm wide (Fig. 1C), while that of the Indian Trichinopoli Formation is 35 mm high and 30 mm wide; they have an apical angle of about 40°.

Differences: RENNIE (1930) described *Dicroloma* (*Perissoptera*) *bailyi* from the Umzamba. But we found no characters to distinguish this species from *L. papilionacea* and *D.* (*P.*) *bailyi* is therefore regarded as a synonym.

Latiala hayamii KASE, 1984 has more convex whorls and deeper sutures than *Latiala papilionacea*. In *Latiala*? *tegulata* (STOLICZKA, 1868) the ribs of the body whorl are continuous down to the rostrum. The Albian-Turonian *Latiala californica* (GABB, 1864) has three clearly visible spiral lines below the suture of the body whorl, a feature unknown in *Latiala papilionacea*. *Latiala lobata* WADE, 1926 from the North American Gulf Coast has more volutions and more axial ribs, especially on the body whorl. The Brazilian *Latiala infortunata* (WHITE, 1887) has a more horn-shaped wing that contrasts the more or less rectangular wing of *Latiala papilionacea*.

Latiala? *tegulata* (STOLICZKA, 1868)
Fig. 1F

*1868 *Alaria tegulata* n. sp. STOLICZKA: 33, pl. 2 figs. 11-13.

Material: Two damaged specimens from Garudamangalam, Trichinopoli Formation, Southern India (GPI 3780).

Description: The shell consists of six to nine whorls with the sutures clearly visible. The spire is slightly higher than the body whorl. Each whorl is sculptured with 16-17 axial ribs. The wing is attached to the penultimate whorl where it is covered by thick callus. The ribs of the body whorl continue onto the rostrum. The shell is 30 mm high, 16 mm wide at the body whorl and has an apical angle of 30°.

Differences: *Latiala papilionacea* has no callus around the suture of the wing like *Latiala*? *tegulata*, and shorter ribs on the body whorl.

Remarks: The wings of our specimens as well as of those described by STOLICZKA (1868) are broken off. Thus, it is not clear whether our specimens belong to the genus *Latiala*, or to *Perissoptera* or to *Graciliala* which have a similar spire but differ in the shape of the wing.

Latiala? cf. *lobata* (WADE, 1926)
Fig. 1G

Material: One specimen from the Kassenberg quarry, Germany (RME A811/18).

Description: The high spired shell has body whorl and spire of equal height. The whorls of the spire are ornamented with about 30 axial ribs and fine spiral lirae, the latter most strongly developed near the sutures. There are only two strong ribs on the body whorl and growth lines which continue onto the wing. The shell is 31 mm high and 24 mm wide.

Differences: From other European species *Latiala*? cf. *lobata* differs in having a much higher number of axial ribs (about 30 in contrast to 12-16 on *Latiala papilionacea*).

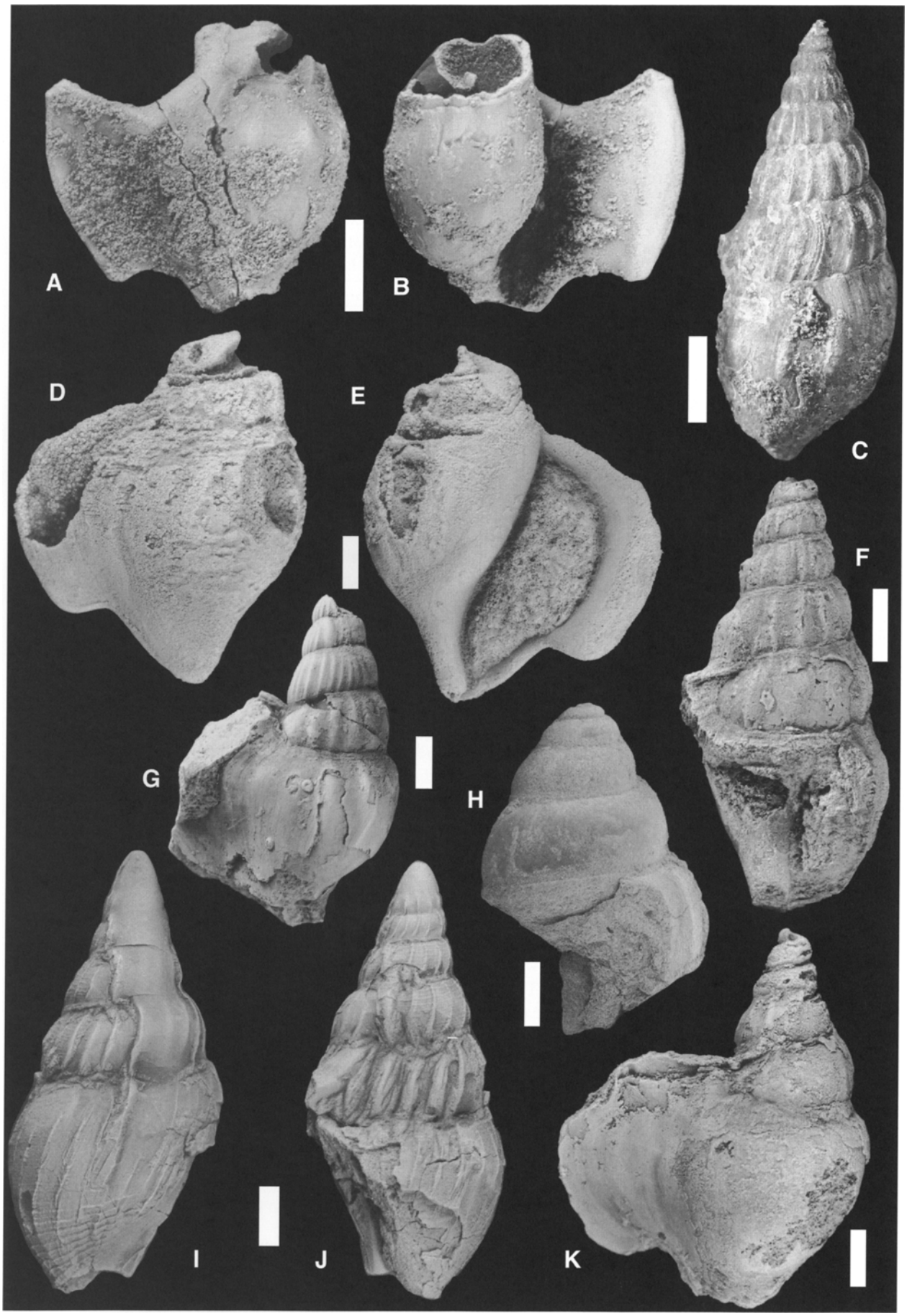
Remarks: Despite its similarities with *Latiala lobata* the specimen from Kassenberg cannot be exactly identified as belonging to *Latiala* since the upper and outer margins of the wing are broken off.

Latiala? *ponsi* n. sp.
Fig. 1H-J

Derivatio nominis: In honour of JOSÉ MARIA PONS from the Universidad Autonoma de Barcelona for his help regarding the geology of the Tremp basin.
Holotype: GPI Type. Kat. Nr. 3901 (Fig. 1I, J).
Paratype: GPI Type. Kat. Nr. 3907 (Fig. 1H).
Locus typicus: The valley system around Torallola, Toralla, and Sensui in the Tremp basin of northern Spain.
Stratum typicum: The Campanian of the Puimanyons Olisthostrom.
Material: More than 500 specimens from the type locality, all with their wing broken off.

Diagnosis: Medium sized aporrhaid gastropod with a band of callus on the ventral side of the spire.

Description: The protoconch consist of 4.5 volutions, is smooth, conical, 1.5 mm wide and 1.35 mm high. Its embryonic whorl measures 0.15 mm across. The adult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shell is high spired with up to ten convex volutions that are ornamented with 16 transverse axial ribs per whorl and fine spiral lirae. Varices may occur irregularly, sutures are marked with a small ridge on later whorls. The aperture is lenticular, ending in an anterior canal. The wing is attached to the penultimate whorl. A band of callus may be present on the ventral side of the spire and also covers the apex. The **holotype** is 24 mm high and 13 mm wide.

Differences: *Latiala*? *ponsi* is distinct from other members of *Latiala* by its callus band on the spire. *Latiala papilionacea* and *Latiala lobata* do not have the wing attached to the penultimate whorl but only to the last whorl. *Latiala*? *tegulata* from India appears closely related to *Latiala*? *ponsi* n. sp. because it has the same number of axial ribs and its wing starts with a similar onset. *Latiala*? *tegulata* differs by having strong ribs on the body whorl.

Genus *Drepanocheilus* MEEK, 1864
Subgenus *Drepanocheilus* (*Drepanocheilus*) MEEK, 1864

Type species: *Rostellaria evansi* COSSMANN, 1904 from the Maastrichtian Fox Hills Sandstone, South Dakota, USA.

Description: The small to medium sized shell has initially smooth whorls and later on an ornament of sloping axial ribs and spiral lirae. The body whorl has two or more keels. The aperture is narrow and ends anteriorly with a short siphonal canal. The upper keel continues onto the single, upward turned wing. The inner lip of the aperture is thickened with callus.

Differences: *Anchura* is quite similar to *Drepanocheilus* but differs in having only one keel on the body whorl and often a forked wing. The Albian *Rostellaria carinata* (MANTELL, 1822) from the Blackdown Greensands, England (MANTELL 1822) can be interpreted to represent a species intermediate between *Drepanocheilus* and *Anchura*. It has two keels like *Drepanocheilus* and a forked wing like *Anchura*.

Fig. 1. – A-E: *Latiala papilionacea* GOLDFUSS; **A, B**. Specimen from the Umzamba Formation, South Africa (SAM PCP 12894); **C**. Another specimen from the Umzamba Formation, South Africa with preserved spire (SAM PCP 12895); **D, E**. Specimen from the Trichinopoli Formation, India (GPI 3782). – **F**: *Latiala*? *tegulata* (STOLICZKA), from the Trichinopoli Formation, India (GPI 3780). – **G**: *Latiala*? cf. *lobata* (WADE) from the Kassenberg quarry, Germany (RME A891/18). – **H-J**: *Latiala*? *ponsi* n. sp., from Torallola, Spain; **H**. Larval shell (GPI 3907); **I, J**. **Holotype** showing the large callus-band (GPI 3901). – **K**: *Perissoptera* cf. *parkinsoni* (MANTELL) from the Trichinopoli Formation, India (GPI 3781). – Scale bars = 5 mm except Fig. H = 0.5 mm.

Drepanocheilus herberti n. sp.
Fig. 2E, G, H

1906 *Aporrhais* sp. – WOODS: 318, pl. 28 fig. 13.

Derivatio nominis: Named after DAVID HERBERT from the Natal Museum in Pietermaritzburg, who kindly supported us in South Africa.
Holotype: SAM PCP 12891 (Fig. 2E).
Paratypes: SAM PCP 12892 (Fig. 2H), and SAM PCP 12893 (Fig. 2G).
Locus typicus: Mouth of Umzamba River, Eastern Cape Province, South Africa.
Stratum typicum: The Santonian lower portion of the Umzamba Formation.
Material: Five specimens from the Umzamba locality, South Africa.

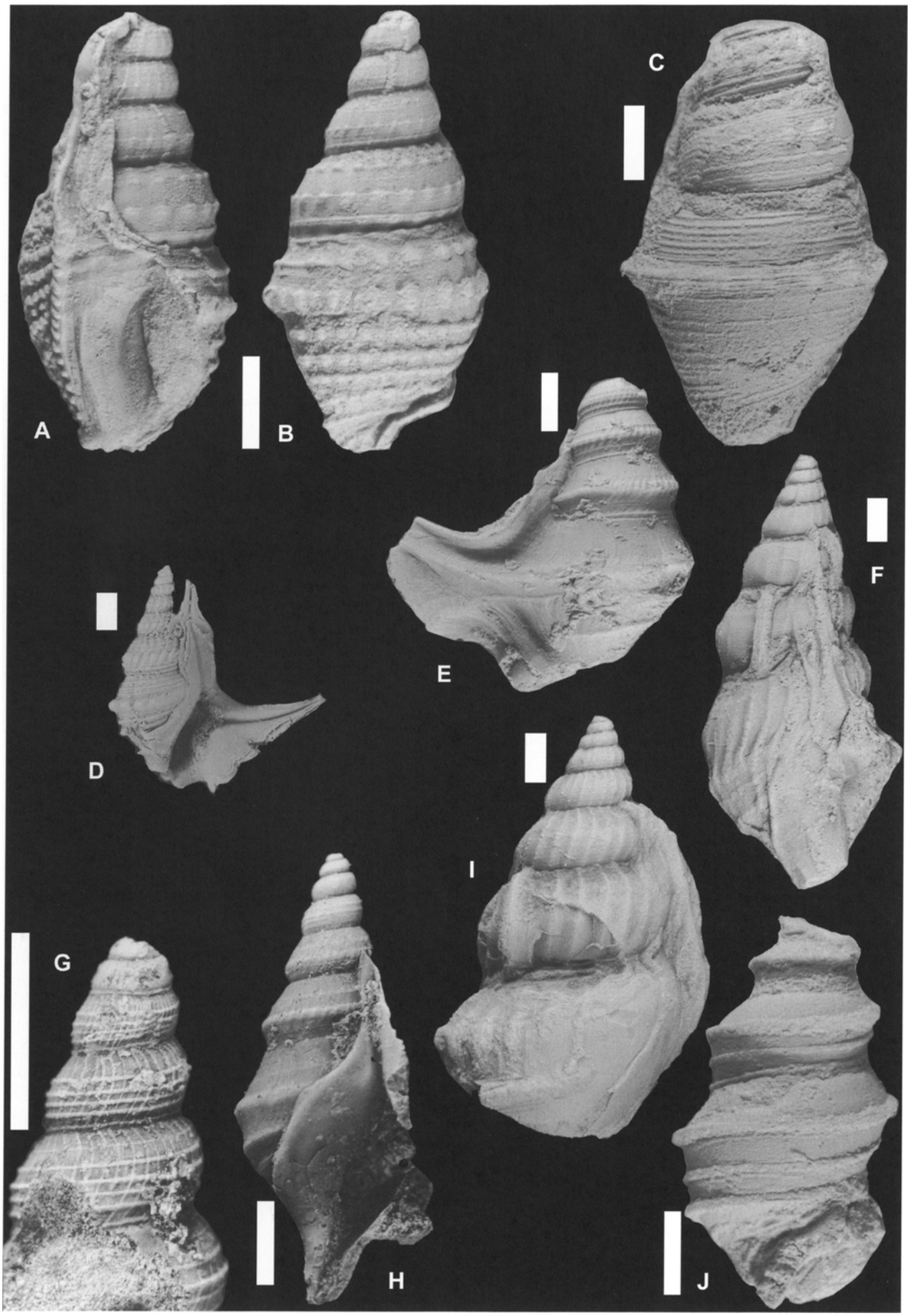
Diagnosis: The small fully grown shell with nine whorls of the teleoconch has an upwards turned dagger-like wing on its outer lip. The ornament consists of one keel that continues onto the wing and two others below it that end at the wing.

Description: The shell comprises nine whorls and has an upward turned, dagger-like wing. The early teleoconch whorls show axial and spiral lines. The last three whorls bear a strong keel in the lower third, have straight sides, and appear angular. The keel continues onto the wing where it corresponds with a groove on the inner side of the wing. There are two more keels present on the body whorl which terminate at the wing. The aperture has lenticular shape and is slightly convex. The posterior spur of the outer lip is attached to the spire and may continue for a distance of up to four whorls. The **holotype** is 11 mm high, 11 mm wide and has an apical angle of 30°.

Differences: This species of *Drepanocheilus* differs from most others not only in size, but also in lacking spiral lirae on the body whorl and in its angular appearance. These characters are commonly present in *Struthiochenopus* ZINSMEISTER & GRIFFIN, 1995 from the Weddellian province. *Drepanocheilus herberti* differs from members of *Struthiochenopus* by having a single dagger-like wing instead of the two digitations on the outer lip present in *Struthiochenopus* which also has only two keels on the bodywhorl. The Santonian *Drepanocheilus herberti* combines typical *Drepanocheilus*-characters (convex early whorls, single-digitated wing) with characters of *Struthiochenopus* (sharp keel on later whorls). Therefore, it might represent the "missing link" between the genera *Drepanocheilus* and *Struthiochenopus*. The geologic range of *Struthiochenopus* starts with the Campanian (ZINSMEISTER & GRIFFIN 1995).

Drepanocheilus triliratus n. sp.
Fig. 2F, I

Derivatio nominis: Named for its three spiral ridges on the body whorl.
Holotype: GPI Type. Kat. Nr. 3903 (Fig. 2F).
Paratype: GPI Type. Kat. Nr. 3902 (Fig. 2I).
Locus typicus: The valley system between Torallola, Toralla and Sensuy near Pobla de Segur in the Tremp Basin, Spain.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Stratum typicum: The Campanian of the Puimanyons Olisthostrom.
Material: Two specimens from Torallola, Spain.

Diagnosis: This *Drepanocheilus* has three beaded spiral cords on its body whorl.

Description: The high spired shell has eight or more volutions bearing fine curved axial ribs and irregularly occurring varices. Three beaded spiral ridges are present on the body whorl. The inner lip of the aperture is reflected, and the posterior canal attached to about three whorls of the spire. The figured **holotype** is 22 mm high and 10 mm wide.

Differences: This species is distinct from the type of the genus by its canal that extends up the spire. The same applies for *Drepanocheilus evansi* COSSMANN, 1904 and *Drepanocheilus nebrascensis* EVANS & SHUMARD, 1854 from the Pierre Shale of the Western Interior Seaway in the USA (see SOHL 1967).

Subgenus *Drepanocheilus* (*Tulochilus*) FINLAY & MARWICK, 1937

Type species: *Drepanocheilus* (*Tulochilus*) *bensoni* FINLAY & MARWICK, 1937 from the Danian (Paleocene) of the Wangaloan Formation, New Zealand.

Description: The shell is small, resembles *Drepanocheilus* (*Drepanocheilus*) in general features, but has the whorls of the spire strongly angled and bears oblique, blunt tubercles. The outer lip expands into a broad hooked wing which is joined to the shell up to the preceding suture. A well-marked, almost straight groove runs from the extremity of the wing to the upper third of the aperture, below which the wing is much thickened.

Drepanocheilus (*Tulochilus*) *jouberti* n. sp.
Fig. 2D

Derivatio nominis: For MADEL JOUBERT from the South African Museum in Cape Town, for her help while visiting the museum and town.
Holotype: SAM PCP 13787 (Fig. 2D).
Locus typicus: Mouth of Umzamba River, Eastern Cape Province, South Africa.
Stratum typicum: The Santonian lower portion of the Umzamba Formation.

Material: One specimen from the Umzamba Formation.

Diagnosis: This *D.* (*Tulochilus*) has a long posterior spur.

Description: The protoconch consists of four smooth whorls, the initial one being very small, the following increasing rapidly in size. The first whorls of the teleoconch are ornamented with axial ribs and fine spiral lirae. The ribs become more oblique on the later whorls. A nodose keel appears in the lower third of the whorl and is well developed from the fourth whorl onward. The ribs disappear on the body whorl, where the strong nodose keel is joined by two smooth keels below it, the second of which is the stronger one. The aperture is long and narrow, ends posteriorly in a grooved spine that is almost as high as the spire. The outer lip is bent upwards ending in a spine that is grooved on its inside. The inner lip is covered by callus. The **holotype** is 13 mm high and wide.

Differences: *Drepanocheilus* (*Tulochilus*) *jouberti* possesses a higher posterior spur and a stronger basal sinus than *Drepanocheilus* (*Tulochilus*) *bensoni* (see FINLAY & MARWICK 1937).

Genus *Perissoptera* TATE, 1865

Type species: *Rostellaria parkinsoni* MANTELL, 1822, by subsequent designation, COSSMANN (1904) from the Albian of Folkstone, UK. The type species has been extensively discussed by SAUL (1998).

Description: The shell is high spired, axially ribbed and the outer lip has a broad central lobe and an upper, posteriorly directed, long and narrow spur. The anterior canal is long and straight.

Differences: *Perissoptera* is distinguished from the otherwise similar *Latiala* and *Graciliala* by the bilobed outer lip.

Perissoptera cf. *parkinsoni* (MANTELL, 1822)
Fig. 1K

Material: One specimen from Kulakalnattam, Trichinopoli Formation, Southern India (GPI 3781).

Description: The medium sized shell has spire and body whorl of equal height. Its ornament consists of 13-15 ribs per volution except for the body whorl which is smooth and ornamented only by growth lines. The whorls become more convex with age. The wing is a little wider than the body whorl and attached to the suture of the penultimate whorl. The shell is 31 mm high, 23 mm wide and has an apical angle of about 40°.

Remarks: What is preserved from our specimen resembles *P. parkinsoni*, but a save determination is impossible without a fully preserved wing.

Genus *Kaunhowenia* ABDEL-GAWAD, 1986

Type species: *Aporrhais* (*Helicaulax*) *carinifera* KAUNHOWEN, 1897 from Maastricht in the Netherlands.

Fig. 2. – A, B: *Kaunhowenia punctata* n. sp. from the Campanian of Torallola, Spain, two views of the **holotype** (GPI 3904). – **C**: *Kaunhowenia catalanica* n. sp. from the Campanian of Torallola, Spain, **holotype** (GPI 3905). – **D**: *Drepanocheilus* (*Tulochilus*) *jouberti* n. sp. from the Umzamba Formation, South Africa, **holotype** (SAM PCP 13787). – **E, G, H**: *Drepanocheilus herberti* n. sp. from the Umzamba Formation, South Africa; **E. Holotype** (SAM PCP 12891); **G**. Paratype with well preserved early sculpture (SAM PCP 12893); **H**. Apertural view on a paratype (SAM PCP 12892). – **F, I**: *Drepanocheilus triliratus* n. sp. from the Campanian of Torallola, Spain; **F. Holotype** (GPI 3903); **I**. Paratype (GPI 3902). – **J**: *Pterocerella* sp. from the Campanian of Torallola, Spain, (GPI 3906). – Scale bars = 2 mm.

Description: This aporrhaid has a corona-like shell webbing that surrounds the spire and an extended outer lip which bears a distinct posterior groove and anterior sinus. In addition, it has a tuberculate ridge in central position on its volutions.

Differences: The tuberculate spiral ridge and the corona-like wing surrounding the spire in fully grown shells distinguishes this genus.

Remarks: When introducing this genus, ABDEL-GAWAD (1986) considered the corona-like wing around the spire to be of great importance although the species figured by KAUNHOWEN (1897) does not show it. It may be present only in fully grown adults. We find the tuberculate ridge in the centre of the volution to be of equal importance and assign the two species described below to *Kaunhowenia* due to this tuberculate ridge.

Kaunhowenia punctata n. sp.
Fig. 2A, B

Derivatio nominis: Named for the tuberculate spiral ridge in the centre of the whorl.
Holotype: GPI Type. Kat. Nr. 3904 (Fig. 2A, B).
Locus typicus: The valley system between Torallola, Toralla and Sensuy near Pobla de Segur in the Tremp Basin, northern Spain.
Stratum typicum: The Campanian of the Puimanyons Olisthostrom.
Material: The **holotype** from the Campanian of Torallola, Spain.

Diagnosis: This *Kaunhowenia* has a beaded spiral ornament.

Description: The high spired shell has more than five convex volutions. Early whorls are ornamented with fine curved axial ribs and spiral striae. These turn into three tuberculate ridges on later whorls, the weak first one lies close to the upper suture, the strongest second in the lower half of the whorl, and the weaker last one near the lower suture. The body whorl is ornamented with seven cords. The aperture has lenticular shape with a heavily callused inner lip. This callus has a denticulate margin and an ornament that resembles that of the underlying body whorl. The wing is attached to the last four whorls of the spire and its inner side is channelled. The shell is 10.5 mm high and 5.5 mm wide.

Differences: This species with its ornament and denticulate inner lip is distinguished by these characters from the other members of *Kaunhowenia*.

Kaunhowenia catalanica n. sp.
Fig. 2C

Derivatio nominis: Named after the Spanish province Catalania, where it was found.
Holotype: GPI Type. Kat. Nr. 3905 (Fig. 2C).
Locus typicus: The valley system between Torallola, Toralla and Sensuy near Pobla de Segur in the Tremp Basin, Spain.
Stratum typicum: The Campanian of the Puimanyons Olisthostrom.
Material: Two specimens from Torallola, Spain.

Diagnosis: This *Kaunhowenia* has tuberculate transverse ribs on the spire.

Description: The high spired shell has more than six volutions and an ornament of transverse, tuberculate ribs forming a ridge that makes the whorls appear angular. The wing is attached to the entire spire. Remains of the spire-surrounding corona are preserved in one of the two specimens. The inner lip of the aperture is callus covered and the rostrum is bent ventrally. The shell is 12 mm high and 8 mm wide.

Differences: The Maastrichtian *Kaunhowenia carinifera* (KAUNHOWEN, 1897) from Poland and Maastricht resembles *Kaunhowenia catalanica* but has stronger spiral ornament. *Kaunhowenia buchi* (MÜNSTER) shows only spiral ornament on the spire but no tuberculate ribs (FRECH 1887).

Genus *Pterocerella* MEEK, 1864

Type species: *Aporrhais* (*Pterocerella*) *tippanus* CONRAD, 1858 from the Maastrichtian of the Ripley Formation in Mississippi, USA (SOHL 1960).

Description: The shell is of moderate height with either smooth whorls or with an ornament of spiral ridges. The aperture has lenticular shape and is inclined to the axis of coiling. The outer lip expands greatly with six thin digitations which are connected with variable amounts of shell webbing.

Remarks: SOHL (1960: 109) found *Cultrigera* BÖHM, 1885 and its synonym *Tridactylus* GARDNER, 1875 to be distinct by "number and arrangement of the digitations and some features of the aperture". As the arrangement of those digitations is quite variable in aporrhaids and the apertures of *Pterocerella* and *Cultrigera* are comparable, *Cultrigera* is herein regarded as a synonym of *Pterocerella*. The genus *Pterocerella* is, thus, known from both sides of the Atlantic Ocean and ranges from the Campanian to the Maastrichtian.

Some species of the Jurassic genus *Alaria* MORRIS & LYCETT, 1850 like *Alaria lorieri*, *Alaria tridigitata*, *Alaria obtusata* and *Alaria arsina* (see PIETTE 1891) possess a similar spire with an ornament only of spiral ridges. They probably belong to the same evolutionary lineage as *Pterocerella*.

Pterocerella sp.
Fig. 2J

Material: One specimen from the Campanian of Torallola, Spain (GPI 3906).

Description: The small, high spired shell has seven volutions. Whorls possess a strong spiral ridge in the middle. On the fifth whorl a small additional ridge initiates below the strong one. The shell is 9 mm high and 5.5 mm wide.

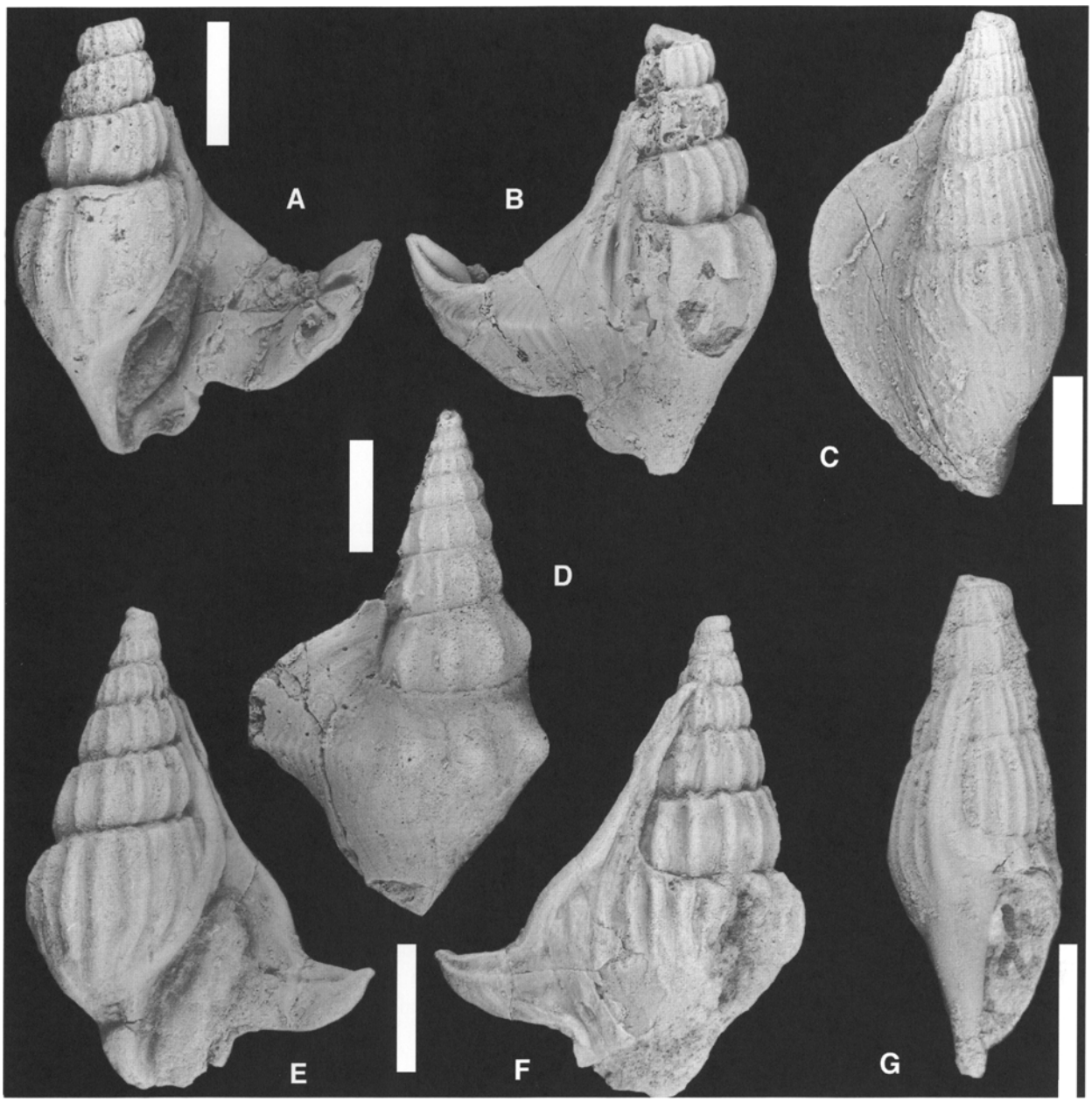

Fig. 3. – **A, B, E, F**: *Graciliala latealata* (RIEDEL) from the Mungo River, Cameroon; **A, B. Holotype** (SMNS 21469); **E, F.** Specimen with short wing but long posterior spur (SNMS 21458). – **C, G**: *Hippocrenes kussi* n. sp. from Egypt; **C. Holotype** with fully grown wing (TUB G 112); **G.** Paratype, represented by a juvenile specimen with only a posterior canal (TUB G 115). – **D**: *Graciliala quaasi* n. sp. from Egypt, **holotype** (TUB G110). – Scale bars = 10 mm.

Differences: The assignment of this specimen to a distinct species is not possible since the outer lip is not preserved. *Pterocerella arachnoides* MÜLLER, 1851 from the Vaals Greensands of Germany has whorls sculptured with a similar number of spiral ridges (HOLZAPFEL 1888).

Genus *Graciliala* SOHL, 1960

Type species: *Anchura calcaris* WADE, 1926 from the Maastrichtian Ripley Formation of the south-eastern United States.

Description: The medium sized, high spired shell has six to eight whorls which are well rounded and sculptured with fine spiral threads and curved transverse ribs that die out below the periphery. The aperture has elongate and lenticular shape with a short, narrow, anterior canal. Its outer lip is expanded with a long, narrow, tapering spur having an internal groove and a corresponding external ridge that dies out on the body. The inner lip is covered with callus over its entire length.

Differences: The genus *Graciliala* differs from *Latiala* and *Perissoptera* in having a keeled wing, from *Drepanocheilus* and *Anchura* in having no keels on the body whorl. When the wing of the outer lip is broken off it is difficult to impossible to distinguish *Latiala*, *Perissoptera* and *Graciliala* from each other.

Remarks: When he introduced this genus, SOHL (1960) found it restricted to the Atlantic coastal plains of North America. *Graciliala latealata* (RIEDEL, 1932) from Cameroon and *Graciliala simplex* (D'ORBIGNY, 1842) from France, as well as *Graciliala quaasi* n. sp. from Egypt extend the geographic range of this genus considerably.

Graciliala quaasi n. sp.
Fig. 3D

Derivatio nominis: In honour of ARTHUR QUAAS who was the first to describe fossils from the Ammonite Hills of the Egyptian Western Desert in 1902.
Holotype: TUB G 110 (Fig. 3D).
Locus typicus: Ammonite Hills, Western Sand Sea, Egypt.
Stratum typicum: The Maastrichtian of the Dakhla Formation.
Material: Nine partly damaged specimens from the Ammonite Hills, western Egypt.

Diagnosis: The spire of the shell is higher than its body whorl, and whorls are ornamented by spiral lirae and axial ribs. The outer lip bears a keeled wing that extends over three volutions.

Description: The high spired shell consists of 8-9 whorls and the spire is about one fourth higher than the body whorl. The whorls show 8-9 fine spiral lines and straight axial ribs which turn into strong elongate tubercles on the last two to three whorls. The base bears only growth lines. The outer lip has a keeled wing that is attached to three former volutions of the shell. The **holotype** is 45 mm high, 29 mm wide and has an apical angle of about 35°.

Differences: No other species of *Graciliala* has ribs which turn into elongate tubercles on the last whorls.

Graciliala latealata (RIEDEL, 1932)
Fig. 3A, B, E, F

*1932 *Helicaulax latealata* n. sp. RIEDEL: 93, pl. 21 figs. 6-9.
1956 *Aporrhais (Helicaulax) latealata* RIEDEL. – DARTEVELLE & BREBION: 38, pl. 3 fig. 1a-c.

Material: Two specimens from the Mungo River, Cameroon (SNMS 21469, SNMS 21458).

Description: The seven volutions of the shell are ornamented with about 16 strong axial ribs. On the body whorl, they count less in number but are stronger and thickened near the suture. The wing of the outer lip of the aperture is horizontal, has a keel on the outer side, and is grooved inside. The wing bends inward and upward at its end, is thickened, and has growth lines. The anterior canal is short. A thin callus covers the inner lip. The posterior spur is attached to up to the three former whorls on the spire. The **holotype** (SNMS 21469) is 35 mm high and 28 mm wide.

Differences: Unlike *Graciliala quaasi*, *Graciliala latealata* shows no spiral lirae on the spire. The posterior spur is unusually high, compared with other species of this genus.

Genus *Anchura* CONRAD, 1860

Type species: *Anchura abrupta* CONRAD, 1860 from the Maastrichtian Ripley Formation of the south-eastern United States.

Description: The medium to large, high spired shell shows ornate sculpture of strong axial and spiral elements, commonly noded. Its aperture is of lenticular shape with long and narrow anterior rostrum that is straight or bent to the left. The outer lip expands into a wing or spine that might fork and/or be ornamented with jags or lobes. The third or fourth spiral cord on the body whorl extends onto the wing, while the first cord might continue onto the occasional posterior spur.

Remarks: Members of the *Anchura* clade first occur and have their highest diversity in the Atlantic Gulf plains and Pacific slope of North America (STEPHENSON 1941, 1952; SOHL 1960; DOCKERY 1993; ELDER & SAUL 1996). *Helicaulax* is considered to represent a subgenus of *Anchura* with long posterior spur and rostrum. PCHELINTSEV (1953) introduced *Pugioptera* as another subgenus with a dagger-like wing and no posterior spur and *Rostellaria requieniana* D'ORBIGNY, 1842 as type species. A rigorous revision is needed to corroborate the validity of this subgenus and even that of *Helicaulax*. It seems that *Anchura* is highly variable in shape and extent of its wing, posterior spur and rostrum. In contrast, the ornamentation of the body whorl formed by axial ribs and spiral cords with knobby intersections, seems very consistent through time and space. ELDER & SAUL (1996) demonstrated that *Anchura* can be used for biostratigraphy. This also demonstrated the ability of *Anchura* to undergo rapid adaptations. Shape and size of wing, posterior spur and rostrum might be adaptations to their local environment and are therefore of low taxonomic value above species level. ELDER & SAUL (1996) pointed out that *Anchura* preferred fine grained sandy sediment of middle or outer shelf environments. This could explain its absence from the Umzamba locality, which represents near shore deposits.

Anchura securifera (FORBES, 1846)
Fig. 4A-B

*1846 *Rostellaria securifera* n. sp. FORBES: 128, pl. 13 fig. 17.
1868 *Aporrhais securifera* FORBES. – STOLICZKA: 28, pl. 2 fig. 1.

Material: Seven specimens from Kulakalnattam and 15 from Garudamangalam, Trichinopoli Formation, Southern India (GPI 3778, 3779).

Description: The medium sized, high spired shell has 6-9 volutions. The spire is a little higher than the body whorl. Ornament consists of strong axial ribs and six spiral cords on the whorls of the spire. On the body whorl

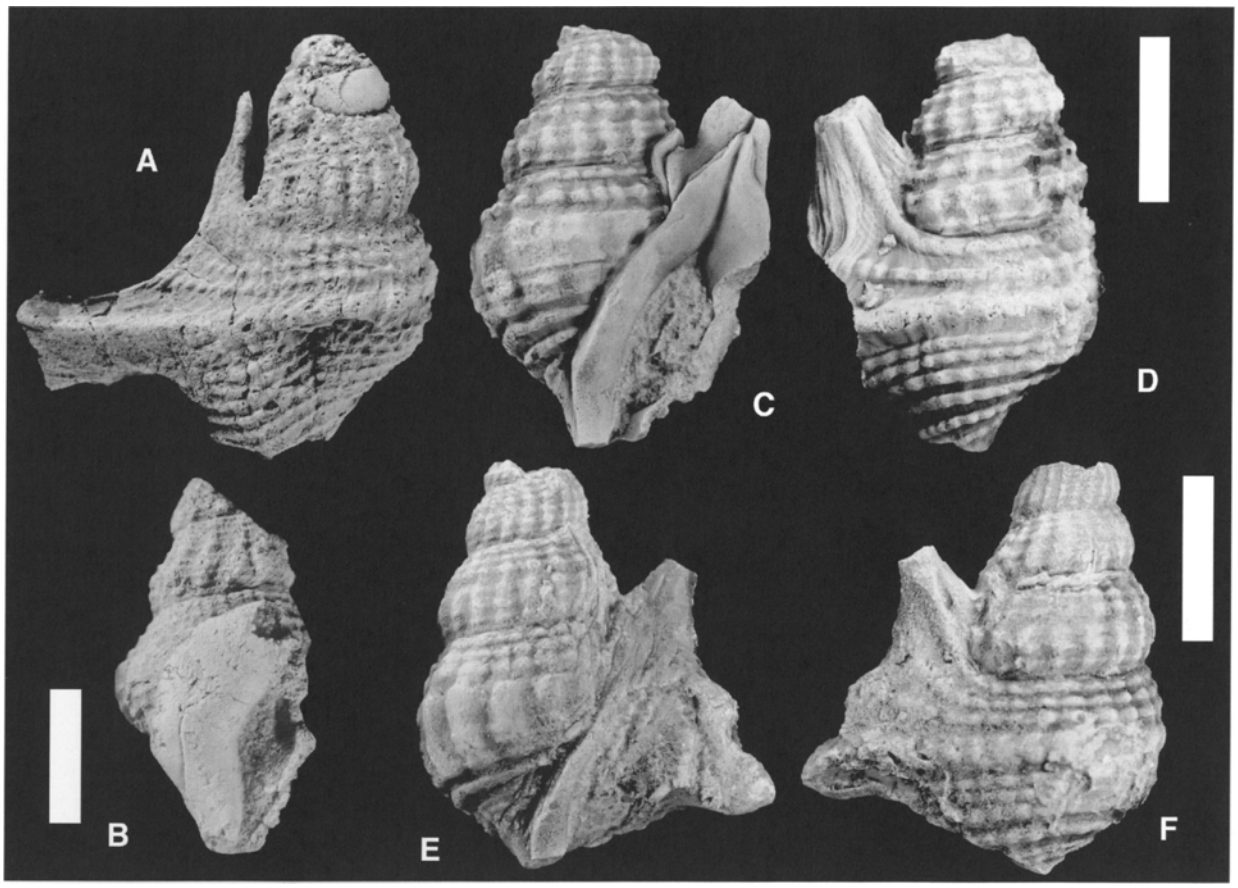

Fig. 4. – **A, B**: *Anchura securifera* (FORBES) from the Trichinopoli Formation, India; **A**. Specimen with parts of the wing preserved (GPI 3778); **B**. Specimen with well developed inner lip callus (GPI 3379). – **C-F**: *Anchura neubaueri* (RIEDEL) from the Mungo River, Cameroon; **C, D**. Two views on the **holotype** (SNMS 21487); **E, F**. Two views on the paratype (SNMS 21456). – Scale bars = 10 mm.

the ornament changes into nodose cords, the upper of which continues into the posterior spur and the fourth (third in one specimen) continues into the keel of the wing of the outer lip. The inner lip is strongly callus covered, narrowing the tight aperture even more. Of the two figured shells GPI 3778 is 30 mm high and 31 mm wide, GPI 3779 is 29 mm high and 19 mm wide. They have an apical angle of about 30°.

Differences: *Anchura neubaueri* is very similar to *Anchura securifera* but has fewer spiral cords and the posterior spur is generally shorter. The Turonian *Anchura jakobi* (COLLIGNON, 1934) from Madagascar differs by having a little finger-like extension between the main wing and the posterior spur of the outer lip of the aperture (COLLIGNON 1934). The Albian *Anchura andersoni* ALLISON, 1955 from northwestern Mexico does not show the carinate ornamentation on the body whorl that is typical of geologically younger species (ALLISON 1955). The same appears to be the case in the Cenomanian *Anchura turricula* STEPHENSON, 1952 from Texas. The European *Anchura requieniana* (D'ORBIGNY, 1842) from the Uchaux basin, France has no posterior spur.

Anchura neubaueri (RIEDEL, 1932)
Fig. 4C-F

*1932 *Chenopus neubaueri* n. sp. RIEDEL: 92, pl. 23 fig. 10; pl. 33 figs. 7-10.
1956 *Aporrhais neubaueri* RIEDEL. – DARTEVELLE & BREBION: 36, pl. 2 fig. 10.

Material: Two specimens from the Mungo River outcrops in Cameroon (SNMS 21456, 21487).

Description: The high spired shell has convex whorls separated by deep sutures. It is sculptured with 18 axial ribs crossed by up to seven spiral cords. The uppermost spiral continues into the ridge of the posterior spur, while the third or fourth spiral forms the ridge on the wing. The aperture is elongate and narrow, ending anteriorly in a canal. The inner lip is strongly callus covered. The shell is 25 mm high and 23 mm wide but parts of spire, rostrum, and wing are missing.

Differences: The posterior spur of *Anchura securifera* is closer to the spire as in *Anchura neubaueri*. *Anchura jakobi* (COLLIGNON, 1934) from Madagascar differs in having a little finger-like projection between the main wing and the posterior spur.

Family Strombidae RAFINESQUE, 1815

Genus *Hippocrenes* MONTFORT, 1810

Type species: *Tibia macroptera* LAMARCK, 1799 from the Eocene of France.

Description: The medium to large sized, high spired shell has straight whorls that are separated from each other by shallow sutures. The aperture is long and narrow, continuing in a narrow canal up to the apex. The rostrum is straight or bent toward the outer lip, the outer margin of the wing is bow-like.

Hippocrenes kussi n. sp.
Fig. 3C, G

Derivatio nominis: Named after JOCHEN KUSS (Universität Bremen) with whom the co-operation in field work in Egypt was very pleasant.
Holotype: G 112, collection of the TU Berlin (Fig. 3C).
Paratype: G 115, collection of the TU Berlin (Fig. 3G).
Locus typicus: Ammonite Hills, Western Sand Sea, Egypt.
Stratum typicum: The Maastrichtian of the Dakhla Formation.
Material: Four specimens from the Ammonite Hills, Western Egypt (TUB G 112, G 115).

Diagnosis: The high spired, strombid gastropod has straight sided whorls and axial ribs. The outer lip is wing-like expanded and attached to the spire.

Description: The high spired shell with straight whorls has an ornament of axial ribs that fade away on the lower part of the body whorl. The body whorl is a little higher than the spire. The wing-like outer lip is attached to the entire spire and forms a half circle covering the last two whorls. One specimen shows varices. The **holotype** is 43 mm high, 23 mm wide, and has an apical angle of about 25°.

Differences: The type species *Hippocrenes macroptera* has a higher wing, just like *Hippocrenes subtilis* PETHÖ, 1906 which also has a bigger apical angle. *Hippocrenes nuda* (BINKHORST) (see KAUNHOWEN 1897: 74, pl. 8 figs. 13-15) from the Maastrichtian of the Netherlands possesses an angular notch between wing and rostrum. In contrast to *Hippocrenes kussi*, "*Aporrhais*" *saharica* QUAAS, 1902 shows spiral lirae on the spire and on the base, but spirals on the base are unknown in *Hippocrenes kussi*.

Remarks on evolution and biogeography of the described genera

The earliest species of *Latiala* was reported from the Aptian/Albian of Japan (*Latiala hayamii* KASE, 1984). Slightly later, in the Albian/Cenomanian *Latiala heliaca* SAUL, 1998 lived in California. In the Cenomanian, *Latiala* had spread to Europe (*Latiala*? cf. *lobata*), and in the Coniacian/Santonian *Latiala papilionacea* appeared in West and South Africa as well as in India (STOLICZKA 1868; WOODS 1906; RENNIE 1930; DARTEVELLE & BREBION 1956). *Latiala* sp. reached the North American Atlantic and Gulf coast in the Campanian (DOCKERY 1993). The genus is also known from Brazil with *Latiala infortunata* which probably is of Maastrichtian age (WHITE 1887). *Latiala* is thus known from the Aptian to the Maastrichtian.

Drepanocheilus lived in the Aptian/Albian at places quite distant from each other. *Drepanocheilus elongatodigitatus* NAGAO, 1939 is known from Japan (KASE 1984) and *Drepanocheilus neglecta* occurred in western Europe (TAYLOR et al. 1983). During the Santonian, *Drepanocheilus herberti* and *Drepanocheilus* (*Tulochilus*) *jouberti* appeared in South Africa. The former might have given rise to the Weddellian genus *Struthiochenopus*. Species of *Drepanocheilus* were quite abundant in the temperate regions and became rarer towards the tropics. This is in contrast to *Anchura* which was widely distributed in tropical regions and less so in temperate regions. When North American species are considered (SOHL 1967: tab. 2) it appears that *Anchura* dominated the more southerly localities, while *Drepanocheilus* dominated the more northerly localities. The subgenus *Drepanocheilus* (*Tulochilus*), previously only described from the Danian (early Paleocene) of New Zealand, can now be traced back into the Santonian of South Africa with *Drepanocheilus* (*Tulochilus*) *jouberti* n. sp. *Drepanocheilus* is one of the few aporrhaid genera that survived the Cretaceous-Tertiary mass extinction and it is known to have occurred from the Aptian to the Eocene (WENZ 1938-44). A Jurassic genus resembling *Drepanocheilus* is *Pietteia* COSSMANN, 1904. It should be taken into consideration as a possible ancestor.

Anchura appeared only shortly after *Drepanocheilus*. It is known from the Albian of the Mexican Pacific coast with *Anchura andersoni* ALLISON, 1955 and the Cenomanian of Texas with *Anchura turricula* STEPHENSON, 1952 (see SAUL 1998). It later appeared in France during the Turonian with *Anchura requieniana* (see ROMAN & MAZERAN 1913) as well as Cameroon with *Anchura neubaueri* and in Central Europe with *Anchura longispina* ANDERT, 1934 in the Coniacian, and in India in the Santonian with *Anchura securifera*. According to ELDER & SAUL (1996), it survived into the Paleocene of California after which it disappeared.

Perissoptera has been documented from the Albian of Europe with *Perissoptera parkinsoni* (MANTELL, 1822), from the Cenomanian of the Western Interior with *Perissoptera prolabiata* (WHITE) (see DOCKERY 1993) and from the Santonian of India (STOLICZKA 1868). In south-eastern North America it occurred in the Campanian with *Perissoptera prolabiata mississippiensis* (DOCKERY, 1993). SAUL (1998) considered "*Perissoptera*" *hannai* ALLISON, 1955 from the Mexican Pacific coast the only *Perissoptera* from the Pacific coast of North America. However, this species has a keeled body whorl and can, therefore, not be assigned to *Perissoptera*. The genus existed from the Albian to the Maastrichtian.

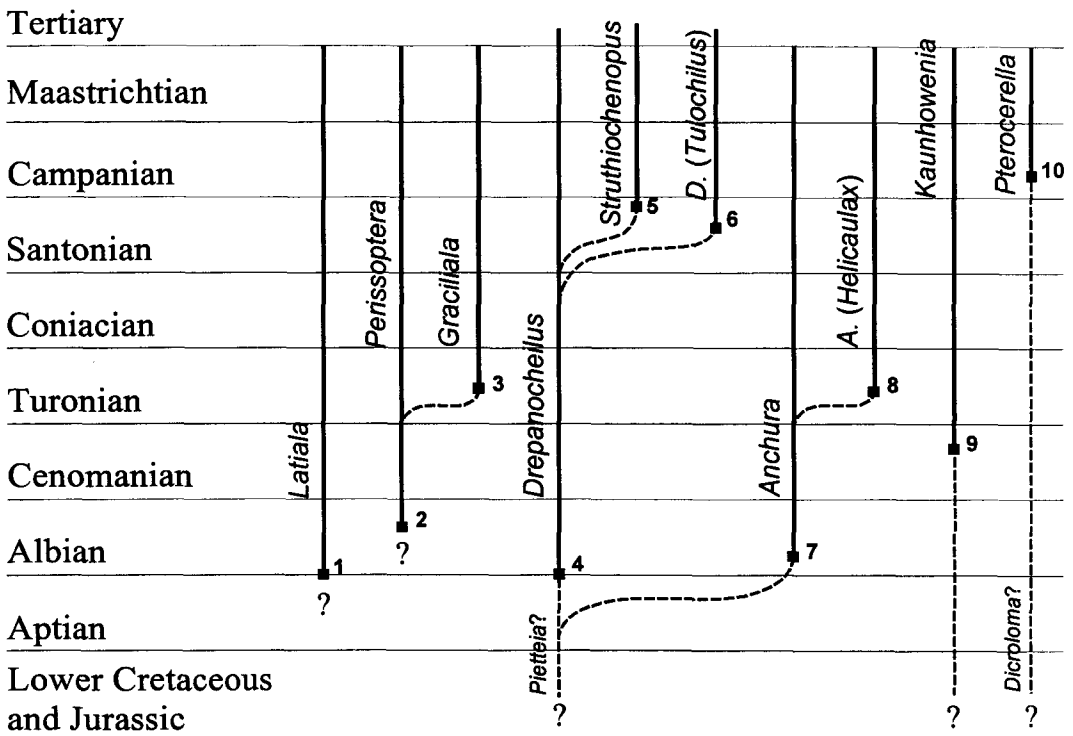

Fig. 5. Possible origin, stratigraphic ranges and suggested phylogenetic relationships of the discussed aporrhaid genera. – **1**: axial sculpture dominant, no keels, wing with a terminal thickening and an upward directed spine; **2**: axial sculpture dominant, no keels on the whorls, an upward directed spine on the wing, and a broad lobe below; **3**: reduction of the lobe to minor digitations; **4**: body whorl with two or more keels, dagger-like wing; **5**: development of keels on the spire; **6**: angular whorls with blunt tubercles; **7**: reduction of the keels except for wing and last whorl; knobbly sculpture on the last whorl; **8**: development of long anterior and posterior projections; **9**: sculpture of tuberculate spiral ridges; **10**: smooth spiral ridges, no axial sculpture, multidigitate wing.

The earliest species of *Graciliala* is *Graciliala simplex* from the French Turonian (ROMAN & MAZERAN 1913). It then appeared in the Coniacian of Cameroon (*Graciliala latealata*) and reached North America in the Campanian (*Graciliala johnsoni* DOCKERY, 1993). *Graciliala* lived in the tropical Tethys and adjacent warm seas and existed from the Turonian to the Maastrichtian. SOHL (1960) suggested that *Graciliala* evolved from *Perissoptera*. This might have taken place by transforming the narrow posterior spur into a broad wing. The "minor digitations that frill the margin" (SOHL 1960: 97) of the outer lip could well be remnants of the once broad lobe of *Perissoptera*.

Kaunhowenia is known throughout the Late Cretaceous of Central Europe (FRECH 1887; MÜLLER 1898; HÄGG 1954; ABDEL-GAWAD 1986). It includes the type species, *Kaunhowenia buchii* (see FRECH 1887), and those described herein. An undetermined species of this genus is very abundant in upper Cenomanian to Turonian sediments in Sergipe, north-eastern Brazil (J. SEELING pers. comm.). Several Jurassic species possess a similar tuberculate ridge including *Chenopus vespa*, *Alaria conulus*, and *Alaria leblanci* (see PIETTE 1891) indicating a Jurassic origin of this genus.

Pterocerella has been observed on both sides of the northern Atlantic Ocean in Campanian to Maastrichtian sediments. With its strong spiral keels and lacking axial sculpture, it differs markedly from the other aporrhaids described herein. It might have its ancestors in the Jurassic *Dicroloma*-relation.

In the Late Cretaceous, *Hippocrenes* is only known form the Maastrichtian. With the discovery of *Hippocrenes kussi* n. sp. on the Egyptian shelf, the genus geographically ranged from the northern to the southern shore of the central Tethys. The type species of *Mauryna* GREGORIO, 1880, *Mauryna bellardi* (GREGORIO) as figured by SAVAZZI (1988: figs. 5-8), could well represent an elongated relative of *Hippocrenes kussi*. *Hippocrenes* and *Mauryna* might therefore be taken into consideration as stem group representatives of the Seraphsidae JUNG, 1974.

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