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# The Pugnellidae, a new stromboidean family (Gastropoda) from the Upper Cretaceous

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With 6 figures

**Abstract:** Members of the new family Pugnellidae have long been considered to represent the earliest members of the Strombidae but have more recently been included with the Aporrhaidae. We here propose them to represent a new family since their low-spired, bulgous shells are quite distinct from the usually slender and high-spired shell of the Aporrhaidae. Eleven species are described here belonging to six genera from which one genus and five species are new. The new genus *Bizarrus* includes large, unornamented *Gymnarus-like* species, and new species are described as *Pugnellus klitzschi*, *Perustrombus africanus*, *Perustrombus indicus*, *Pugnellus? bartheli* and *Pyktes popenoei*.

The here described Pugnellidae are from the Coniacian/Santonian of Mungo River in Cameroon, the Santonian Umzamba Formation in the Eastern Cape Province of South Africa, the Campanian-Maastrichtian Ariyalur Group in Tamil Nadu, southern India, the Maastrichtian Quiriquina Formation of central Chile and the Maastrichtian Ammonite Hill Formation in the Western Desert of Egypt. Their radiation and possible phylogenetic relations to other Late Cretaceous stromboids are discussed. The origin of this family appears to lie in eastern Asia from where they spread through the Indopacific, Tethys and Atlantic Oceans during the Cenomanian-Santonian before they finally reached eastern North America in the Campanian.

**Kurzfassung:** Vertreter der neuen Familie Pugnellidae wurden teils als früheste Strombidae angesehen, in jüngerer Zeit aber auch zu den Aporrhaidae gestellt. Aufgrund ihrer massiven Schale und gedrungenen Spitze lassen sie sich jedoch gut von den meist schlanken, hochturmigen Aporrhaidae abgrenzen. Wir beschreiben hier elf Arten aus sechs Gattungen, darunter eine neue Gattung und fünf neue Arten. In der neuen Gattung *Bizarrus* werden große, *Gymnarus*-artige Arten mit glatter Schale zusammengefaßt; die neuen Arten sind: *Pugnellus klitzschi*, *Pugnellus? bartheli*, *Perustrombus africanus*, *Perustrombus indicus* und *Pyktes popenoei*.

Sie entstammen der Mungokreide von Kamerun (Coniac-Santon), der Umzamba Formation an der Ostküste Südafrikas (Santon-Campan), der Ariyalur Gruppe im südindischen Tamil Nadu (Campan-Maastricht), der Quiriquina Formation Zentralchiles (Maastricht) und den Ammonitenbergen in der Libyschen Wüste von Ägypten (Maastricht). Ihre Beziehungen untereinander und zu anderen oberkretazischen Stromboidea, ihre Radiation sowie mögliche phylogenetische Zusammenhänge werden diskutiert. Die Pugnellidae scheinen ihren Ursprung in Ostasien zu haben, von wo sie sich im Cenoman-Santon über den Indopazifik, Atlantik und die Tethys ausbreiteten und im Campan die nordamerikanische Atlantik- und Golfküste erreichten.

## Introduction

Many *Pugnellus*-related species and genera have been described from around the world since *Pugnellus densatus* was first described by CONRAD (1 860) but their taxonomic position has long been cloudy. *Pugnellus* and related forms used to be placed in the Strombidae (WENZ 1938; SOHL 1960) but POPENOE (1983) considered them to represent Aporrhaidae according to similar juvenile shell shape. POPENOE placed *Gymnarus* in a new subfamily Aporrhainae and *Pugnellus* in a new subfamily Arrhoginae. But during our evaluation of Late Cretaceous gastropods it became apparent that *Pugnellus* could very well represent a descendant of *Gymnarus* so that their placement in separate subfamilies appears to be unacceptable. DOCKERY (1993) agreed with their placement in the Aporrhaidae due to the similarities he recognized in the juvenile sculpture found in *Pugnellus* and modern *Aporrhais*. We introduce the new family Pugnellidae to include *Pugnellus* and related taxa and consider them to be closely related to the Aporrhaidae, from which they probably descended.

KOROTKOV (1992) introduced four new Aporrhaid families based mainly on the number of digits that are present on the outer lip of the adult shell. He placed the genera *Anchura* and *Helicaulax* in different families even

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thouh they are only distinguished from each other by the length of their posterior spur and rostrum, while *Helicaulax* and *Gymnarus* were placed in the same family, even thouh they have several more morphological features by which they can be separated from each other. Taxonomy based on such minute differences appears of little use and is not accepted here.

## Material

The gastropods of the Late Cretaceous on the Indian Ocean coast of South Africa were described first by WOODS (1906) and later by RENNIE (1930). KLINGER & KENNEDY (1980) determined the age of these layers as Santonian/Campanian in a revision of their ammonite fauna. Since most of the Campanian layers present in the outcrop are exposed in the slippery, overgrown upper part of the cliff North of the Umzamba river mouth the fossils described here (and also those of WOODS and RENNIE) can be dated as predominantly of Santonian age.

The main outcrop lies next to the North of the Umzamba river mouth and consists of sandstone cliffs from which the fossils have been liberated from the rather hard rock by salt erosion initiated by splash during high tides and mechanical erosion due to surf during occasional spring tides. The locality lies at the mouth of the Umzamba River in the northeastern corner of the former Transkei (Pondoland), now Eastern Cape Province. We collected most of the fossils described here in summer 1995. The beds are rich in fossils, consist of silty to sandy carbonate-indurated sediment, contain boulders and fossil wood, and although they reflect frequent but minor changes in regard to the former sea-level, they were all deposited within the tidal range and slightly below it. These fossils are deposited in the South African Museum in Cape Town (labeled SAM).

The Indian fossils were collected during field work in 1994 by K. BANDEL and D. KORTUM, in the vicinity of the town Ariyalur in the Tiruchirapalli District of Tamilnadu in SE India from the Campanian/Maastrichtian Ariyalur Group. Its stratigraphy was described in detail by GOVINDAN & RAVINRAN (1996). The sediments of the Ariyalur Group near Ariyalur are about 600 m thick. The lower Sillakuddi Formation is a thick, rather sandy deposit with a dominance of fluvial and shallow marine sand beds. The following Kallankurichchi Formation is formed by calcareous deposits in its lower 40 m used for the production of cement and grades into the sandy Ottakkovil Formation above.

According to GOVINDAN & RAVINRAN (1996) the limestones of the Kallankurichchi Formation are of Early Maastrichtian age. The formation begins with a fluvial conglomerate with pebbles being utilized by oysters for attachment. These shore deposits are succeeded by limestones well exposed in the quarries of the cement factory about 5 km east of Ariyalur. The lower limestones here consist of a matrix containing many bryozoan and bivalve fragments and orbitolinids, and are characterized by large *Gryphaea*-like exogyrids. Its top has been transformed into a hardground, and a sequence of sandy to marly limestones with beds of complete and fragmented inoceramids follows above. It ends again in a very conspicuous hardground from which the here described stromboid was extracted. It rested in a pit that had probably been excavated by burrowing crustaceans. Some more limestone follows above before the Ariyalur Group becomes more sandy. The Indian fossil is deposited in the museum of the Geologisch- Paläontologisches Institut of the University of Hamburg (labeled GPI).

The Egyptian fossils from the Ammonite Hills (Dakhla Formation) in the Western Sand Sea were collected by BARTHEL and HERRMANN-DEGEN as part of their year-long research within the SFB 69, in Berlin. They are from the locality that had originally been described by QUAAS (1902) and again in more detail by BARTHEL & HERRMANN-DEGEN(1981). These rocks exposed between the high dunes of the Western Egyptian Desert are of Maastrichtian age. BANDEL & KOWALKE (1997) described microreef-forming Vermetidae (*Laxispira*) from the same locality which indicate a rather shallow environment, probably influenced by the tropical Tethys Sea. These fossils are deposited in the TU Berlin (labeled TUB).

The Chilean gastropods from the Quiriquina-Formation were collected during spring 1997 together with ARTURO QUINZIO and RAMIRO BONILLA at Isla Quriquina near Concepción (Talcahuano). Some specimens were taken from the collection of Biro in the Geological Institute of the University of Concepción (labeled GIUC). The outcrop and its fauna has been described in detail by STINNESBECK (1986) and also age determination was carried out by him aided by ammonites. The fauna thus lived during Maastrichtian time very close to a rocky shore on sandy ground in the southwestem Pacific Ocean.

From the Late Cretaceous deposits of Cameroun the types described by RIEDEL (1932) were loaned from the Staatliches Museum für Naturkunde in Stuttgart (labeled SMNS). All five species where found in the locality 'Bombe'. The age of this locality is problematic since only two ammonites where found. In RIEDEL's discussion (RIEDEL 1932: 18-19) he assumed that it ranges from Emscher (= Coniacian) to Maastrichtian. According to REYMENT (in: DARTEVILLE & BREBION 1956) they are of Coniacian age. A recent visit to the exposures of Cretaceous rocks at the shore of the Mungo River near the village of Bombe (1998) demonstrated that RIEDEL's material was quite exceptional and nothing like it can be found there today.

We were able to compare our material with species collected from the Ripley Formation and its Coon Creek and Coffee Sand members in Mississippi and Tennessee. The material is largely from the collection of DAVID DOCKERY III (DOCKERY 1993) and from collections made jointly with him in Coon Creek (Tennessee) and Union County Lake in Mississippi (Maastrichtian) and Coffee Sand in Friendship, Mississippi (Campanian).

## Systematic Palaeontology

Phylum Mollusca LINNAEUS 1758
Class Gastropoda CUVIER 1797
Subclass Caenogastropoda COX 1959
Superfamily Stromboidea RAFINESQUE 1815
Family Pugnellidae n. fam.

Derivatio nominis: The family is named after *Pugnellus* which represents the genus of the group that is best known and has been established for the longest time.

Diagnosis: Species belonging to the Pugnellidae are characterized by a low spire, an enlarged and reinforced outer lip, often with horn-like extensions, and a callus-coated inner lip. The callus is commonly spread out to cover large parts of the shell.

Differences: The Colombellariidae are also low-spired but commonly show a denticulate inner and outer lip the latter not as much reinforced as that of the Pugnellidae. The Aporrhaidae from which the Pugnellidae may have descended are usually high-spired and possess spines or lobe-like extensions on the outer lip instead of the more horn-like extension of the Pugnellidae. The outer lip of

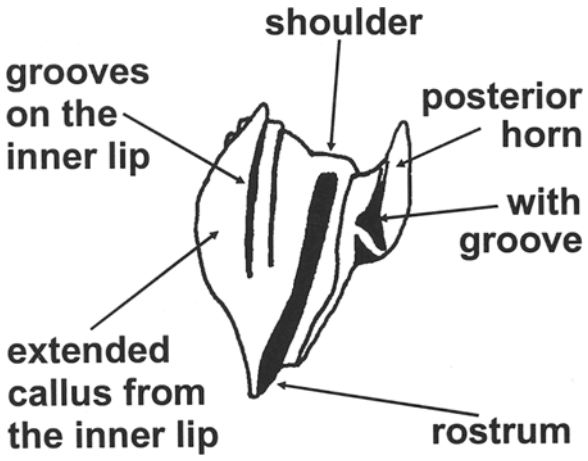


**Fig. 1.** Some distinct pugnellid characters.

the Struthiolariidae is not extended and thickened as in the Pugnellidae. From the Strombidae only *Strombus* looks quite similar, even the 'stromboid notch' is often present among members of the Pugnellidae, but *Strombus* lacks the massive callus, especially that portion that covers the upper whorls of the spire. In addition, *Strombus*-like fossils are not known from strata older than Miocene (ABBOTT 1960), a time when the last Pugnellidae had already become extinct.

The protoconch of *Pugnellus* shows close affinities to that of the Aporrhaidae, as was pointed out by DOCKERY (1993: 66). According to this author the protoconch of *Pugnellus densatus* is conical and composed of four smooth convex whorls. The protoconch of *Strombus*, in contrast, is high-spired and shows tuberculose ornamentation (BANDEL 1993; BANDEL et al. 1997: fig. 3, 4 A-D).

Remarks: Members of the Pugnellidae are quite abundant in Late Cretaceous and Paleogene deposits of the Indopacific, Atlantic, Weddellian provinces and the southern margin of the Tethys, but are apparently absent from Europe and the Boreal realm. *Lispodesthes* and *Tundora* as well as *Tessarolax* and *Ceratosiphon* may also belong to this family, but they need to be studied in more detail before this suggestion can be confirmed.

Assigned genera: *Pugnellus*, *Pyktes*, *Gymnarus*, *Bizarrus*, *Perustrombus*, *Torgnellus*, *Tephlon*, *Conchothyra*, and *Antarctodarwinella*.

## Genus *Gymnarus* GABB 1868

Type species: *Pugnellus manubriatus* GABB 1864 from the Cenomanian Cottonwood Creek, Siskiyou County, California.

Description: The medium-sized shell has a body whorl that makes up about two thirds of total shell height. Ornament consists of axial ribs on the body whorl, sometimes fine spiral lirae are present as well. The outer lip is expanded, with a thick outer margin, shoulder and posterior horn. The inner lip is also strongly callus-covered and callus commonly covers parts of the spire and body whorl as well. The rostrum is short and sometimes bent to the right.

Differences: *Pugnellus* and *Perustrombus* differ from *Gymnarus* and the other genera of the Pugnellidae in having no posterior horn on the outer lip. *Pyktes* has a second extension on the outer lip. *Bizarrus* and *Torgnellus* have a posterior horn but there is no ornament on the whorls.

Remarks: POPENOE (1983) suggested *Gymnarus* to represent the Indopacific faunal province, but members of this genus managed to reach the Atlantic Ocean as early as Coniacian time since *Gymnarus fraasi* (RIEDEL 1932) is found in Cameroon.

*Pugnellus hauthali* WILCKENS 1905 from southern Patagonia is an interesting species intermediate between *Gymnarus*, *Tephlon*, *Conchothyra* and *Bizarrus*. Regarding its callus cover it resembles *Bizarrus dietrichi* (RIEDEL 1932), aperture and ornamentation is similar to *Gymnarus auriculatus* (WOODS 1906), and the shape of the outer lip is similar to that of *Tephlon* and even more so to *Conchothyra parasitica* HUTTON 1877.

The earliest species of *Lispodesthes* (*L. panda* STEPHENSON 1953 and *L. patula* STEPHENSON 1953) from the Cenomanian have two keels on their body whorl instead of axial ribs as are found in *Pugnellus*. This feature makes a close relation to *Gymnarus* very questionable, and *Lispodesthes* appears to be more closely related to *Tessarolax* and *Tundora*.

### *Gymnarus auriculatus* (WOODS 1906)
Fig. 2 A-C

1906 *Pugnellus auriculatus* n.sp. – WOODS: 319, pl. 38, fig. 15 a, b.

Material: One big specimen (SAM PCP11335), a rostrum and an outer lip from the Umzamba beds, South Africa were found. Two smaller specimens from the South African Museum in Cape Town with unknown locality were included, which, according to their mode of preservation and a very similar figure in RENNIE's (1930) description, most probably had also been collected from the Umzamba locality (SAM PCP 12888).

Description: The shell consists of five whorls ornamented with axial ribs and fine spiral lirae. A row of tubercles is separated from the uppermost part of the axial ribs due to a depression found here from the penultimate whorl onwards, and on smaller specimens is only seen on the body whorl. Growth lines are the only ornament on the lower part of the body whorl. The outer lip has a thick shoulder, followed by a deep sinus that is succeeded by a strong upward-curved horn. The thickened outer margin of the outer lip has a small sinus in its lower part. The inner lip is covered by thick callus and extends upward to the second whorl. Its callus covers at least a fifth of the whole shell. The aperture is narrow, a little concave, and runs out into the rostrum which is twisted to the right at its end.

The largest specimen is 52 mm high, 32 mm wide and has an apical angle of about 90°.

Differences: *Gymnarus auriculatus* closely resembles *G. granuliferus* (STOLICZKA 1868) from Ariyalur in India but its upper sinus of the outer lip is less deep. The two smaller specimens of the studied *Gymnarus auriculatus* show great affinities to *G. contortus* (STOLICZKA 1868) from India. STOLICZKA (1868) stated that the main difference is size. Among modern representatives of *Strombus* adult individuals commonly show quite different sizes within the same species, when they are fully grown. This has also been observed in detail in case of *Strombus pugilis* and *S. raninus* from the Caribbean Sea (BANDEL & WEDLER 1987). It is found also in other occurrences of *Strombus* and relatives living in tropical seas (own observation). *Gymnarus manubriatus* has smooth ribs that continue from suture to suture. Apart from this character both species are very similar.

*Gymnarus congolensis* (BREBION 1956)
Fig. 2 D, E

1930 *Pugnellus contortus* CONRAD – RENNIE: 218, pl. 25, figs. 24-26.
1956 *Pugnellus densatus* var. *congolensis* n.var. – BREBION: 87, pl. 1, figs. 2, 3.

Material: Two specimens from the Umzamba Formation, South Africa, deposited in Cape Town (SAM PCP 12889).

Description: The low spire of the shell is completely covered with callus, and the body whorl is at least twice as high as the spire. Five to six axial ribs on the body whorl form the ornament just before onset of the outer lip. The shoulder is covered by thick callus. The outer margin of the outer lip is thickened and grooved axially on the inside. It shows an upward bent keel on the outside. The inner lip is also covered by much callus and axially grooved. The callus on the left side extends over and covers the apex as well as the entire ventral side of the shell. The aperture is narrow and of rectangular shape. The holotype is 30 mm high, 16 mm wide, and has an apical angle of about 60°.

Differences: *Gymnarus fraasi* from Cameroon is a close relative. It has a step-like spire and a strong, horizontal keel on the outside of the outer lip. *G. congolensis* and *G. fraasi* differ from the other known species of *Gymnarus* in having no ornament on the spire and a straight rostrum. These two shell characters also occur in North American species of *Pugnellus*.

Remarks: RENNIE (1930) misidentified this species as *Pugnellus contortus* since this latter Indian species has a more elongated posterior horn and a more bulging body whorl.

*Gymnarus fraasi* (RIEDEL 1932)
Fig. 2 F-I

1932 *Pugnellus fraasi* RIEDEL n. sp.: 96, pl. 21, figs. 1-5; pl. 20, figs. 5, 7, 8; pl. 21, fig. 7.
1956 *Pugnellus fraasi* RIEDEL – DARTEVILLE & BREBION: 35.

Material: Three specimens from the Mungo River in Cameroon, deposited in Stuttgart (SMNS 21443, 21471, 21465).

Description (partly according to RIEDEL 1932): The broad, spindle-shaped shell has four visible volutions and an apical angle of about 40°. The body whorl shows 4-7 transversal ribs in the upper third, that form tubercles next to the suture. The spire is smooth and volutions are convex and separated by deep sutures. The outer lip is grooved on the outside with a horizontal keel in the middle. This keel sometimes disintegrates into tubercles. The inner side of the outer lip is grooved and the margin is formed by a strong vertical keel. The inner lip is heavily coated with the callus covering the entire left side of the shell and is axially grooved. The first specimen figured by RIEDEL (SMNS 21443) is herein assigned as holotype and is 30 mm high and 23 mm wide.

Differences: *Gymnarus fraasi* is distinguished from *Gymnarus congolensis* by the horizontal keel on the wing and the deep sutures of the spire.

Genus *Pugnellus* CONRAD 1858

Type species: *Pugnellus densatus* CONRAD 1860 from the Maastrichtian Ripley Formation of Mississippi, USA.

Description: The low-spired stromboids developed at maturity a thick and expanded outer lip. Their aperture is of sublenticular shape with the anterior canal generally short. The outer lip is reinforced and thick, the inner lip smooth. Callus coats the body in latest stages and obscures the original shape of the shell and its ornament and covers the spire (according to SOHL 1960: 111).

Differences: *Pugnellus* has no horn on the outer lip which distinguishes it from *Gymnarus*. It differs from *Perustrombus* in the spire/body whorl relation which is one to three in case of *Pugnellus* and one to five in case of *Perustrombus*.

Remarks: The rostrum of the Indian Ocean *Pugnellus* is strongly bent upwards in contrast to the short ones of North American *Pugnellus*. These show strong affinities to the West African *Gymnarus*.

*Pugnellus klitzschi* n. sp.
Fig. 2 M-O

Derivatio nominis: In honor of EDUARD KLITZSCH who headed the research group that worked in the Egyptian Desert within the SFB 69 of Berlin.
Holotype: TUB: G 114, from the SFB 69, Fig. 2 M-O.
Locus typicus: Ammonite Hills, Western Sand Sea, Egypt.
Stratum typicum: Dakhla Formation, Maastrichtian.
Material: Six specimens from the Ammonite Hills, Western Egypt, deposited in Berlin (TUB G 114).

Diagnosis: The fully grown shell is covered by callus and ornamented by four to five axial ribs on the body whorl that is provided with an expanded and thickened outer lip and an inner lip with sinuous axially oriented groove in its callus cover.

Description: The shell is completely covered by callus. Four to five axial ribs are present on the body

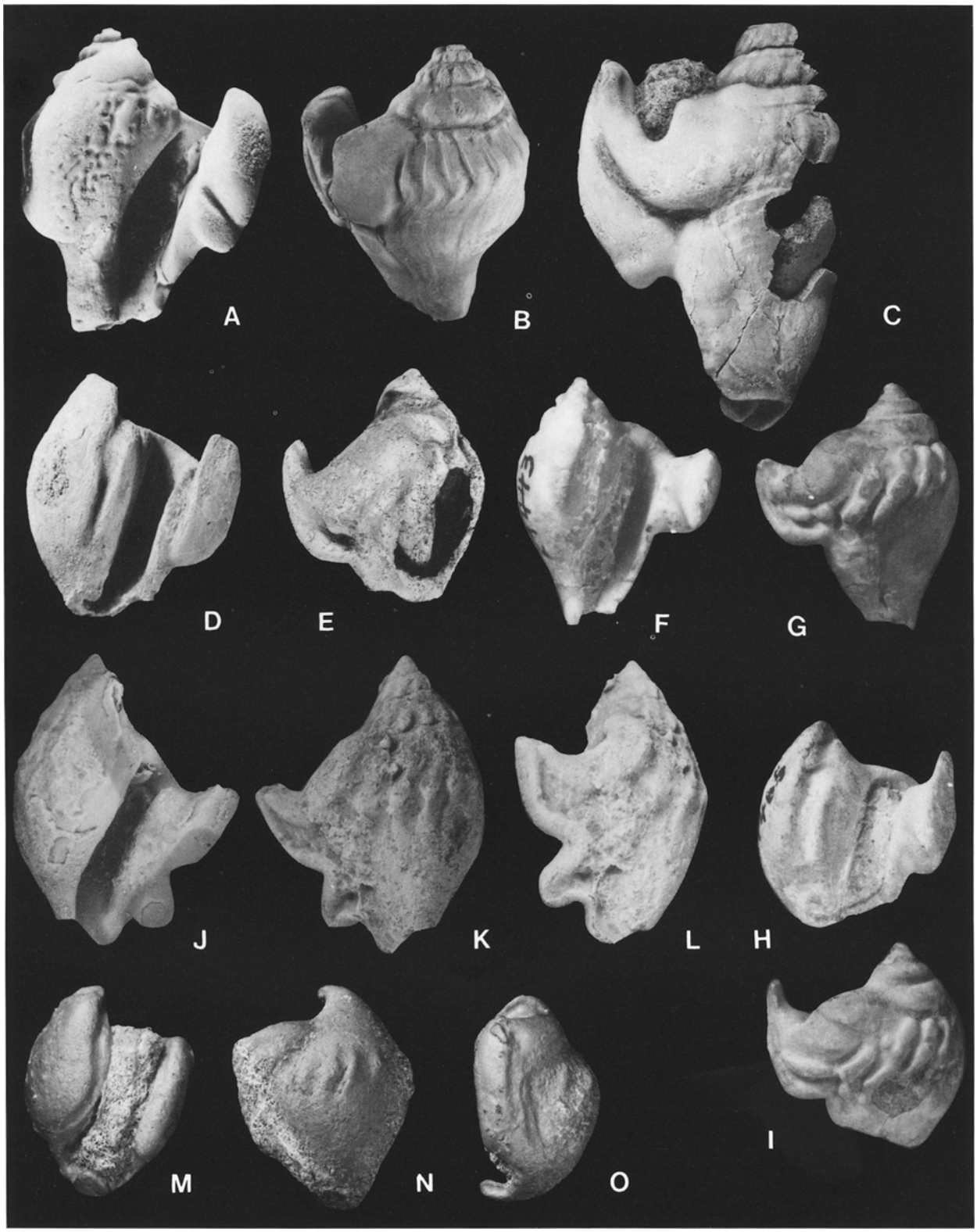


**Fig. 2. A-C:** *Gymnarus auriculatus* (WOODS), ventral (A) and dorsal (B) view of a specimen (SAM PCP 11335), h: 33 mm, w: 26 mm; C: dorsal view of a specimen found at the Umzainba (SAM PCP 12888), h: 52 mm, w: 23 mm. – **D, E:** *Gymnarus congolensis* (BREBION), ventral (D) and dorsal (E) view of a specimen from the Umzamba Formation (SAM PCP 12889), h: 26 mm, w: 23 mm. – **F-I:** *Gymnarus fraasi* (RIEDEL), ventral (F) and dorsal (G) view on a specimen with broken posterior horn but almost complete rostrum (SMNS 21443), h: 24 mm, w: 23 mm, ventral (H) and dorsal (I) view on a specimen with intact posterior horn (SMNS 21465). – **J-L:** *Pyktes popenoei* n. sp., ventral (J) and dorsal (K) view, L: view of the outer lip of the holotype from the Umzamba Formation (SAM PCP 12890), h: 30 mm, w: 23 mm. – **M-O:** *Pugnellus? klitzschi* n. sp., ventral (M) and dorsal (N) view of the holotype from the Ammonite Hills (G 114), h: 26 mm, w: 19 mm; O: side view of the same specimen, showing the upward bend rostrum.

whorl just before the outer lip. The spire makes up about one quarter of the total shell height. The shoulder and outer margin of the outer lip are thickened with callus, and the anterior canal is bent upwards forming a horn. Callus of the inner lip shows an S-like axial groove. The aperture is long and narrow, widening at both ends. The holotype measures 26 mm in height and is 20 mm wide.

Differences: *Pugnellus klitzschi* differs from the American species from the Ripley Formation (see SOHL 1960; DOCKERY 1993) and Navarro Group of Texas (STEPHENSON 1941) by its upward bent rostrum and the smooth inner margin of the outer lip. The closest relative is *Pugnellus uncatus* STOLICZKA 1868 which has a higher spire and more ribs on the body whorl.

*Pugnellus? bartheli* n. sp.
Fig. 3 I

Derivatio nominis: Named in honor of WERNER K. BARTHEL who collected these fossils in the Sand Sea.
Holotype: TUB: G 113, from the SFB 69; Fig. 3 I.
Locus typicus: Ammonite Hills, Western Sand Sea, Egypt.
Stratum typicum: Dakhla Formation, Maastrichtian.
Material: Two specimens from the Ammonite Hills, western Egypt; they are deposited in Berlin (TUB G 113).

Diagnosis: The shell is almost totally covered by callus, and the body whorl is twice as high as the spire. There are two grooves present on the inner lip of the aperture. The holotype is 30 mm high and 15 mm wide.

Differences: The two grooves on the inner lip separate *Pugnellus? bartheli* from any other *Pugnellus*-like fossil. The outer lip of both available specimens is broken so it is not possible to assign the new species with certainty to the genus *Pugnellus*.

Genus *Perustrombus* OLLSON 1944

Type species: *Perustrombus wheeleri* OLLSON 1944 from the Paita region. northern Peru. Maastrichtian.

Description: The medium-sized shell has a short spire and adult shells are completeley covered with callus. The aperture is long with parallel sides. The rostrum is straight and the outer margin of the outer lip is thickened.

Differences: *Perustrombus* differs from *Pugnellus* in the spire/body whorl relation which is one to three for *Pugnellus* and one to five for *Perustrombus*.

Remarks: Apart from the type species and the two new species described below, *Strombus? dallianus* WHITE 1887 from Brazil might belong here.

*Perustrombus africanus* n. sp.
Fig. 3 G. H

Derivatio nominis: It is named after the African continent on which it was found.
Holotype: TUB: G 111, from the SFB 69; Fig. 3 G-H.
Locus typicus: Ammonite Hills, Western Sand Sea, Egypt.
Stratum typicum: Dakhla Formation, Maastrichtian.
Material: 16 specimens from the Ammonite Hills, Western Egypt, deposited in Berlin (TUB G 111).

Diagnosis: The fully grown shell with thickened outer lip is ornamented by four inclined axial ribs and has as finger-like extention of callus onto the spire.

Description: The medium-sized, massive shell has a thickened outer lip and a short spire. The whorls of the spire are flattened smooth, the body whorl is ornamented with growth lines and four sloping axial ribs. The shoulder is heavily thickened and callus sometimes continues like a little finger onto the spire. The holotype is 38 mm high, 23 mm wide and has an apical angle of 75°.

Differences: *Perustrombus africanus*, in contrast to the other species of this genus, has ribs on the body whorl.

*Perustrombus indicus* n. sp.
Fig. 3 J, K

Derivatio nominis: It is named after the Indian subcontinent where it was found.
Holotype: GPI 3654; Fig. 3 J-K.
Locus typicus: Ariyalur, Southern India.
Stratum typicum: Kallankurichchi Formation, Ariyalur Group, Early Maastrichtian.
Material: One specimen from Ariyalur, Southern India, deposited in Hamburg (GPI 3654).

Diagnosis: The fully grown shell is smooth and has a short spire. The aperture is narrow and the outer lip is callus-covered and grooved on its dorsal side.

Description: The medium-sized shell has no ornament, the spire is completely covered by callus. The aperture is long and small and a little wider on its posterior end. The margin of the outer lip is thickened with a band of callus that is grooved on the dorsal side with the groove disappearing toward the spire. The inner lip is only lightly callused. The holotype is 27 mm high and 18 mm wide.

Differences: *Perustrombus indicus* differs from *Perustrombus africanus* by the lack of an ornament, a shorter spire and the outer lip being closer to the body. The Peruvian *Perustrombus wheeleri* has no groove in the callus of the outer lip.

Genus *Bizarrus* n. gen.

Type species: *Pugnellus dietrichi* RIEDEL 1932 from the Coniacian of the Mungo River, Cameroon.
Derivatio nominis: For its bizarre shape.

Diagnosis: Medium- to large-sized *Gymnarus*-like species that lack any ornamentation on the spire or the body whorl, possess a posterior horn and cover their entire shell with callus. The aperture is narrow and of rectangular or lenticular outline. The lower part of the outer lip may show a ventrally inclined fold.

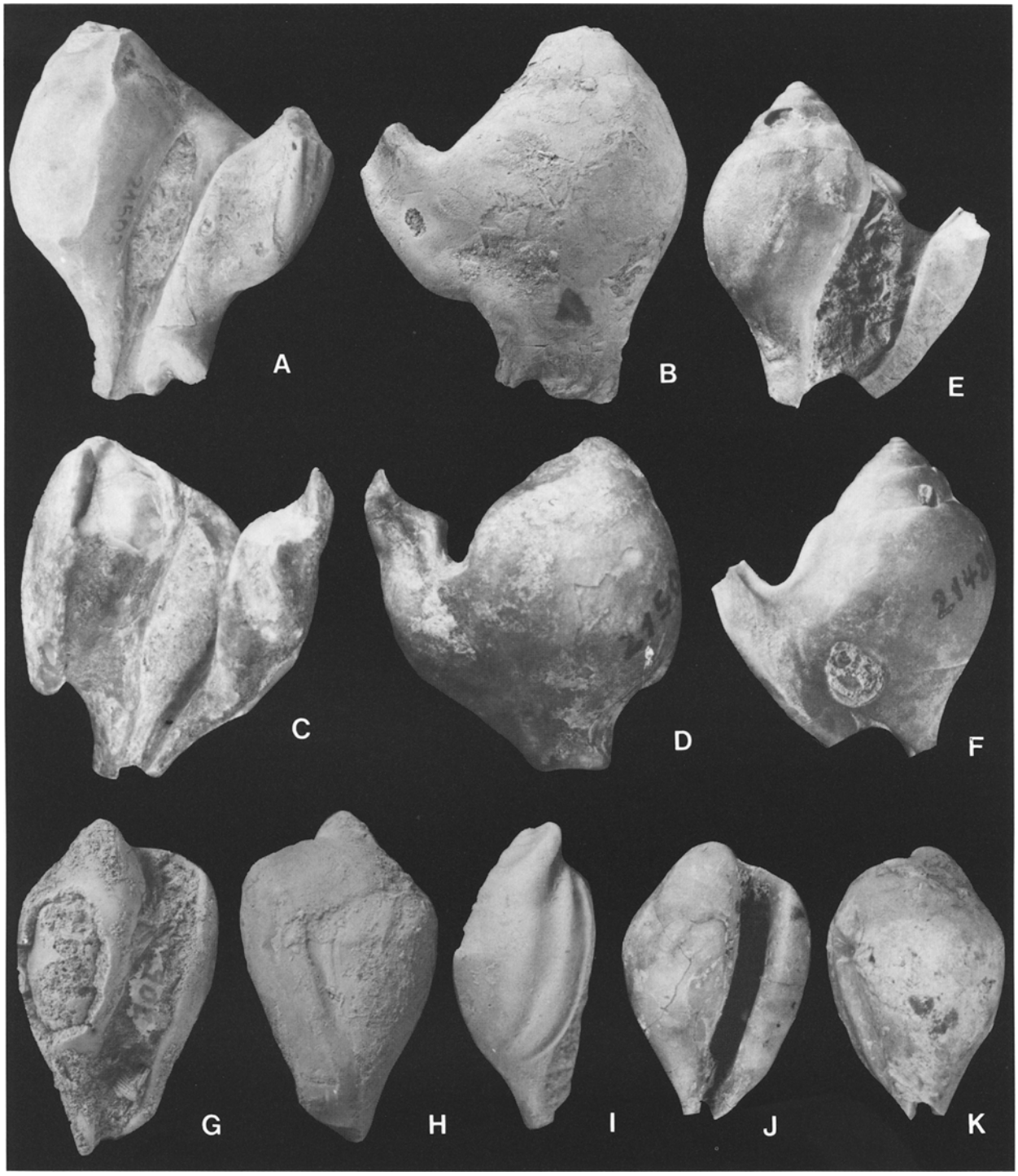


**Fig. 3. A, B:** *Bizarrus incertus* (RIEDEL), ventral and dorsal view of RIEDEL's holotype (SMNS 21503), h: 56 mm, w: 48 mm. – **C-F:** *Bizarrus dietrichi* (RIEDEL), ventral (C) and dorsal (D) view on RIEDEL's holotype (SMNS 20508), h: 33 mm, w: 30 mm; ventral (E) and dorsal (F) view of a specimen without callus cover (SMNS 21488), h: 32 mm, w: 28 mm. – **G, H:** *Perustrombus africanus* n. sp., ventral (G) and dorsal (H) view of the holotype from the Ammonite Hills (G 111), h: 38 mm, w: 23 mm. – **I:** *Pugnellus*? *bartheli* n. sp., ventral view showing the two grooves in the callus cover (G 113), h: 30 mm, w: 15 mm. – **J, K:** *Perustrombus indicus* n. sp., ventral (J) and dorsal (K) view of the holotype from the Ariyalur Formation (GPI 3654), h: 27 mm, w: 18 mm.

Differences: *Bizarrus* is distinguished from most other pugnellid genera by its smooth surface, its entire callus cover and the more bulging body whorl. *Lispodesthes* can be of similar shape but has two projections on the outer lip instead of one as *Bizarrus*.

Remarks: The species of *Bizarrus* used to be placed with the genera *Gymnarus* and *Pugnellus*. DOCKERY (1993) placed *Pugnellus abnormalis* WADE 1926 in the genus *Gymnarus* suggesting that the ribs had disappeared under the callus. But an immature specimen of *Bizarrus*

*dietrichi* (RIEDEL 1932) from Cameroon with no callus cover shows no ornament of ribs or any other ornamentation (Fig. 3 E, F). All known species – with one dubious exception – are from the Atlantic Ocean and are not older than Coniacian, and these are: *Pugnellus abnormalis* from Mississippi, *Pugnellus dietrichi* and *Pugnellus incertus* from the Coniacian of Cameroon. The latter also appears in the Maastrichtian phosphates of Morocco (SALVAN 1954).

An illustration of *Pugnellus nitidus* DELPEY 1948 (DELPEY 1948: pl. 5, figs. 12, 13), from Madagascar shows strong similarities with *P. dietrichi* (smooth whorls and the shape of callus on the inner lip and the weak indication of a keel on the body whorl); its age has been determined as Santonian-Campanian. But it could also represent a corroded and worn specimen of either *Gymnarus auriculatus* or *G. granuliferus.*

*Bizarrus dietrichi* (RIEDEL 1932)
Fig. 3 C-F

1932 *Pugnellus dietrichi* n.sp. – RIEDEL: 98, pl. 20, figs. 1, 2, 4, 10; pl. 33, fig. 11.
1956 *Pugnellus dietrichei* RIEDEL – DARTEVILLE & BREBION: 35.

Material: Two specimens from the Mungo River in Cameroon, deposited in Stuttgart (SMNS 20508, SMNS 21488).

Description (according to RIEDEL 1932): The shell consists of 3-4 smooth volutions, the body whorl is without rostrum and 1.5 higher than the spire. Whorls are convex and the outer lip extends into a small wing that is grooved on the outside. On the inside a lobe is situated from the margin inwards, and a strong vertical groove bends around it. This creates a coiled appearance of the wing. The aperture is oval and narrow, the callus of the inner lip is grooved vertically, and the callus of the left side forms a downward inclined lobe. Five volutions are visible on a specimen that had just reached maturity. The first specimen figured by RIEDEL is herein assigned as holotype and is 33 mm high and 30 mm wide.

Differences: According to RIEDEL (1932) *Bizarrus dietrichi* differs from *B. abnormalis* by the lobe in the wing and the lobe of callus extending from the inner lip, which is confirmed.

*Bizarrus incertus* (RIEDEL 1932)
Fig. 3 A, B

1932 *Pugnellus incertus* n.sp. – RIEDEL: 99, pl. 20, fig. 9.
1954 *Pugnellus incertus* RIEDEL – SALVAN: 153, pl. 9, figs. 18-19.
1956 *Pugnellus incertus* RIEDEL – DARTEVILLE & BREBION: 34.

Material: One specimen from the Mungo River in Cameroon, deposited in Stuttgart (SMNS 21503).

Description: The large pugnellid gastropod has its shell covered entirely with callus. Four volutions are visible and the aperture is narrow and a little concave. The outer lip is provided with a strong posterior horn that is grooved on the outside. The lower part of the outer lip has a ventrally directed fold. The shell is 56 mm high and 48 mm wide.

Differences: The ventrally directed fold on the outer lip of *Bizarrus incertus* is similar to that of *B. abnormalis*, but the body whorl of *B. incertus* is more bulbous and the horn points into a more upward direction.

Genus *Pyktes* POPENOE 1983

Type species: *Pyktes aspris* POPENOE 1983 from the Coniacian of Oak Run Valley, Shasta County, California.

Description: The pugnellid shell has two labral projections. The posterior projection is situated posteriorly in regard to the whorl periphery, it is broad and laterally directed proximally, bent posteriorly in the middle. The anterior projection is short, spatulate or plug-like and situated about midway between posterior projection and anterior end of the body whorl. The anterior labrum is broad and low. The shell of an adult is covered with callus. Ornament is nearly absent or markedly spiral, strongest on whorl shoulder (according to POPENOE 1983: 753).

Differences: *Pyktes* differs from most other *Pugnellus*-like genera by its two labral projections. *Lispodesthes* also has two labral projections but possesses spiral keels on the body whorl instead of axial ribs.

Remarks: POPENOE (1983: 755) described an evolutionary trend with increasing number of ribs and apical angle for the Californian species from the Turonian to the Maastrichtian. According to the author, *Pugnellus bilobatus* BREBION 1956 from the Upper Campanian or Maastrichtian of Logbatjeck, Cameroon resembles *G. fraasi* and *G. contortus.* It has smooth transversal ribs on the body whorl (unlike *Pyktes popenoei* that shows prominent tubercles in the middle of the rib) and a big apertural angle (spindle vs. direction of aperture). We place this species with *Pyktes* due to its two labral projections.

*Pyktes popenoei* n. sp.
Fig. 2 J-L

1906 *Pugnellus* sp. – WOODS: 320, pl. 38, fig. 16.

Derivatio nominis: In honor of WILLIS PARKINSON POPENOE who published his last study on the Californian Cretaceous Aporrhaidae in 1983.
Holotype: SAM: PCP 12890; Fig. 2 J-L.
Locus typicus: Mouth of Umzamba River, Eastern Cape Province, South Africa.
Stratum typicum: Umzamba Formation, Santonian.
Material: Two specimens from the Umzamba, South Africa, deposited in Cape Town (SAM PCP 12890).

Diagnosis: The shell has abroad body whorl twice as high as the spire which is ornamented by spiral lirae in the early shell and later on also by axial ribs. The thickened outer lip is characterized by one big horn-like lobe pointing upward and a smaller peg pointing downward.

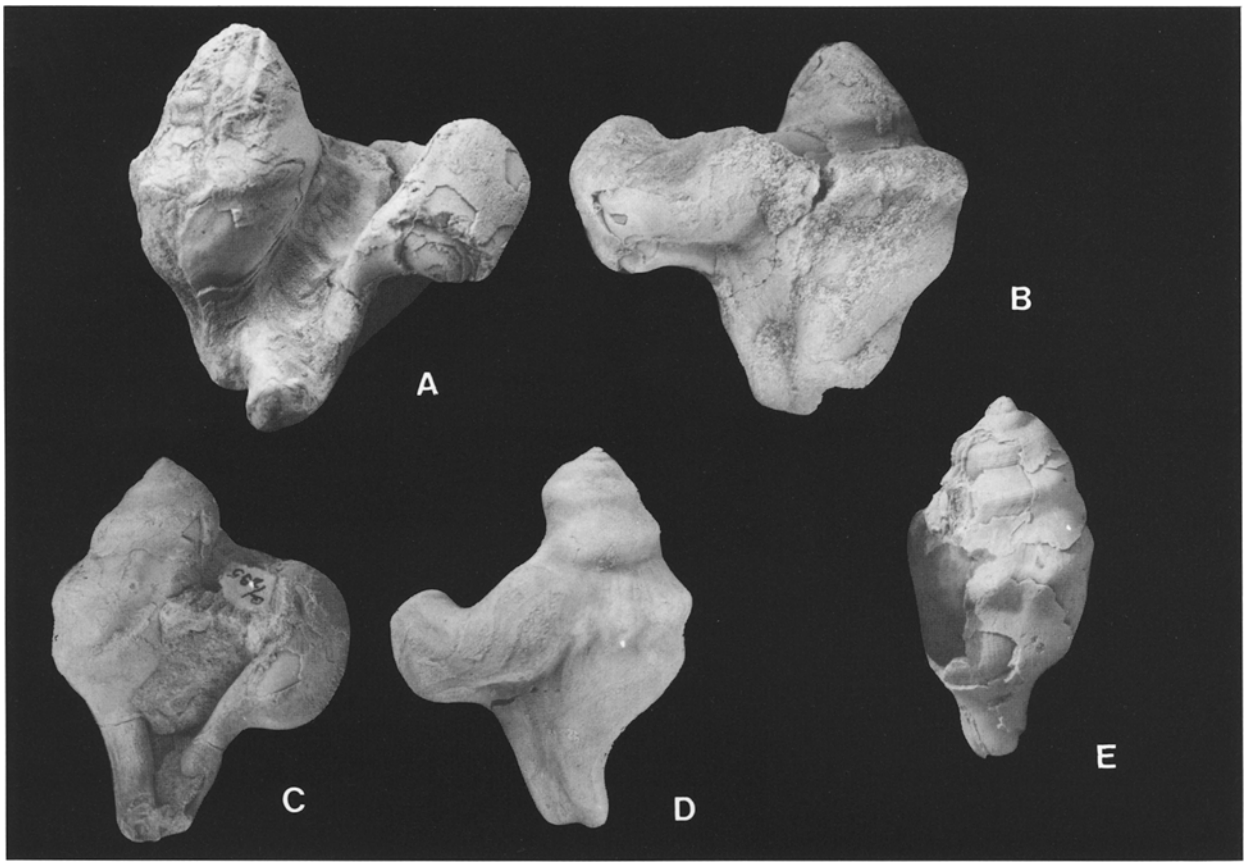


**Fig. 4.** *Tephlon tumidus* (GABB). – **A, B:** Specimen with exceptionally broad outer lip (GIUC Q 459), h: 28 mm, w: 31 mm. – **C:** ventral view of a 'normal' specimen (GIUC Q 259), h: 36 mm, w: 28 mm. – **D:** dorsal view of a 'normal' specimen (GIUC Q 2063), h: 36 mm, w: 27 mm. – **E:** specimen with the callus partly broken off, showing the fine carinae on the shell (GIUC Q 2061), h: 34 mm, w: 17 mm.

Description: The body whorl of the shell is at least twice and half as high as the spire. The shell consists of eight whorls, the early ones are convex and with fine spiral lines. From the fourth whorl onward they are more straight and with twelve ribs per volution. Ribs slope to the left at their lower part and form a prominent row on the body whorl. The margin of the outer lip is thickened, as is the heavy shoulder. One big horn points upward, a smaller peg downward, both extensions are grooved on their dorsal side. The aperture is long and narrow with parallel sides, the inner lip is slightly callus-covered. The holotype is 30 mm high, 23 mm wide with an apical angle of 65°.

Remarks: POPENOE (1983) suggested that the number of ribs on the body whorl of *Pyktes* increased during the Upper Cretaceous. According to this, only the Turonian *Pyktes daiphron* can be regarded as a possible ancestral species of the group. It is older and has less ribs than *P. popenoei* and *P. aspris*. But the latter has more ribs than *P. popenoei* even though it is older. Their evolutionary lines may have split here in an Californian and an eastern branch.

Another possibility is that *P. popenoei* and *P. daiphron* share a common ancestor that should have lived during the Cenomanian or even earlier.

## Genus *Tephlon* POPENOE 1983

Type species: *Pugnellus tumidus* GABB 1860 from the Maastrichtian Quiriquina Formation, Quiriquina Island, southern central Chile.

Description: The pugnellid gastropod has noded tabulate whorls, dominantly spiral sculpture and is equipped with a single spur-shaped posterolateral labral spine bent posteriorly in the middle. Adult shells are usually covered with heavy callus (according to POPENOE 1983: 761).

### *Tephlon tumidus* (GABB 1860)
Fig. 4 A-E

1960 *Pugnellus tumidus* n.sp. – GABB: 197, pl. 3, figs. 13, 14.
1887 *Pugnellus tumidus* GABB – PHILIPPI: 34, pl. 1, fig. 3.
1895 *Pugnellus tumidus* GABB – MÖRICKE: 96, pl. 7, figs. 15, 16.
1904 *Pugnellus tumidus* GABB – WILCKENS: 205, pl. 18, figs. 2a, b.

Material: 27 specimens and some fragments, collected from Quiriquina Island near Concepción and from the collection of the Geological Institute of the University of Concepción.

Description: The pugnellid shell with six volutions is ornamented by fine spiral lirae and a prominent ridge in the middle of the whorl. This ridge turnes into a row of 4-

7 more or less separated, transverse tubercles on the body whorl. The shoulder is heavily thickened with callus. The rostrum has an inner and an outer groove and is bent upwards at its end. The margin of the outer lip is broad and turned upwards. The inner lip is covered by callus, and the apertural part of the penultimate whorl is partly resorbed. Adult shells are entirely covered by callus. The specimen figured as 4 C-D measures 36 mm in height and 28 mm in width.

Differences: *Tephlon tumidus* is a rather unusual pugnellid that has a fairly high spire and differs markedly from all others especially by the ridge on its spire.

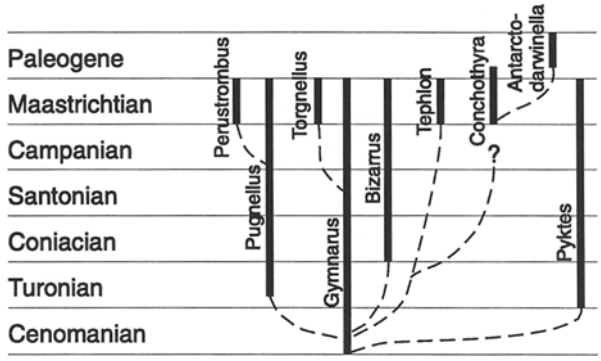


**Fig. 5.** Possible phylogenetic relations within the Pugnellidae.

## Remarks on the evolution and palaeogeography of the Pugnellidae

*Gymnarus* first appeared in the Cenomanian of Japan (*G. yabei* NAGAO 1939) and reached California during the Turonian (*G. manubriatus* GABB 1868; POPENOE 1983). It then spread through the Indopacific as far as Southern India (Santonian *G. granuliferus* STOLICZKA 1868) which at that time lay in the cooler waters of the Southern Hemisphere. There it is also present in South Africa (*G. auriculatus*), is known from the Senonian of Angola and Congo (*G. congolensis*), reached Cameroon in Coniacian times (*G.fraasi*) and might have been present in the Coniacian of Mississippi with *G. calcaris* (WADE 1926) according to STEPHENSON (1947). It also appeared in southern Patagonia (*G. hauthali* WILCKENS 1910) that at that time belonged to the Weddellian province. *Gymnarus* thus existed from the Cenomanian to the Maastrichtian.

The first *Pugnellus* s.s. appeared in southeastern North America (*P. densatus* and *P. goldmani*) during Late Campanian to Early Maastrichtian. It seems to have descended from species like the West African *Gymnarus* (*G. fraasi* or *G. congolensis*) by reduction of the posterior horn or from the Tethys Ocean species of *Pugnellus* (*P. uncatus* STOLICZKA 1868) by straightening the rostrum. We are not yet able to state wether the similarities between the American and the eastern Tethys varieties of *Pugnellus* are a product of convergence or represent an evolutionary lineage. *Pugnellus* lived from probably Turonian time to the Maastrichtian.

*Perustrombus* is only known from the Maastrichtian where it reached a wide distribution ranging from southern India (*P. indicus*) along the Tethyan shores to Egypt (*P. africanus*) to the southeastern Pacific and northern Peru (*P. wheeleri* OLLSON 1944). It appears to have evolved from the Indian Ocean varieties of *Pugnellus* by total reduction of the extensions on the outer lip and seems to have preferred the warmer to temperate Tethyal realm.

*Pyktes* appeared in the Turonian of California (*P. daiphron* POPENOE 1983) where it persisted until the Maastrichtian with *P. hamulus* POPENOE 1983, and is known from the Santonian of South Africa (*P. popenoei*) and the Campanian-Maastrichtian of Cameroon (*P. bilobatus* according to DARTEVILLE & BREBION 1957). These two quite separate occurrences suggest that *Pyktes* evolved early in the area of southeast Asia and differentiated into two branches because of the great distance between the eastern margin of the Pacific and the western margin of the Indian Ocean.

*Bizarrus* first appeared in the Coniacian of Cameroon (*B. incertus* and *B. dietrichi*). Apart from one dubious species from the Santonian-Campanian of Madagascar (*Pugnellus nitidus* DELPEY 1948) it is only known from the North Atlantic. It reached North America in the Campanian (*B. abnormalis* according to DOCKERY 1993) and is known from the Maastrichtian of Morocco (*B. incertus* according to SALVAN 1954). It probably descended from *Gymnarus* by reduction of the ribs and by enlarging the posterior horn. *Bizarrus* lived from the Coniacian to the Maastrichtian.

*Tephlon* occurs only in the Maastrichtian of Quiriquina/ Central Chile (*T. tumidus*) and it may very well represent a long-isolated descendant of an early Indopacific *Gymnarus*.

*Torgnellus* is endemic in northern Peru (*T. peruvianus* OLLSON 1944) and appears to be a descendant of the West African *Gymnarus* that reduced all ornament on spire and body whorl.

In case of the genera *Conchothyra* and *Antarctodarwinella* some suggestions regarding their placement can be made. *Pugnellus hauthali* WILCKENS 1905 from the Senonian of Southern Patagonia can be interpreted to represent an intermediate species between *Gymnarus* and the Weddellian *Conchothyra*, which in turn could quite possibly represent the ancestor to *Antarctodarwinella*. The two latter genera are quite problematic in regard to their belonging in the Struthiolariidae.

ZINSMEISTER & CAMACHO (1980) stated about *Antarctodarwinella:* "Although *Antarctodarwinella* shares a number of features in common with representatives of the

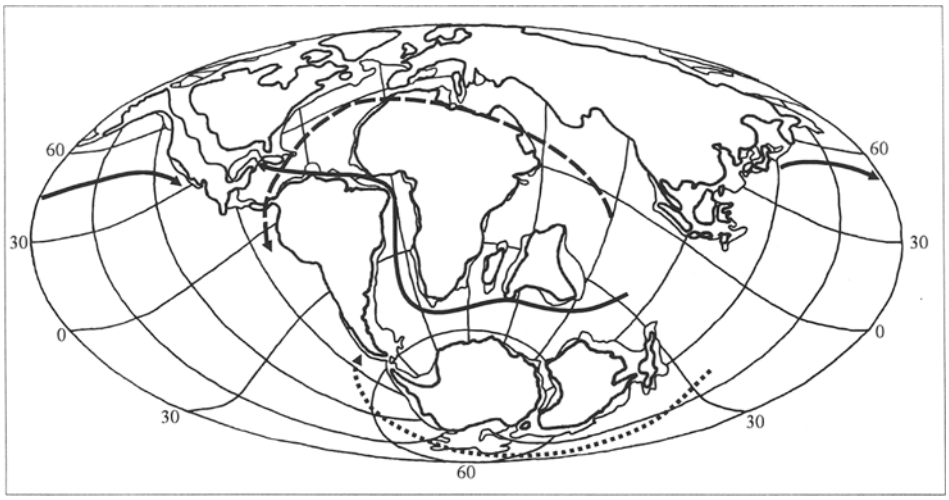


**Fig. 6.** Possible migration routes of the Pugnellidae in the Upper Cretaceous and Paleogene. Solid lines: temperate genera such as *Gymnarus*, *Pugnellus*, *Pyktes* and *Bizarrus*; dashed line: Tethyan genera such as *Perustrombus* and *Pugnellus*?; dotted line: Weddellian genera such as *Tephlon*, *Conchothyra* and *Antarctodarwinella*.

Struthiolariidae, a massive callus, blunt, slightly produced wing and obsolete spiral sculpture indicates that it may have diverged at an early date from the main evolutionary line of *Struthiolarella*. The close similarity of *Antarctodarwinella* with *Conchothyra* suggests that it may have evolved from *Conchothyra* and not *Struthiolarella*." The same authors stated about *Conchothyra*: "The *Conchothyra* stock which was abundant in the Late Cretaceous and Early Tertiary disappeared prior to the beginning of the Eocene and apparently did not give rise to any later struthiolariids in the southwestern Pacific."

We suggest to proceed further along this line of reasoning and exclude *Antarctodarwinella* and *Conchothyra* from the Struthiolariidae and place them in the Pugnellidae. In this case the range of the Pugnellidae would be extended to the Eocene and the Struthiolariidae could be considered a monophyletic family descending from the Paleocene *Perissodonta* of New Zealand. No Cretaceous ancestors have been found or suggested for *Perissodonta* so far.

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