

Systematic revision of Palaeocene brackish water Gastropoda from Mons, Belgium, based on their early ontogenetic shells

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Abstract

The systematic position of Early Mid-Palaeocene brackish water Gastropoda from the Dano-Montian of Mons, South-east Belgium, is revised. Representatives of the subclasses Neritimorpha (with the new genus *Monsneritina* - Neritoidea, Neritidae), Caenogastropoda (with the new genus *Monspotamides* - Cerithioidea, Potamididae) and Heterostropha are characterised with regard to their paleoecology. Three different modes of early ontogenetic development are recognised and paleoecological inferences are discussed.

Key-words: Palaeocene, Belgium, brackish water Gastropoda, early ontogenetic development, palaeoecology

Résumé

Les gastéropodes saumâtres d'âge Paléocène Moyen du Dano-Montien de Mons, Belgique, sont revus. Des représentants des sous-classes des Neritimorpha, avec un nouveau genre *Monsneritina* (Neritoidea, Neritidae), des Caenogastropoda, avec un nouveau genre *Monspotamides* (Cerithioidea, Potamididae) et des Heterostropha sont décrits avec leur développement initial et leur paléocologie est discutée. Trois modes différents de développement ontogénétique initial sont reconnus et les inférences paléocologiques sont discutées.

Mots-clefs: Paléocène, Belgique, Gastéropodes saumâtres, développement, paléocologie

Zusammenfassung

Brackwassergastropoden aus dem frühen Mittelpaläozän des Dano-Montiums von Mons, SE Belgien, werden hinsichtlich ihrer systematischen Stellung revidiert. Vertreter der Unterklassen Neritimorpha inklusive *Monsneritina* n. g. (Neritoidea, Neritidae), Caenogastropoda inklusive *Monspotamides* n. g. (Cerithioidea, Potamididae) und Heterostropha werden hinsichtlich ihrer Paläoökologie charakterisiert. Drei Modi frühontogenetischer Entwicklung werden beschreiben und paläoökologische Schlussfolgerungen werden diskutiert.

Stichworte: Paläozän, Belgien, Brackwassergastropoden, frühontogenetische Entwicklung, Paläoökologie

Introduction

The Early Mid-Palaeocene sediments of Mons, Southeast Belgium, were brought to the attention of geologists, when the mining engineers F.L. Cornet and A. Briart recognised a section within a domestic well on the Goffint property in 1865. In 1874, the Geological Society of France initiated a second pit a few metres to the west on the Coppée estate. These original sinkings were terminated at a depth of about 20 m, when the ground water floor was reached. In 1969 another boring was initiated by the Belgian Geological Survey, located 10 m south of the Goffint pit. The sections – detailed descriptions of the stratigraphy and sketches of the locality were given by MARLIÈRE (1977) – commence with Dano-Montian deposits (68.7 m thick in the 1969 boring) are then succeeded by a Landenian (Late Palaeocene) silty glauconitic sand, which is overlaid by Quaternary deposits. In the 1969 boring the Maastrichtian basement (“Craie de Spiennes”) is also exposed. The Dano-Montian consists of more or less solid limestones with marly intercalations. The upper part of the section (“Calcaire grossier de Mons”) is fossiliferous, containing assemblages of marine, brackish water and fluvial Mollusca.

The well-preserved molluscan fauna has been analysed by several previous workers. BRIART & CORNET (1870-1887) contributed an early comprehensive work on the gastropod fauna. COSSMANN (1915, 1924) first described the gastropods and subsequently the scaphopod and cephalopod fauna. More recently GLIBERT (1973) and VILATTE in MARLIÈRE (1977) have described the gastropod fauna at Mons. The bivalve fauna has been described by COSSMANN (1908), CHAVAN (1936, 1940) and more recently by GLIBERT & VAN DE POEL (1973) and by VILATTE in MARLIÈRE (1977). In addition to the Mollusca further studies of the invertebrate fauna at Mons have described the ostracods (MARLIÈRE, 1958; DAMOTTE, 1964; GODFRIAUX & MARLIÈRE, 1973).

The brackish water gastropod fauna at Mons contains representatives of the subclasses Neritimorpha (order Neritida, superfamily Neritoidea), Caenogastropoda (Littorinimorpha, Risooidea, Littorinoidea; Cerithiimorpha,

Cerithioidea; Pseudamauridae; Neogastropoda, Buccinoidea, Columbelloidea) and Heterostropha (Archaeopulmonata, Ellobioidea). Members of these taxa are characterised by three distinct modes of early ontogenetic development (for terminology and measurements of early ontogenetic shells see BANDEL, 1982; KOWALKE, 1998a):

1. Embryonic development with subsequent hatching of veliger larvae which are feeding on phytoplankton. In these the protoconch comprises a small embryonic shell, which is terminated by a thickened rim indicating the moment of hatching of the veliger from the egg. The subsequent larval shell formed by a planktotrophic veliger usually consists of two or more whorls bearing a characteristic ornament, which differs from the sculpture of the adult shell. The protoconch is usually terminated by a well developed sinusigera notch, indicating the course of the pediveligers outer apertural lip.
2. Embryonic development with subsequent hatching of lecithotrophic larvae. This type of embryogenesis results from a yolk-rich development which produces a bulbous embryonic shell, that is succeeded by a larval shell usually less than two whorls. The shell is produced by a free-swimming larva, that does not feed on phytoplankton but on the remaining embryonic yolk. The transition from the embryonic to the larval shell is indistinct. The sculpture of the larval shell is less characteristic than that occurring in planktotrophic larvae, and often represents a simplified version of that found in the adult. The transition to the adult shell is characterised by a rim on the shell, which is slightly thickened and very slightly sinuous.
3. Direct development without inclusion of a free larval stage. In this instance the large embryonic shell comprises usually not more than one and a half whorls. It is terminated by a more or less distinct rim indicating the course of the outer lip of the embryo's aperture. This is a case of early ontogenetic development, in which the gastropods hatch from the eggs as crawling young.

In this systematic revision of the brackish-water gastropods from Mons, their early ontogenetic shells are described and the paleoecological implications of these are discussed.

The figured specimens are deposited at the Institut Royal des Sciences Naturelles de Belgique (IRSNB FI 6404-6421).

Systematic Palaeontology

- Class Gastropoda
Subclass Neritimorpha
Superfamily Neritoidea RAFINESQUE, 1815
Family Neritidae RAFINESQUE, 1815
Subfamily Neritinae RAFINESQUE, 1815
? *Nerita heberti* SZÖTS, 1953

1953 *Nerita heberti* SZÖTS, p. 30, 141 f., pl. 2, figs. 3-5.

1953 *Nerita hantkeni* SZÖTS, p. 30, 142, pl. 2, figs. 6-7.

1973 *Otostoma* cf. *bicoronatum* DESHAYES, 1864. – GLIBERT, p. 17, pl. 2, fig. 8.

Remarks. – GLIBERT (1973) described a species, based on a single specimen from the Coppée pit, coll. Houzeau, IRSNB 5330, as *Otostoma* cf. *bicoronatum*. This would rather appear to belong to *Nerita* LINNAEUS, 1758. The figured specimen closely resembles *Nerita heberti* from the Lutetian of Hungary and juvenile specimens of *N. heberti* that were described as the synonymous *Nerita hantkeni* by SZÖTS (1953). *Nerita bicoronata* differs from *N. heberti* by eight coarse columellar teeth of equal size, whereas the two uppermost adapical columellar teeth of *N. heberti* are always more strongly developed than the lower ones. *Otostoma* d'ARCHIAC, 1859 with the type species *Otostoma ponticum* d'ARCHIAC, 1859 (WENZ, 1938-1944, p. 418 f., fig. 1020) differs by its very large oblique aperture, the fine axial ridges crossed by equally strong spiral cords and the more or less prominent nodes at the points of intersection of the axial and spiral sculpture.

Genus *Theodoxus* MONTFORT, 1810

Theodoxus fabulus (BRIART & CORNET, 1887)

Pl. 1, Figs. 1-4

1887 *Neritina fabula* BRIART & CORNET, p. 35, pl. 21, fig. 3 a-f.

1915 *Neritina fabula* BRIART & CORNET. – COSSMANN, p. 45, pl. 3, figs. 54-58.

1973 *Theodoxus* (*Vittocliton*?) *fabulus* (BRIART & CORNET). – GLIBERT, p. 18, pl. 2, fig. 10.

Material. – 12 specimens, Coppée pit, coll. Houzeau, IRSNB IG 6544, IRSNB FI 6404.

Description. – The neritoid shell consists of about 3.5 convolute whorls measuring up to 12 mm in width and 8 mm in height. The spire is only slightly emerging. The sculpture of the teleoconch whorls consists of dense zigzag shaped dark brown stripes on a cream white ground. The aperture is ovate and characterised by a rounded, moderately thickened outer lip and a smooth slightly concave columellar septum, which is not dentate. The columellar edge is not thickened by callus.

The protoconch of about 1.25 whorls measures 0.62-0.63 mm at its maximum diameter; its initial cap is 0.07-0.08 mm in width. The diameter of the first whorl is 0.4-0.5 mm. Sculpture of the embryonic shell consists of an indistinct axial groove-ridge pattern that is concentrated on the lower half of the whorls. After 1.25 whorls crowded growth lines are visible and these grade into the regular dense prosocyrte growth lines that occur on the teleoconch whorls.

Remarks. – *T. fabulus* represents the oldest known species of the genus *Theodoxus* with preserved protoconch. The size and dimensions of the protoconch are indicative of direct development with the hatching of crawling young, without the occurrence of a free planktonic veliger stage.

This mode of early ontogenetic development with the formation of an embryonic shell having a characteristic groove-ridge pattern is a typical feature of the genus *Theodoxus*. It has been described in the type species *Nerita fluviatilis* LINNAEUS, 1758 by BANDEL (1982). The morphology of the teleoconch with a smooth columellar septum also indicates a relationship to the genus *Theodoxus*. *Vittoclithon* BAKER, 1923 based on the recent Southeast Asian type species *Neritina meleagris* LAMARCK, 1816 is recognised as a synonym of *Neritina* LAMARCK, 1816, which differs by the coarser dentition of the columella and by involute protoconchs with characteristic sculpture reflecting an indirect development (BANDEL & RIEDEL, 1998; HARZHAUSER et al., in press).

Genus *Monsneritina* n. g.

Type species. – *Neritina montensis* BRIART & CORNET, 1887 from the Dano-Montian of Mons.

Derivatio nominis. – Combination name using Mons, the type locality of the type species, with the modern genus *Neritina*, which has a similar teleoconch morphology.

Diagnosis. – The small shell is formed of a few rounded convolute whorls that increase strongly in diameter. The inner walls of the protoconch and of the teleoconch are dissolved. Sculpture of the teleoconch consists of dense prosocyrct growth lines and irregularly arranged brown stripes and dots on a cream white ground. The parietal and basal lip of the aperture are characterised by wing-like extensions. The slightly curving columella bears two columellar plaits in the posterior third of the aperture that continue into the interior portion of the aperture with a few coarse teeth anterior of them.

The protoconch in the type species consists of about three convolute whorls. The first 1.5 whorls are totally covered by the succeeding ones and the last 1.5 whorls are less convolute. The surface of the whorls seems to be smooth. The protoconch is terminated by a thickened projecting rim.

Differences. – The shape of the juvenile shell and the morphology of the protoconch are similar to the type species of the genus *Neritina*, *Nerita pulligera* LINNAEUS, 1758 from Southeast Asia as described by BANDEL & RIEDEL (1998, p. 179, fig. 4 C-E). *N. pulligera* differs by the lack of columellar plaits and by a higher number of weaker columellar teeth (WENZ, 1938-1944: p. 428, fig. 1052 a, b). The protoconch differs by its weak axial ridges on the larval shell. *Neritoplica* OPPENHEIM, 1892 with as type species *Neritina uniplicata* J. de C. SOWERBY, 1823 (WENZ, 1938-1944, p. 422, fig. 1031) differs by its rounded shell without wing-like extensions of the peristome, and having only one prominent columellar plait without any accompanying teeth. *Theodoxus* MONTFORT, 1810 differs by its smooth columella and its direct mode of early ontogenetic development with an inflated

embryonic shell. *Deianira* STOLICZKA, 1859, with type species *Rotella bicarinata* ZEKELI, 1852 from the Late Cretaceous Gosau-Formation of Austria has prominent columellar plaits and is distinguished by its rotelliform teleoconch, which is strongly carinate and where the inner teleoconch whorls are not dissolved (WENZ, 1938-1944, p. 434, fig. 1069).

Monsneritina montensis (BRIART & CORNET, 1887)

Pl. 1, Figs. 5-7

1887 *Neritina montensis* BRIART & CORNET, p. 36, pl. 21, fig. 4 a-c.

1915 *Neritina montensis* BRIART & CORNET. – COSSMANN, p. 46, pl. 3, figs. 59-62.

1973 *Neritoplica* (?) *montensis* (BRIART & CORNET). – GLIBERT, p. 18, pl. 2, fig. 9.

1977 *Theodoxus* (*Vittoclithon*) *montensis* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 45f.

Material. – 86 specimens, from the Goffint pit, coll. Cornet, IRSNB IG 5496; 121 specimens, from Coppée pit, coll. Houzeau, IRSNB IG 6544, IRSNB FI 6405.

Description. – The small shell measures up to 8 mm in width and 6 mm in height, consisting of about five rounded, strongly convolute whorls. The inner walls of the protoconch and of the teleoconch are dissolved. Sculpture of the teleoconch consists of dense prosocyrct growth lines and brown coloured irregularly arranged stripes and dots on a creamy-white background. The parietal and basal lips of the large aperture are characterised by wing-like extensions. The slightly curving columella bears two columellar plaits in the posterior portion that continue into the interior portion of the aperture and are accompanied anteriorly by 5-6 coarse teeth.

The neritimorph protoconch consists of about three convolute whorls, which attain a maximum diameter of 0.48-0.5 mm. The first 1.5 whorls are totally covered by the later ones that are more or less convolute – the succeeding whorl covers the lower half of the preceding one. The whorl surface is corroded, but seems to be smooth. The protoconch is terminated by a thickened projecting rim.

Remarks. – The protoconch is indicative of a planktonic veliger stage. The shape of the juvenile shell and the morphology of the protoconch are similar to the early shell of the type species *N. pulligera* of the genus *Neritina*. The wing-like extensions of the peristome similarly occur in modern *Neritina* (BANDEL & KOWALKE, 1999). *Monsneritina* n. g. appears to be ancestral to *Neritina*, which is known from fossils in Neogene tropical deposits. *Monsneritina* may have derived from the Cretaceous *Neritoplica* which characterised shallow marine and brackish habitats of the Tethys and which has the similar feature of a columellar plait continuing into the interior portion of the aperture (KOWALKE & BANDEL, 1996).

Subclass Caenogastropoda

Order Littorinimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily Rissooidea GRAY, 1847

Family Rissoidae GRAY, 1847

Genus *Alvania* RISSO, 1826Subgenus *Arsenia* MONTESERATO, 1890*Alvania (Arsenia) craticula* (BRIART & CORNET, 1887)

Pl. 2, Figs. 3-5

1887 *Rissoa craticula* BRIART & CORNET, p. 8, pl. 19, fig. 5 a-c.1924 *Alvania craticula* (BRIART & CORNET). – COSSMANN, p. 82, pl. 5, figs. 58-59.1973 *Alvania (Arsenia) craticula* (BRIART & CORNET). – GLIBERT, p. 24, pl. 3, fig. 71977 *Alvania (Alvania) craticula* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 55f., pl. 2, figs. 11-12.

Material. – One specimen, Coppée pit, coll. Achat Piret, IRSNB FI 6406; 7 specimens, Coppée pit, coll. Vincent & Collard, IRSNB IG 3439; 20 specimens, Coppée pit, coll. Lefèvre, IRSNB IG 6433.

Description. – The small rissoiform shell comprises five rounded, rapidly increasing whorls up to 3 mm in height and 1.8 mm in width. The sculpture of the teleoconch consists of 14-16 straight to slightly opisthocyrt axial ribs, which are crossed by eight weaker spiral cords. The base is ornamented by six spiral cords. The last whorl forms about 60% of the total height of the shell. The ovate aperture is characterised by an incised parietal notch. A slit like umbilicus is present.

The conical protoconch consists of 2.3 rounded whorls measuring 0.34 mm in height and 0.36 mm in maximum diameter. The maximum diameter of the first whorl is 0.16-0.17 mm and the width of the initial cap is 0.04 mm; this first whorl is slightly pointed. The sculpture of the protoconch is not well preserved. The second whorl is characterised by remains of spiral rows of tubercles on the adapical half and spiral lines on the abapical half of the whorl. The protoconch is terminated by a slightly sinuous thickened rim.

Remarks. – The protoconch is indicative of a free planktonic veliger stage and closely resembles that of the type species of the Recent subgenus *Arsenia*, *Turbo puncturus* MONTAGU, 1803 from the Mediterranean Sea, which has been recently described from the plankton of Banyuls-sur-Mer (Pyrénées-Orientales, S.France) by KOWALKE (1998a, p. 70, pl. 9, fig. 9). The dimensions of the protoconch and the shape of the embryonic shell are similar, although the protoconch of the type species is slightly smaller.

Alvania (Arsenia) montensis GLIBERT, 19731924 *Turbella? pulchra* COSSMANN, p. 81, pl. 5, figs. 54-55.1973 *Alvania (Arsenia) montensis* GLIBERT, p. 24f., pl. 3, fig. 8.

Material. – 2 specimens, Coppée pit, IRSNB IG 3439.

Description. – A small turreted rissoiform shell of five slightly rounded whorls measuring up to 2.2 mm in height and up to 1.2 mm in width. The whorls are characterised by a sutural ramp. The sculpture of the teleoconch whorls consists of 26-27 straight axial ribs that are crossed by six equally strong spiral cords; the teleoconch base is ornamented by six spiral cords. The height of the last whorl forms 60% of the total height of the shell. The ovate aperture is characterised by an incised parietal notch. A slit-like umbilicus is visible.

The protoconch consists of 1.75 rounded whorls measuring 0.46 mm in height and with a maximum diameter of 0.45-0.46 mm. The diameter of the first whorl is 0.31 mm and the width of the initial cap 0.1 mm. Sculpture is not preserved.

Remarks. – *A. (A.) montensis* differs from *A. (A.) craticula* by its direct mode of early ontogenetic development that omits a free swimming planktonic veliger stage. The inflated embryonic shell indicates a development within the egg capsule and hatching of crawling young. The teleoconch differs from that of *A. (A.) craticula* by its shouldered whorls and by the more regular ornament of equally strong axial and spiral elements. The teleoconch sculpture is similar to that in the type species of the subgenus *Arsenia*, *A. (A.) punctura* (WENZ, 1938-1944, p. 617, fig. 1719). This differs by its less shouldered teleoconch whorls, in possessing a more rounded aperture, and by its indirect early ontogenetic development that has a free planktonic veliger stage.

Family Stenothyridae FISCHER, 1885

Genus *Stenothyrella* WENZ, 1938*Stenothyrella pupiformis* (BRIART & CORNET, 1887)

Pl. 2, Figs. 6-8

1887 ?*Bithinia pupiformis* BRIART & CORNET, p. 28, pl. 20, fig. 13 a-c.1924 *Stenothyra pupiformis* (BRIART & CORNET). – COSSMANN, p. 76, pl. 5, figs. 28-29.1973 *Stenothyra pupiformis* (BRIART & CORNET). – GLIBERT, p. 23f., pl. 3, fig. 4.

Material. – 25 specimens, Goffint pit, coll. Cornet, IRSNB IG 5496, IRSNB FI 6407.

Description. – A very small solid shell with an elongated ovate shape of 4-5 slightly rounded rapidly increasing whorls, up to 1.8 mm in height and 0.8 mm in width. The shell is characterised by a short conical spire with a stout apex. The last whorl forms about 60% of the total height of the shell and narrows in its adapertural portion. Sculpture of the teleoconch whorls consists of dense slightly prosocyrty growth lines. The small aperture is oblique and drop-shaped with an acute parietal edge. It is characterised by a slightly thickened parietal lip. A slit-like umbilicus is visible.

The protoconch comprises 1.5 flat smooth whorls, is 0.19-0.2 mm in height and 0.26-0.27 mm in maximum

diameter. The maximum diameter of the first whorl is 0.19 mm and the width of the initial cap 0.06 mm. The onset of the teleoconch is indicated by crowded growth lines.

Remarks. – The smooth bulbous protoconch is indicative of a direct development with individuals hatching as crawling young. *Stenothyrella pupiformis* differs from the type species *Nematura lubricella* SANDBERGER, 1863 (WENZ, 1938-1944, p. 588, fig. 1610) from the Late Oligocene of Hackenheim (Rhine-Hesse, Germany) by its smaller size and by the more oblique aperture. *Stenothyra* BENSON, 1856 with the type species *Nematura deltae* BENSON, 1836 (WENZ, 1938-1944, p. 588, fig. 1609) differs by its larger size, by a less solid shell with more rounded whorls, its acute apex and by the very large bulbous body whorl.

Superfamily Littorinoidea GRAY, 1840

Family Littorinidae GRAY, 1840

Genus *Dissochilus* COSSMANN, 1888

Dissochilus lineatus (BRIART & CORNET, 1887)

1887 *Lacuna lineata* BRIART & CORNET, p. 6, pl. 19, fig. 12a-c.

1924 *Dissochilus Houzeaui*. – COSSMANN, p. 90, pl. 5, figs. 86-87.

1973 *Dissochilus lineatus* (BRIART & CORNET). – GLIBERT, p. 19, pl. 2, fig. 12 a-c.

1977 *Medoriopsis (Medoriopsis) lineata* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 46f., pl. 2, fig. 10.

Description. – The slender littorinid shell measures up to 9 mm in height and up to 3.5 mm in width. It consists of six to seven high, only slightly rounded whorls. The last whorl amounts about 50% of the total height of the shell. Sculpture consists of 14-16 thin spiral cords, which may bear a fine nodulation and which are regularly arranged all over the whorls. The base is fine spirally sculptured. The height of the aperture forms about 30% of the total height of the shell. It has elongated oval to subangular shape and it is characterised by a small but well developed anterior notch and by a pointed posterior edge. The aperture is slightly detached from the spire. A slit-like umbilicus is present.

Remarks. – GLIBERT (1973) assigned *Dissochilus lineatus* to the family Lacunidae. According to PONDER (1976) and REID (1986a) Lacunidae and Littorinidae lack significant conchological and anatomical differences and thus should be united. *Dissochilus houzeaui* as described by COSSMANN (1924) is represented by adult specimens with larger more slender shells and stronger developed sculpture (see GLIBERT, 1973, p. 19, pl. 2, fig. 12c). VILATTE in MARLIÈRE (1977) described a juvenile specimen as *Medoriopsis (Medoriopsis) lineata*. The large embryonic shell is a single whorl and indicates its direct development. As mentioned by GLIBERT, the shape of the aperture in this species suggests it probably belongs to *Dissochilus* rather than to *Medoriopsis*

COSSMANN, 1888. *Medoriopsis*, with the type species *Lacuna effusa* DESHAYES, differs by possessing a stouter shell and in the lack of any spiral sculpture on the teleoconch (WENZ, 1938-1944, p. 514, fig. 1348). *D. lineatus* closely resembles slender brackish water littorinids, e.g. the genera *Littoraria* and *Mainwaringia* NEVILL, 1885 from West African and Indo-Pacific mangroves (REID, 1985, 1986a, b; BANDEL & KOWALKE, 1999). *Littoraria* is distinguished by its large broad conical shell. *Mainwaringia*, with the Recent type species *M. leithii* (E. A. SMITH, 1875), has a very similar shell size and outline but differs in having a larger more rounded aperture with a weaker columellar board.

Genus *Cavilabium* COSSMANN, 1888

Cavilabium microscopicum COSSMANN, 1924

Pl. 2, Figs. 1-2

1924 *Cavilabium microscopicum* COSSMANN, p. 89, pl. 6, figs. 45-46.

1973 *Littorina (Cavilabium) microscopicum* (COSSMANN). – GLIBERT, p. 19f., pl. 3, fig. 1.

Material. – One specimen, Coppée pit, coll. G. Vincent & Collard, IRSNB FI 6408; 23 specimens, Coppée pit, coll. Th. Lefèvre, IRSNB IG 6433.

Description. – A minute shell with six strongly convolute whorls up to 2 mm in height and 1.2 mm in width. The sculpture on the whorls forming the teleoconch consists of dense prosocline growth lines with about eight spiral rows of slightly elongated pits on the anterior and posterior third of the whorls. The central third is smooth. The aperture is drop-shaped and with an incised parietal edge. The parietal and columellar lips are bent.

The 2.2 whorls of the protoconch are almost planispirally coiled, have a maximum diameter of 0.57 mm and are terminated by an un-thickened rim. The limited 0.75 whorl forming the embryonic shell is sculptured by a pattern of grooved ridges and has a maximum diameter of 0.12 mm with an initial cap 0.04-0.05 mm wide. The diameter of this whorl is 0.15-0.16 mm. An indistinct rim terminates the embryonic shell. The larval shell of this species appears to be smooth.

Remarks. – The larval shell is evidence of a planktonic veliger stage. *C. microscopicum* is distinguished from the type species of *Cavilabium*, *Littorina bezanconi* COSSMANN, 1888 found in the Lutetian of the Paris Basin, by its less stout spire and its smaller aperture. *Littorina* FÉRUSAC, 1819, type species *Turbo littoralis* LINNAEUS, 1758, differs in its larger size and by having more rounded whorls. The protoconchs of *Littorina (Littorina) littorea* (LINNAEUS, 1758) (KOWALKE, 1998a, p. 66f., pl. 9, figs. 1-2) from the North Sea and *L. (Melarhaphé) neritoides* (LINNAEUS, 1758) (KOWALKE 1998a, p. 67, pl. 9, fig. 3) from the Mediterranean Sea, are of a similar size, but can be separated by their more conical shape and the

fine pitted sculpture present on their embryonic and larval shells.

The small trochoidal littorinids *Bembicium* PHILIPPI, 1846 and *Paesiella* NEVILL, 1885 that occupy similar brackish habitats to *Cavilabium*, are often associated with mangroves. *Bembicium* which has an angular trochoidal shell occurred in the Late Oligocene of Australia and is known to be a direct developer (REID, 1988). *Paesiella* differs from *Cavilabium* by its protoconch with a larval shell that has sculpture of wavy spiral ridges and which is terminated by a marked sinusigera notch (REID, 1988; KOWALKE, 1998a, p. 68, pl. 9, fig. 16).

Order Cerithiimorpha

Superfamily Cerithioidea FÉRUSAC, 1819

Family unknown

Genus *Krumbachiella* KOWALKE & BANDEL, 1996

Krumbachiella typica (BRIART & CORNET, 1887)

- 1887 *Keilostoma typica* BRIART & CORNET, p. 14, pl. 19, fig. 10a-c.
 1924 *Paryphostoma typicum* (BRIART & CORNET). – COSSMANN, p. 87, pl. 6, figs. 1-2.
 1973 *Keilostoma typicum* BRIART & CORNET. – GLIBERT, p. 27, pl. 3, fig. 13.

Description. – The large elongated conical shell comprises about ten preserved straight to slightly convex whorls measuring more than 40 mm in height. The whorls are step-like, separated by deep sutures, with telescope-like covering of the preceding ones. Whorls are smooth aside from closely spaced slightly prosocyrte growth lines. The height of the last whorl forms about 40% of the total height of the shell. The rounded lozenge-shaped aperture is pointed and slightly notched in its posterior portion. It is characterised by a prominent varix-like thickening.

Remarks. – GLIBERT (1973) assigned “*Keilostoma*” *typicum* BRIART & CORNET, 1887 to the family Rissoidae (Rissooidea). The large size and telescope-like morphology of the teleoconch of this shell distinguishes it from any rissoid genus and indicates a relationship with the Cerithioidea. The shell morphology of this species does not agree with the generic description of *Keilostoma* DESHAYES, 1848 and the type species *Bulimus turriculus* BRUGUIÈRE, 1789 from the French Lutetian (WENZ, 1938-1944, p. 625, fig. 1750). *Keilostoma* does not have a telescope-like arrangement of its teleoconch whorls, which are ornamented by strong spiral cords. COSSMANN (1924) assigned the species to the genus *Paryphostoma* BAYAN, 1873, which actually represents a synonym of *Keilostoma* (see WENZ, 1938-1944, p. 625). “*Keilostoma*” *typicum* closely resembles *Krumbachiella* KOWALKE & BANDEL, 1996 with the type species *Eulima conica* ZEKELI, 1852 from the Late Cretaceous Gosau-Formation of the Northern Alps (KOWALKE & BANDEL, 1996, p. 30 f., pl. 2, fig. 4, 7). The early ontogenetic shell of that species, indicating a direct development, has been described by KOWALKE (1998a, p. 40, pl. 4, fig. 9).

Krumbachiella typica differs from the type species only in its larger size. The protoconch of *K. typica* is unknown.

Genus *Cornetia* MUNIER-CHALMAS in FISCHER, 1885

Cornetia malaisei (BRIART & CORNET, 1870)

- 1870 *Fusus Malaisei* BRIART & CORNET, p. 19, pl. 2, fig. 2 a-c.
 1885 *Cornetia modunensis* MUNIER-CHALMAS in FISCHER, p. 701.
 1887 *Cornetia modunensis* MUNIER-CHALMAS in FISCHER. – BRIART & CORNET, p. 32, pl. 2, fig. 1a-f.
 1924 *Fusus Malaisei* BRIART & CORNET. – COSSMANN, p. 91, pl. 6, figs. 58-59.
 1924 *Cornetia modunensis* MUNIER-CHALMAS in FISCHER. – COSSMANN, p. 91, pl. 5, figs. 81-85.
 1973 *Cornetia malaisei* BRIART & CORNET. – GLIBERT, p. 34, pl. 5, fig. 7.
 1977 *Cornetia modunensis* MUNIER-CHALMAS in FISCHER. – VILATTE in MARLIÈRE, p. 75f., pl. 4, fig. 16.
 1977 *Cornetia? malaisei* BRIART & CORNET. – VILATTE in MARLIÈRE, p. 76f., pl. 4, fig. 17.

Description. – The low conical shell comprises four to five preserved rounded whorls rapidly increasing in diameter. It measures up to 26 mm in height and 20 mm in width. Sculpture of the teleoconch whorls consists of four strongly developed spiral keels crossed by 7-12 equally strong or finer straight to slightly opistocyrte axial ribs. Points of intersection of the spiral and axial sculpture are slightly thickened. The base is sculptured by three spiral keels. The height of the large last whorl forms about 60% of the total height of the shell. The large rounded to inclined oval aperture is characterised by a small but well developed anterior notch.

Remarks. – The genus *Cornetia* was placed within the Thiaridae, subfamily Paludominae by GLIBERT (1973, p. 34). Paludominae are based on the Recent Southeast Asian genus *Paludomus* SWAINSON, 1840 with the type species *Melania conica* GRAY, 1847 (WENZ, 1938-1944, p. 703, fig. 2026). *Paludomus conicus* shares the low conical shape of the teleoconch with *Cornetia*, but differs by tear-shaped aperture that has a strongly pointed acute parietal edge and by its lack of prominent axial sculpture on the teleoconch. *Cornetia* is based on *C. modunensis* BRIART & CORNET, 1887 from the Dano-Montian of Mons which is a synonym of *C. malaisei* (BRIART & CORNET, 1870) (GLIBERT, 1973, p. 34, pl. 5, fig. 7). GLIBERT (1973) mentioned the synonymy of these taxa, but VILATTE in MARLIÈRE (1977) continued to use the separate species names. *C. modunensis* includes morphs of *C. malaisei* that have closer finer axial ribs. This feature is generally variable in *C. malaisei* and has a range of 7-12 axial ribs per whorl (GLIBERT, 1973; VILATTE in MARLIÈRE, 1977). *Cornetia* is very similar to the Cretaceous - Eocene genus *Pyrgulifera* MEEK, 1877, type species *Melania humerosa* Meek from the Cenomanian of Wyoming (WENZ, 1938-1944, p. 705, fig. 2033) and is most prob-

ably synonymous, but the protoconch is unknown and its exact position within the Cerithioidea is unclear.

Family Melanopsidae H. & A. ADAMS, 1854

Genus *Melanopsis* FÉRUSSAC, 1807

Melanopsis briarti COSSMANN, 1888

- 1873 *Melanopsis buccinoidea* FÉRUSSAC. – BRIART & CORNET, p. 71, pl. 7, figs. 7-9a-c.
 1888 *Melanopsis Briarti* COSSMANN, p. 286.
 1897 *Melanopsis Briarti* COSSMANN. – MUNIER-CHALMAS, p. 86.
 1924 *Melanopsis Briarti* COSSMANN. – COSSMANN, p. 91, pl. 5, figs. 88-93.
 1973 *Melanopsis briarti* MUNIER-CHALMAS. – GLIBERT, p. 34, pl. 5, fig. 6.
 1977 *Melanopsis briarti* COSSMANN. – VILATTE in MARLIÈRE, p. 74f.

Description. – The melanopsid shell measures up to 15 mm in height and up to 7 mm in width. It comprises about eight preserved whorls, separated by straight sutures. The last whorl has elongated oval shape, the spire is conical. The height of the last whorl forms about 80% of the total height of the shell. The large aperture has slender oval shape. It is characterised by a slight anterior sinus and by a pointed posterior portion. A prominent parietal callus pad is present.

Remarks. – *Melanopsis briarti* has been assigned to the family Thiaridae, subfamily Melanopsinae by GLIBERT (1973, p. 34). Melanopsidae actually represent a family of the Cerithioidea well separated from the Thiaridae by conchological and anatomical features (HOUBRICK, 1988; KOWALKE, 1998a). BRIART & CORNET (1873) assigned this species to *M. buccinoidea*. This Recent species from the Eastern Mediterranean differs in its considerably larger shell, which is characterised by a weaker callus regularly covering the columellar and parietal portion of the aperture and which is lacking the heavy callus pad in the parietal portion of the aperture (see HELLER *et al.* 1999, fig. 4a). From the general shell characteristics *M. briarti* could well be ancestral to Neogene smooth melanopsids of the Central Paratethys and of the Mediterranean region (HARZHAUSER & KOWALKE, 2001; HARZHAUSER *et al.*, in press). *M. buccinoidea* may represent a relic of this diverse Cainozoic relation.

Family Cerithiidae FÉRUSSAC, 1819

Subfamily Cerithiinae FÉRUSSAC, 1819

Genus *Pseudovertagus* VIGNAL, 1904

Subgenus *Pseudaluco* CLARK & DURHAM, 1946

Pseudovertagus (Pseudaluco) dumonti

(BRIART & CORNET, 1873)

Pl. 3, Figs. 1-3

- 1873 *Cerithium dumonti* BRIART & CORNET, p. 61, pl. 12, fig. 11, a-c.
 1873 *Cerithium tenuiplicatum* var. BRIART & CORNET, p. 58 (partim), pl. 10, fig. 12, a-c.

1973 *Clava (Striovertagus) dumonti* (BRIART & CORNET). – GLIBERT, p. 41, pl. 6, fig. 5.

1977 *Clava (Striovertagus) dumonti* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 93f., pl. 6, figs. 10-13.

Material. – 21 specimens, Goffint pit, coll. Cornet, IRSNB IG 5496; Coppéc pit, 40 specimens, coll. Lefèvre, IRSNB IG 6433, IRSNB FI 6409; 31 specimens, coll. Vincent & Collard, IRSNB IG 3439, IRSNB FI 6410.

Description. – This turreted fusiform shell can be up to 20 mm in height and 8 mm in width. It has about 20 shouldered whorls with flat flanks that are separated by deep sutures. Sculpture of the first teleoconch whorl consists of three spiral cords, which disappear on the fourth whorl. 12-14 straight axial ribs develop on the third teleoconch whorl but become weaker by the sixth whorl and later vanish, resulting in a smooth shell. The aperture is ovate with its posterior-anterior axis being oblique to the main axis of the shell. The inner apertural lip may be covered by callus, the outer lip is sometimes accompanied by a varix and a slight posterior notch is developed. The columella is characterised by a very weak columellar plait. A short but well developed anterior channel is bent backwards.

The protoconch comprises 1.5 rounded whorls that are 0.31 mm in height and attain a maximum diameter of 0.27 mm. It is terminated by a slightly sinuous rim. The maximum diameter measured for the first whorl was 0.23 mm. The initial cap is 0.09 mm wide. Sculpture is not preserved in any of the specimens.

Remarks. – The protoconch is indicative of a short lecitotrophic larval stage: the embryonic and larval shell are not differentiated but the protoconch is terminated by a slightly sinuous rim. The larva probably only spent a short time within the plankton, feeding on embryonic yolk and without additional feeding on phytoplankton.

Pseudovertagus (Pseudaluco) dumonti has been assigned to *Clava (Striovertagus)* by GLIBERT (1973). *Clava* is a synonym of the modern genus *Rhinoclavis* SWAINSON, 1840 that can be recognised by its elongate sharply reflexed anterior canal, a well developed anal canal and a prominent columellar plait (HOUBRICK, 1978). *Striovertagus* CHAVAN, 1948 is a synonym of *Pseudaluco* with a type species *Cerithium jusseui* MAYER-EYMAR, 1870 from the Lutetian of the Paris Basin.

Pseudovertagus (Pseudaluco) tenuiplicatus (BRIART & CORNET, 1873) differs by its larger apical angle, the less shouldered whorls and by a greater number of closely spaced axial ribs (GLIBERT, 1973, pl. 6, fig. 6). *P. (P.) punctifibrus* (BRIART & CORNET, 1873) (GLIBERT, 1973, pl. 6, fig. 8) and *P. (P.) quequeti* (BRIART & CORNET, 1873) (GLIBERT, 1973, pl. 6, fig. 9) with dense fine axial and spiral sculpture on each of the teleoconch whorls could well be conspecific with *P. (P.) duponti* (BRIART & CORNET, 1873) (GLIBERT, 1973, pl. 6, fig. 7) representing different ontogenetic stages of a single species. *P. (P.) dejaeri* (BRIART & CORNET, 1873) with coarse axial and

spiral ribs on each teleoconch whorl has been attributed to *Thericium* by GLIBERT (1973, p. 44, pl. 6, fig. 10) and VILATTE in MARLIÈRE (1977, p. 84, pl. 7, figs. 1, 5-7, 9-10). *Thericium* is a synonym of *Cerithium* BRUGUIÈRE, 1789, and differs from *Pseudovertagus* in its aperture with a parietal tooth and a crenulate outer lip.

Pseudovertagus (*Semivertagus*) (COSSMANN, 1889), type species *Cerithium unisulcata* LAMARCK from the Lutetian of the Paris Basin, differs by its teleoconch sculpture of close spiral cords and its lack of a columellar plait (WENZ, 1938-1944, p. 763, fig. 2211). BRIART & CORNET (1873) described other specimens as *Cerithium abnormis*, *C. elisae*, *C. gibberosa*, *C. edmonti* and *C. abnormae*, which according to GLIBERT (1973) represent species of *Semivertagus*. These "species" could well represent different ontogenetic stages of a single species *Pseudovertagus* (*Semivertagus*) *urania* (d'ORBIGNY, 1850) (GLIBERT, 1973, p. 40, pl. 6, fig. 4).

Family Potamididae H. & A. ADAMS, 1854

Remarks. – Potamididae are confined to brackish water habitats, especially mangroves, at least since the Late Cretaceous (Coniacian). The oldest known potamidids with preserved protoconchs have been described from the Late Coniacian - Early Santonian of the Northern Alpine Gosau Formation by KOWALKE & BANDEL (1996). These inhabitants of brackish biotopes were well separated from the convergent Procerithiidae that occur in fully marine habitats. Recent Potamididae characterise pan-tropical mangroves, with the exception of the genus *Potamides* MONTFORT, 1810, of which *Potamides conicus* (BLAINVILLE, 1829) the only modern representative, a relict species of a diverse Cainozoic lineage, is widespread in comparably cold waters of the Mediterranean Sea and the Red Sea (KOWALKE, in press a).

Genus *Granulolabium* COSSMANN, 1889

Granulolabium ovalituberosum

(BRIART & CORNET, 1873)

Pl. 3, Fig. 4

- 1873 *Cerithium ovalituberosum* BRIART & CORNET, p. 31, pl. 8, fig. 6, a-c.
 1873 *Cerithium sexlinum* BRIART & CORNET, p. 33, pl. 9, fig. 7, a-c.
 1873 *Cerithium montense* BRIART & CORNET, p. 50, pl. 11, fig. 10 a-c.
 1973 *Pirenella* (s. s.) *montensis* (BRIART & CORNET). – GLIBERT, p. 35, pl. 5, fig. 8.
 1977 *Pirenella* (*Pirenella*) *montensis* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 79f., pl. 4, figs. 1-4.

Material. – 5 specimens, Coppée pit, coll. Lefèvre, IRSNB IG 6433; 7 specimens, Coppée pit, coll. Chavan, IRSNB IG 21735; 72 specimens, Coppée pit, coll. E. de Jaer, IRSNB IG 8261, IRSNB FI 6411.

Description. – An elongate tower-shaped shell up to 14 mm in height and 4.5 mm in width. It usually consists

of 8-10 preserved whorls, slightly rounded in the early teleoconch, but flattened in the later teleoconch. A protoconch is not preserved. The earliest preserved whorl measuring 0.4 mm in width has sculpture of three spiral cords, of which the most abapical is the strongest. This sculpture persists on the following two whorls. The next whorl characteristically has three equally strong cords and a weaker cord just above the abapical suture. This teleoconch whorl also bears 10 straight weak axial ribs that cross the upper three spiral cords. These ribs may persist over each following whorl, or they may decrease during the subsequent ontogeny. More or less prominent elongate nodes form at the intersection of the spiral and axial sculpture. The following whorls are characterised by the formation of weaker but distinct spiral cords in the intercalations of the primary spirals. On the last 2-4 teleoconch whorls the uppermost adapical intercalated secondary spiral may become as strong as the primary spiral cords. The base is ornamented by up to five spiral cords, of which the two peripheral cords are always the most strongly developed. The aperture has well developed short anterior and posterior channels. The slightly convex columella lacks a plait and may be covered by callus.

Remarks. – This species is characterised by a certain variability of the sculpture (GLIBERT, 1973). Different morphs with intermediate features have originally been assigned to different species by BRIART & CORNET (1873): Morphs with broad axial ribs and thus pronounced elongated nodes have been called *Cerithium ovalituberosum*; those with more regular axial and spiral sculpture were called *Cerithium montense*; and those with stronger spiral sculpture and weak axial ribs had been assigned to *Cerithium sexlinum*.

Pirenella GRAY, 1847 is a synonym of *Potamides* BRONGNIART, 1810, based on the European Oligocene species *Cerithium lamarkii*, BRONGNIART, 1810 (KADOLSKY, 1984; KOWALKE 1998a; KOWALKE, in press a). *Granulolabium* differs from *Potamides* in lacking a twisted columella and a columellar plait. This genus is distinguished by the formation of secondary spiral cords intercalated between the main primary spirals, whereas *Potamides* characteristically has four spiral cords and no secondary spirals.

Genus *Monspotamides* n. g.

Type species. – *Cerithium varians* BRIART & CORNET, 1873 from the Dano-Montian of Mons.

Derivatio nominis. – Named after the type locality Mons and the closely related type genus of the Potamididae.

Diagnosis. – This small to medium sized broad conical shell commonly has about ten flat whorls. The last whorl forms about half of the total height of the shell. The teleoconch is ornamented by 4-5 spiral cords of which the initial two spiral cords are always the most strongly developed. Additional spiral sculpture consists of numer-

ous very fine spiral threads. These spirals are crossed by straight to slightly opisthocyrt axial ribs, with nodes formed at the points of intersection. The uppermost adapical row of nodes is strongly developed and produces a step-like outline to the shell. The base is ornamented by three spiral cords with the uppermost adapical as the most prominent. The subangular aperture has a well developed anterior channel and a thin slightly rounded outer lip. The straight columella bears a weak columellar plait. In the type species the protoconch consists of 1.5 rounded whorls ornamented by spiral ridges and intercalated fine spiral threads. It is terminated by a thin slightly sinuous rim.

Differences. – *Tympanotonos* SCHUMACHER, 1817, type species *Murex fuscatus* LINNAEUS, 1758 from the West African Coast (WENZ, 1938-1944, p. 739, fig. 2141), differs by its large, acute conical shell, a sculpture of spiral rows of nodes or spines and by the thickened aperture bearing a heavy callus pad (KOWALKE, in press b). The genus *Terebralia* SWAINSON, 1840, type species *Strombus palustris* LINNAEUS, 1758 from the Indo-Pacific (WENZ, 1938-1944, p. 746, fig. 2157), differs by its elongate conical shell, by its thickened aperture with a heavy callus and an extended outer lip (KOWALKE, in press b). *Potamidides* BRONGNIART, 1810, type species *Cerithium lamarckii* from the European Oligocene (WENZ, 1938-1944, p. 736, fig. 2132), differs by its slender elongate shell, its regular sculpture of four spiral keels, the crowded sinuous growth lines on the later teleoconch whorls and by the lower body whorl with its considerably smaller and rounded aperture (KOWALKE, in press a). *Granulolabium* differs by its slender shell, the intercalation of secondary spiral cords in the sculpture of the teleoconch whorls, and by its less angular aperture that lacks a columellar plait.

Monspotamidides varians (BRIART & CORNET, 1873)

Pl. 3, Figs. 5-7

- 1873 *Cerithium varians* BRIART & CORNET, p. 34, pl. 9, fig. 3 a-c.
 1873 *Cerithium Larteti* BRIART & CORNET, p. 39, pl. 8, fig. 9 a-c (= juvenile *varians*).
 1973 *Tympanotonos varians* (BRIART & CORNET). – GLIBERT, p. 36, pl. 5, fig. 9.
 1977 *Sandbergeria varians* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 83f., pl. 5, fig. 1-5.

Material. – 6 specimens, Coppée pit, coll. Lefèvre, IRSNB IG 6433; 86 specimens, Coppée pit, coll. Houzeau, IRSNB IG 6544; 173 specimens, Goffint pit, coll. Cornet, IRSNB IG 5496, IRSNB FI 6412 – IRSNB FI 6413.

Description. – This broad conical shell measures up to 11 mm in height and 5 mm in width and consists of about ten flat whorls. The height of the last whorl forms about half of the total height of the shell. The onset of the teleoconch is indicated by the formation of two strong spiral cords. On the fourth whorl another weak spiral cord is visible just above the abapical suture and 1-2 further cords are formed below the adapical suture on the fifth

whorl. The two initial spiral cords are always the strongest. Additional spiral sculpture consists of numerous very fine spiral threads, usually only visible in juvenile specimens. The spiral cords are crossed by 14-16 axial ribs, which are visible on the fourth whorl and grade into straight to slightly opisthocyrt axial ribs. These increase in number up to 20 in the course of the ontogeny. Nodes are formed at the intersection of spiral and axial sculpture. The uppermost adapical row of nodes is the strongest developed, thus the shell may have step-like outline. The base is ornamented by three spiral cords, of which the outer one is most prominent. The sub-angular aperture has a well developed anterior channel. The straight columella bears a very weak columellar plait.

The protoconch consists of 1.5 rounded whorls measuring about 0.26-0.28 mm in height and 0.28-0.3 mm in diameter, with an initial cap of 0.08-0.09 mm in width. The diameter of the first whorl is 0.23-0.24 mm. Sculpture consists of six coarse spiral ridges which are visible on the first half whorl and numerous very fine spiral threads are intercalated between these. The protoconch is terminated by a slightly sinuous thin rim.

Remarks. – Dimensions of the protoconch indicate a lecithotrophic larval stage. Embryonic and larval shells are not differentiated and the protoconch is terminated by a slightly sinuous rim.

VILATTE in MARLIÈRE (1977) assigned this species to the genus *Sandbergeria*, which differs by a higher number of finer axial ribs and by its large oval aperture with a slight anterior notch lacking a prominent canal (COSSMANN 1906), and belongs to the family Scaliolidae (Cerithioidea).

Genus *Hadraxon* OPPENHEIM, 1892

Hadraxon regularicostatum (BRIART & CORNET, 1873)

Pl. 3, Figs. 8-9

- 1873 *Cerithium regularicostatum* BRIART & CORNET, p. 32, pl. 8, fig. 8, a-c.
 1973 *Harrisianella (Teliostomopsis) regularicostata* (BRIART & CORNET). – GLIBERT, p. 38, pl. 5, fig. 15.
 1977 *Harrisianella (Teliostomopsis) regularicostata* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 85f., pl. 5, figs. 18-19.

Material. – 21 specimens, Goffint pit, coll. Cornet, IRSNB IG 5496, IRSNB FI 6414 – IRSNB FI 6415.

Description. – The very slender shell contains more than 20 slightly rounded whorls. It measures up to 15 mm in height and up to 4 mm in width. The first whorl of the teleoconch is characterised by dense growth lines and by the formation of two median spiral cords. Two weaker spiral cords appear above the adapical and below the abapical cord on the second teleoconch whorl. Twelve weak slightly opisthocyrt axial ribs occur and become equal in strength to the cords on the two subsequent whorls. In the course of the sixth teleoconch whorl an-

other spiral cord appears between the uppermost and the second adapical cord and a sixth spiral cord develops on the eighth teleoconch whorl. The axial elements become the most dominate element of sculpture at the eighth teleoconch whorl. The points of intersection of spiral and axial sculpture may be nodose. On late teleoconch whorls the axial ribs do not cross the uppermost adapical and the lowermost abapical cords. The base is ornamented by three spiral cords. The height of the last whorl forms less than 30% of the total height of the shell. It has a small roundish fragmented aperture with a notch or short channel in the anterior portion.

The protoconch is fragmented. It comprised about 1.8 rounded whorls measuring about 0.3 mm in both height and in maximum diameter. The initial cap is about 0.1 mm wide. The sculpture is not preserved. The transition to the teleoconch is indicated by a thickened sinuous rim.

Remarks. – The morphology of the protoconch indicates a lecithotrophic larval development. The dimensions of the protoconch and the sinuous transition to the teleoconch reflect a free swimming larval stage, during which the larva fed on embryonic yolk without additional feeding on phytoplankton.

Hadraxon resembles the Eocene Genus *Harrisianella* OLSSON, 1929, type species *H. peruviana* OLSSON (WENZ, 1938-1944, p. 752, fig. 2178) from the Eocene of Peru, with similar slender multi-whorled shell and low body-whorl, which has been classified within the Diastomatidae by WENZ, (1938-1944). *Harrisianella* differs in its cylindrical shell with flatter whorls, and by the teleoconch sculpture of sickle shaped axial ribs, that are deeply incised below the adapical suture, resulting in a prominent row of tubercles beneath that suture. The aperture of *Harrisianella* differs in having a distinct columellar plait. *Harrisianella* is actually considered an Eocene Tethyan subgenus of *Cerithidea* SWAINSON, 1840 by KOWALKE (in press b), a potamidid genus with Recent Indo-Pacific and tropical American distribution.

Teliostomopsis CHAVAN, 1952 is a synonym of *Hadraxon* OPPENHEIM, 1892, type species *Hemisinus csingervallensis* TAUSCH, 1886, with similar dimensions to *H. regularicostatum*. But *H. csingervallense* from the Santonian of Hungary differs from *H. regularicostatum* by its greater number of closely spaced spiral cords and by the vanishing of axial ribs on late teleoconch whorls (BANDEL & RIEDEL, 1994, pl. 6, figs. 5-7). The protoconch of the type species conforms to a direct development without the occurrence of a free larval stage (BANDEL & RIEDEL, 1994, pl. 6, figs. 1-3).

Genus *Diastomella* CHAVAN, 1952

Diastomella luciani (BRIART & CORNET, 1873)

Pl. 4, Figs. 2-3

1873 *Cerithium Luciani* BRIART & CORNET, p. 38, pl. 5, fig. 13.

1973 *Diastomella luciani* (BRIART & CORNET). – GLIBERT, p. 38, pl. 5, fig. 13.

1977 *Diastomella luciani* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 86f., pl. 5, figs. 6-9.

Material. – 10 specimens, Coppée pit, coll. Vincent, IRSNB IG 3423, IRSNB FI 6416.

Description. – A small turriculate shell of about 10 slightly rounded whorls that are up to 6 mm in height and up to 2.5 mm in width. The sculpture of the first teleoconch whorl consists of two median spiral keels and numerous very fine spiral threads. On the sixth teleoconch whorl another spiral keel becomes visible just above the adapical suture. Six straight to slightly opisthoclinal axial ribs appear on the third teleoconch whorl and cross the two upper spiral keels. Prominent nodes are formed at the points of intersection of the spiral and axial sculpture. This type of sculpture persists over all the teleoconch whorls. The height of the last whorl forms about 40% of the total height of the shell. Only fragments of the aperture are preserved and these seem to indicate the lack of any thickening and the presence of a well developed anterior channel.

The protoconch of 1.5 slightly rounded whorls measures 0.21-0.22 mm in height and 0.24 mm in maximum diameter. The first whorl has a maximum diameter of 0.19 mm and the width of the initial cap is 0.09 mm. Sculpture is not preserved.

Remarks. – The protoconch is indicative of direct development without the inclusion of a free-swimming veliger stage.

Diastomella tenuicula (BRIART & CORNET, 1877)

Pl. 4, Fig. 1

1877 *Cerithium tenuiculum* BRIART & CORNET, p. 61, pl. 17, fig. 6 a-c.

1973 *Diastomella tenuicula* (BRIART & CORNET). – GLIBERT, p. 38, pl. 5, fig. 15.

1977 *Diastomella tenuicula* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 86f., pl. 5, fig. 6-9.

1977 *Diastomella chavani* VILATTE in MARLIÈRE, p. 88, pl. 5, figs. 10-11, 14.

Material. – Material is present from the Coppée pit, coll. Lefèvre, IRSNB IG 6433, IRSNB FI 6413.

Description. – The small slender shell measures up to 6 mm in height and 1.9 mm in width. It comprises 9-10 slightly rounded whorls. Sculpture consists of two strong spiral keels and another weaker keel just above the abapical suture, which is visible with the course of the sixth whorl. The spiral elements are crossed by about 20 very fine straight axial ribs. The last whorl forms about 40% of the total height of the shell. The aperture has oval shape and a well developed anterior channel is present.

Remarks. – The shell with similar height like *D. luciani* differs in having a considerably more slender shell with a teleoconch sculpture of two spiral keels that are crossed

by a higher number of very weak axial ribs. *D. chavani* is probably a synonym of *D. tenuicula* and a morph with sharp pronounced keels and no other differences. *D. luciani* and *D. tenuicula* have been placed within the family Diastomatidae by GLIBERT (1973) and VILATTE in MARLIÈRE (1977). *Diastoma* DESHAYES, 1861, type species *Melania costellata* Lamarck from the Lutetian of the Paris Basin (WENZ, 1938-1944, p. 749, fig. 2169) differs by its larger size and possessing a less regular sculpture in which the axial ribs diminish on late teleoconch whorls. It is further distinguished by a large half-moon shaped aperture without an anterior canal, but with an incised pointed parietal edge and a distinct columellar plait. *D. luciani* and *D. tenuicula* could well be placed within the family Potamididae.

Family Pseudamauridae KOWALKE & BANDEL, 1996

Remarks. – The Pseudamauridae (Caenogastropoda) occurred in brackish-water and are known from the Late Cretaceous until becoming extinct after the Chattian (Late Oligocene). They are distinguished from the convergent Naticidae (Neomesogastropoda) by their fine-pitted spiral ornament and a protoconch with a larval sculpture of dense collabral axial ribs typical of planktotrophic development (KOWALKE & BANDEL 1996, KOWALKE 1998b).

Genus *Ampullina* BOWDICH, 1822

Remarks. – *Ampullella* COX, 1931 is a synonym of *Ampullina* BOWDICH, 1822 (WENZ, 1938-1944, p. 1020; KABAT, 1991, p. 426). A species described as *Ampullella lavalleei* (BRIART & CORNET, 1877) by GLIBERT (1973, p. 59, pl. 7, fig. 9) does not agree with the generic description of *Ampullina*. This large thin shelled teleoconch with an acute spire angle, short pointed spire, apically flat whorls and a large body whorl with wide rounded aperture should be assigned to the genus *Crommium* COSSMANN, 1888, type species *Ampullina willemetii* DESHAYES, 1825 from the French Lutetian (WENZ, 1938-1944, p. 1025, fig. 2937).

Ampullina montensis COSSMANN, 1915

Pl. 4, Figs. 4-5

1873 ? *Natica parisiensis* BRIART & CORNET, p. 2, pl. 6, fig. 1 a-c.

1915 *Ampullina montensis* COSSMANN, p. 67, pl. 4, figs. 43-45.

1973 *Globularia montensis* (COSSMANN). – GLIBERT, p. 59.

Material. – 9 specimens, Goffint pit, coll. Cornet, IRSNB IG 5496, IRSNB FI 6418 – IRSNB FI 6419.

Description. – A small, globose, solid shell with a regular step-like spire, up to 8 mm in height and 6 mm in width, of about six rounded whorls. The spire forms about 20% of the total height of the shell. Sculpture consists of crowded slightly prosocyrct growth lines and closely

spaced spiral rows of very fine indistinct pits. The very large body whorl is well rounded and it is characterised by an oblique drop-shaped aperture, which is slightly bent anteriorly. The curved columella is slightly concave at its anterior end and the edge may be covered by callus. A slit like umbilicus is present. The first whorl is very bulbous, has a maximum diameter of 0.54-0.55 mm and the width of the initial cap is 0.3 mm. The transition to the teleoconch is indistinct.

Remarks. – The dimensions of the first whorl indicate a direct development with a yolk rich embryogenesis and subsequent hatching of crawling young. A free larval stage was absent.

A. montensis differs from the type species *A. depressa* LAMARCK, 1804 from the French Eocene by its smaller size and by its less prominent callus pad (WENZ, 1938-1944, p. 1020, fig. 2925). *Globularia* SWAINSON, 1840, the type species *Ampullaria sigaretina* LAMARCK, 1804 (KABAT, 1991, p. 430), differs by its larger size, a shorter more acute spire and by the large half moon shaped aperture with a columella, which curves convexly in its parietal portion and concavely in its anterior portion. *A. montensis* could well be placed within the family Pseudamauridae.

Genus *Amaurellina* FISCHER, 1884

Amaurellina julei (BRIART & CORNET 1873)

Pl. 4, Figs. 6-7

1873 *Natica Julei* BRIART & CORNET, p. 7, pl. 6, fig. 16, a-c.

1915 *Amauropsella Julei* (BRIART & CORNET). – COSSMANN, p. 68, pl. 4, figs. 51-53.

1973 *Amaurellina* (s. s.) *julei* (BRIART & CORNET). – GLIBERT, p. 60, pl. 7, fig. 10.

Material. – 14 specimens, Coppée pit, coll. Houzeau, IRSNB IG 6544, IRSNB FI 6420.

Description. – A rounded conical shell, up to 9 mm in height and 6 mm in width, of about five rounded whorls. The step-like spire forms about 30% of the total height of the shell. Sculpture consists of closely spaced prosocyrct growth lines and very fine spiral rows of pits. The large body whorl is characterised by an oblique elongate oval aperture. The peristome is thin and fragmented. The columella has a slight concave curvature. A narrow umbilicus is present. The first whorl has a maximum diameter of 0.54-0.55 mm and the width of the initial cap is 0.2 mm. The transition to the teleoconch is indistinct.

Remarks. – The dimensions of the first whorl are indicative of a direct development without the intermission of a free larval stage, with the hatching of crawling young after a yolk-rich embryogenesis.

A. julei differs from the type species *A. spirata* LAMARCK, 1804 that occurs in the Lutetian of the Paris Basin (WENZ, 1938-1944, p. 1025, fig. 2936), by its consider-

ably smaller shell. It can be distinguished from *Ampullina montensis* by its more elongate, less solid shell, by its slightly higher spire and by its less bulbous embryonic shell. It could well be placed within the family Pseudamauridae. However, a direct comparison of the early ontogenetic shells is not possible, because *A. julei* lacks a larval shell with distinctive ornament.

Order Neogastropoda

Superfamily Buccinoidea RAFINESQUE, 1815

Family Buccinidae RAFINESQUE, 1815

Genus *Suessonia* COSSMANN, 1899

Suessonia montensis (BRIART & CORNET, 1870)

Pl. 4, Figs. 8-9

1870 *Buccinum Montense* BRIART & CORNET, p. 30, pl. 2, fig. 9, a-d.

1973 *Cominella montensis* (BRIART & CORNET). – GLIBERT, p. 67, pl. 8, fig. 5.

1977 *Cominella montensis* (BRIART & CORNET). – VILATTE in MARLIÈRE, p. 120f., pl. 8, figs. 7-12.

Material. – 20 specimens, Coppée pit, coll. Rutot, IRSNB IG 5611, IRSNB FI 6421.

Description. – A solid, moderately slender buccinid shell of ovate to spindle shape consisting of about 10 slightly rounded whorls up to 16 mm in height and 7 mm in width. The first teleoconch whorl is sculptured by ten indistinct spiral cords that are crossed by 12 strong slightly opisthocyrt axial ribs. The number of axial ribs increases up to 16 during ontogeny. The uppermost spiral cords (1 - 4) are always the most strongly developed. The base is ornamented by ten well-defined, closely spaced spiral cords. The last whorl forms about 50-60% of the total height of the shell. The narrow ovate aperture has a well-developed anterior canal, slightly bent to the left side, has a characteristic slightly rounded outer lip and a thickened columellar lip.

The protoconch consists of four slightly rounded whorls, which appear to be smooth. It measures 1.4 mm in height and has a maximum diameter of 0.83-0.84 mm. The first whorl has a maximum diameter of 0.26 mm and the width of the initial cap is 0.1 mm. The transition from the embryonic to the larval shells is not preserved. A broken sinuous rim characterises the transition to the teleoconch.

Remarks. – The protoconch is indicative of a free planktonic veliger stage. *S. montensis* differs from the type-species *Fusus exigua* DESHAYES, 1865 from the French Ypresian by its less slender shell, and its teleoconch sculpture of closer and more slender axial ribs. The protoconch with similar dimensions differs by comprising about 0.5 additional larval whorls. GLIBERT (1973, p. 68, text-fig. 39) gave a sketch of the protoconch of *Suessonia exigua* and compared it to the early ontogenetic shell of "*Fusus*" *strictus* BRIART & CORNET, 1870 (GLIBERT, 1973, p. 67f., text-fig. 67, pl. 11, fig. 20) in

which the teleoconch morphology resembles that of the Recent fusine genus *Microcolus* COTTON & GODFREY, 1931 from West Australia (WENZ, 1938-1944, p. 1257, fig. 3582) and differs by its indication of a direct development. *S. montensis* has been assigned to *Cominella* GRAY, 1850 by GLIBERT (1973) and VILATTE in MARLIÈRE (1977). However, *Cominella*, type species *Buccinum testudineum* LAMARCK, 1799 from Recent, New Zealand (WENZ, 1938-1944, p. 1181, fig. 3357) differs by its larger shell with teleoconch whorls that are slightly concave in the upper portion and convex in the lower portion. The sculpture consists of strongly sinuous axial ribs. The aperture of *Cominella* differs by its broad egg shape, the ridge above the fasciole and the presence of a well-developed pointed posterior channel. NUTTALL & COOPER (1973) assigned the species to *Polliia* G.B. SOWERBY, 1834, type-species *Buccinum undosum* LINNAEUS, 1758 from Recent, South Pacific (WENZ, 1938-1944, p. 1197, fig. 3406). This differs by a lower conical shell, a higher last whorl forming about 75% of the total height of the shell, a well-rounded extending outer lip and by the presence of columellar plaits.

Family Melongenidae GILL, 1871

Genus *Levifusus* CONRAD, 1865

Levifusus amplus (BRIART & CORNET, 1870)

1870 *Pleurotoma ampla* BRIART & CORNET, p. 51, pl. 4, fig. 8.

1877 *Fusus Potieri* BRIART & CORNET, p. 19, pl. 14, fig. 9 a-c.

1887 *Pleurotoma Dewalquei* BRIART & CORNET, p. 29, pl. 15, fig. 2.

1973 *Levifusus amplus* (BRIART & CORNET). – GLIBERT, p. 68, pl. 8, fig. 7.

Description. – The large melongenid species measures up to 65 mm in height and 35 mm in width. The shell has about five preserved whorls. Sculpture consists of ten tuberculate spiral cords with numerous fine spiral threads intercalated. A median spiral cord is strongest developed. The spiral sculpture is crossed by about ten broad slightly opisthocyrt axial ribs. In the points of intersection of the median spiral and the axial ribs strong short spines are developed. The last whorl forms about 70% of the total height of the shell. The large ovate aperture with rounded outer lip is characterised by a well-developed siphonal channel, which is slightly bent to the left side.

Remarks. – GLIBERT (1973) described the species as *Levifusus amplus*. According to KOLLMANN & PEEL (1983) *L. amplus* and another closely related New genus, cf. *Levifusus* CONRAD, species 1 from the Paleocene of Nûgssuaq, West Greenland (KOLLMANN & PEEL, 1983, p. 82, fig. 183) differ from the type-species of *Levifusus*, *Fusus trabeatus* CONRAD, 1865 from the Claibornian (Eocene) of Alabama (WENZ, 1938-1944, p. 1222, fig. 3473), in their less inflated last whorl and by lacking a carina in the lower part and by a straight siphonal canal. The inclusion of *L. amplus* within a new genus is not

followed here. KOLLMANN & PEEL indicated that the carina may be generally weak or even absent in other species of the genus *Levifusus*, thus represents a variable feature. The slightly more inflated body whorl of the type species and another weak carina of the lower part of the whorl may be taken into account to separate species but are not very distinctive on genus level. Furthermore the siphonal channel is not straight in case of the specimen figured by GLIBERT (1973), but it is slightly bent. Thus *L. amplus* could well be congeneric with the type-species of *Levifusus*, *L. trabeatus*.

Superfamily Columbelloidea SWAINSON, 1840

Family Fascioliariidae GRAY, 1855

Genus *Dolicholaturus* BELLARDI, 1884

Dolicholaturus striatulus (BRIART & CORNET, 1870)

- 1870 *Turbinella striatula* BRIART & CORNET, p. 10, pl. 1, fig. 6 a-c.
 1877 *Turbinella granulosa* BRIART & CORNET, p. 10, pl. 14, fig. 1 a-c.
 1973 *Latirus (Dolicholaturus) striatulus* (BRIART & CORNET). – GLIBERT, p. 69, pl. 8, fig. 8.

Description. – The fascioliariid shell measures up to 35 mm in height and 13 mm in width. It has about eight preserved slightly rounded whorls. Sculpture consists of numerous fine tuberculate spiral threads crossed by 6–8 strong straight axial ribs. The last whorl forms about 60% of the total height of the shell. The large narrow aperture is characterised by a straight columella, bearing two plaits in its posterior portion, and by a well-developed straight siphonal channel.

Remarks. – GLIBERT (1973, p. 69, pl. 8, fig. 8) described the species as *Latirus (Dolicholaturus) striatulus*, which differs from the type-species of *Dolicholaturus*, *Turbinella bronni* MICHELOTTI, 1861 (WENZ, 1938–1944, p. 1243, fig. 3543), from the Tortonian of Italy by its more rounded teleoconch whorls, and by the formation of finer closely-spaced spiral cords. *Dolicholaturus* should be regarded as a genus which differs considerably from *Latirus* MONTFORT, 1810, type-species *Murex gibbulus* GMELIN, 1792 from Recent, Australia (cf. WENZ, 1938–1944, p. 1241, fig. 3538), in its crenulated outer apertural lip, the lack of columellar plaits and in its very short siphonal channel. Fascioliariidae are often connected to mangrove environments, e.g. the Recent South Atlantic genus *Leucozonia* GRAY, 1847 (BANDEL & KOWALKE, 1999).

Subclass Heterostropha

Order Archaeopulmonata

Superfamily Ellobioidea H. & A. ADAMS, 1855

Family Ellobiidae H. & A. ADAMS, 1855

Remarks. – The diverse ellobiid fauna of Mons consists of members of the subfamilies Ellobiinae, Pedipedinae and Pythiinae (GLIBERT, 1973).

Genus *Ellobium* RÖDING, 1798

Ellobium olivaeformis (BRIART & CORNET, 1873)

- 1887 *Melampus olivaeformis* BRIART & CORNET, p. 108, pl. 25, fig. 12 a-c.
 1887 *Melampus cochleatus* BRIART & CORNET, p. 109, pl. 25, fig. 13 a-c.
 1973 *Melampus olivaeformis* BRIART & CORNET. – GLIBERT, p. 91, pl. 11, figs. 4a, b.

Description. – The elongated conical shell is characterised by an ovate body whorl and by a short conical spire and has about six preserved whorls. It measures up to 15 mm in height and 7.5 mm in width. The shell appears to be smooth aside from closely spaced slightly prosocyrct growth lines. The last whorl is very large, forms about 80% of the total height of the shell. The narrow half-moon shaped aperture is very high, reaching more than half of the total height of the shell. It is characterised by a slight broad anterior notch and by a pointed posterior portion. It bears a prominent horizontally arranged parietal plait and a weaker columellar plait, which is orientated towards the spire. The columellar and parietal portion of the aperture are covered by callus.

Remarks. – BRIART & CORNET (1887) described *Melampus olivaeformis* and *M. cochleatus* and assigned these species to the genus *Melampus* MONTFORT, 1810 [Melampinae, attributed to Melampodinae by GLIBERT (1973) and WENZ & ZILCH (1959–1960)]. GLIBERT (1973) mentioned the variability of the species regarding the morphology of the last whorl and the height of the spire and mentioned that these species are conspecific, with *M. cochleatus* representing varieties with stout apices and more rounded body whorl (p. 91, pl. 11, figs. 4a, b). GLIBERT confirmed the systematic placement of *M. olivaeformis* within the genus *Melampus*. *Melampus*, type species *Voluta coffea* LINNAEUS, 1758, Recent, from tropical America (WENZ & ZILCH, 1959–1960, p. 65f., fig. 211) differs in its less conical more rounded and elongate ovate shape, in having one strong columellar plait, 1–5 weaker parietal plaits and its weak teeth on the interior labial part of the aperture. *M. olivaeformis* most likely belongs to the genus *Ellobium*, type species *Voluta aurismidae* LINNAEUS, 1758, Recent, from Southeast Asia (WENZ & ZILCH, 1959–1960, p. 77, Fig. 250), with a similar shell shape, and the characteristic presence of an oblique columellar plait together with a stronger more horizontal parietal plait. *Ellobium olivaeformis* (BRIART & CORNET, 1873) differs from the type species by its smaller size, and by the absence of weak spiral granulations on the teleoconch whorls.

Genus *Auriculastra* MARTENS, 1880

Auriculastra ovata (BRIART & CORNET, 1887)

- 1887 *Blauneria ovata* BRIART & CORNET, p. 106, pl. 25, fig. 13.
 1973 *Stolidoma ovata* (BRIART & CORNET). – GLIBERT, p. 93, fig. 13.

Description. – The small elongated conical shell with a large cylindrical last whorl and a short conical spire has about six to seven preserved whorls. It measures up to 7 mm in height and up to 3 mm in width. The spire whorls are slightly rounded. The shell appears to be smooth aside from close-spaced slightly prosocyrat growth lines. The last whorl forms about 70-80% of the total height of the shell. The large narrow aperture is characterised by a slight but broad anterior notch and by a pointed posterior portion. It is characterised by a prominent plait in the upper columellar portion. The aperture lacks a callus.

Remarks. – BRIART & CORNET (1887) originally assigned the species to *Blauneria* SHUTTLEWORTH, 1854, which differs by its very thin, left wined shell with turreted spire. GLIBERT (1973) assigned the species to the genus *Stolidoma*. *S. ovata* differs from the type species of the genus *Stolidoma* DESHAYES, 1863, *S. crassidens* DESHAYES, 1863 from the French Thanetian (WENZ & ZILCH, 1959-1960, p. 73, fig. 237) by its less elongate shell, larger body whorl and shorter, more acute apex and by the lack of columellar and parietal callus. The columellar plait is less oblique and rather more horizontal. GLIBERT (1973) figured *Stolidoma acuta* (BRIART & CORNET, 1887) (GLIBERT, 1973, p. 93, pl. 11, fig. 11) and *S. cylindrata* (BRIART & CORNET, 1887) (GLIBERT, 1973, p. 93, pl. 11, fig. 12), subfamily Pythiinae. The systematic place of these species within the genus *Stolidoma* could be confirmed. The protoconch of *S. acuta* (GLIBERT, 1973: pl. 11, fig. 11) consists of two whorls with the initial 1.5 whorls being heterostrophic and is about 0.2 mm in both height and its maximum diameter. This indicates an indirect development with a planktonic veliger stage. The teleoconch shape of *S. ovata* indicates it most likely belongs to the genus *Auriculastra* MARTENS, 1880 (subfamily Ellobiinae), type species *Auricula subula* QUOY & GAIMARD, 1832 (WENZ & ZILCH, 1959-1960, p. 76, fig. 249; BANDEL & RIEDEL, 1998, p. 188, fig. 8A). *Auriculastra ovata* differs from the type species by its smaller size and its stronger columellar plait.

Genus *Semiauricula* COSSMANN, 1889

Semiauricula granda (BRIART & CORNET, 1887)

1887 *Auricula grandis* BRIART & CORNET, p. 90, pl. 25, fig. 1 a-b.

1973 *Ellobium grande* (BRIART & CORNET). – GLIBERT, p. 93f., pl. 11, fig. 14.

Description. – The slender elongate cylindrical shell comprises about five slightly rounded whorls measuring up to 35 mm in height and 18 mm in width. Sculpture consists of closely-spaced slightly prosocyrat growth lines and of 8-10 straight axial ribs which vanish on the last whorl. The last whorl forms about 60-70% of the total height of the shell. The height of the large ovate aperture amounts about half of the total height of the shell. It is thickened by callus and characterised by a very weak columellar plait and a weak parietal plait.

Remarks. – BRIART & CORNET (1887) had assigned *S. granda* to *Auricula* LAMARCK, 1799, a synonym of *Ellobium*, to which it has been attributed by GLIBERT (1973). The species is distinguished from the type species *Ellobium aurismidae* by its elongate slender cylindrical shell with lower body-whorl and probably belongs to the genus *Semiauricula* COSSMANN, 1889 (subfamily Ellobiinae), type species *Auricula adversa* DESHAYES, 1863 from the French Thanetian. *Semiauricula granda* differs from the similarly sized type species by the stronger axial ribs present on the teleoconch whorls and its weaker columellar and parietal plaits.

Embryogenesis, Larval Ecology and Paleoecology

Sixteen brackish water gastropod species from Mons are known from their protoconch morphologies. Only five species are characterised by an indirect mode of early ontogeny with a free-swimming planktotrophic larval stage (*Monsneritina montensis*, *Alvania* (*Arsenia*) *craticula*, *Cavilabium microscopicum*, *Suessonia montensis*, *Stolidoma acuta*). Three species are characterised by a lecithotrophic larva, which only spend a very short time within the plankton, as indicated by larval shells that have less than one whorl (*Pseudovertagus* (*Pseudaluco*) *dumonti*, *Monspotamides varians*, *Hadraxon regularicostatum*). Eight species underwent a direct development with the formation of large embryonic shell that indicates a yolk-rich embryogenesis with the subsequent hatching of crawling young without a planktonic veliger stage (*Theodoxus fabulus*, *Alvania* (*Arsenia*) *montensis*, *Stenothyrella pupiformis*, *Dissochilus lineatus*, *Diastomella luciani*, *Diastomella tenuicula*, *Ampullina montensis*, *Amaurellina julei*).

The predominance of direct developers and lecithotrophic species indicates a calm, coastal swamp environment with reduced water energy (KOWALKE & BANDEL, 1996). The coastal swamps probably extended far landwards. This is also indicated by the presence of a diverse archaeopulmonate fauna (e.g. *Ellobium olivaeformis*, *Auriculastra ovata*, *Semiauricula granda*). Archaeopulmonata characterise the landward part of coastal swamps and mangroves, settling the uppermost intratidal to supratidal portion (BANDEL & RIEDEL, 1998; BANDEL & KOWALKE, 1999). This zone is also preferred by littorinids (*Dissochilus lineatus*, *Cavilabium microscopicum*). A good connection to the open sea existed as shown by the species with lecithotrophic and planktotrophic development, as these have had a marine larval stage after hatching from egg masses within their adult brackish habitat. The occurrence of *Theodoxus fabulus* and *Melanopsis briarti* may point to a major fresh water influx. This is also indicated by the presence of diminutive forms of Potamididae (*Granulolabium ovalituberosum*, *Monspotamides varians*, *Hadraxon regularicostatum*, *Diastomella luciani*, *Diastomella tenuicula*) and Pseudamauridae (*Ampullina montensis*, *Amaurellina julei*) that reach only half the size of their known Cretaceous, Eocene or

Recent relatives (KOWALKE 1998a, b; KOWALKE, in press a, b). The occurrence of *Cornetia*, that most probably represents a synonym of *Pyrgulifera*, indicates a calm, landward portion of the coastal swamps – a similar environment has been reconstructed for the *Pyrgulifera*-habitat of the Late Cretaceous of the Gosau and the Bakony Mountains (BANDEL & RIEDEL, 1994; KOWALKE & BANDEL, 1996).

Most of the brackish water gastropods described were herbivorous, either grazing on plants or microalgae as their modern relatives: Neritidae occur on hard substrates as well as on soft bottom habitats (BANDEL & RIEDEL, 1998; BANDEL & KOWALKE, 1999). Within the Littorinidae, *Dissochilus* closely resembles modern *Littoraria* or *Mainwaringia*. These live on mangrove vegetation and are mainly active at low tide (REID, 1985, 1986a, b). *Cavilabium* in contrast resembles small littorinids such as *Bembicium* and *Risellopsis*, that prefer coastal hard substrates (REID, 1988). *Pseudovertagus* (*Pseudaluco*) *dumonti* (Cerithiidae) could have lived on intertidal hard substrates, or else on the roots of mangrove trees as their modern relatives belonging to the cerithiid genus *Clypeo-*

morus JOUSSEAUME, 1888 (cf. HOUBRICK, 1985). Potamididae usually move during low tides preferring muddy portions of the coastal swamp. This type of habitat is also settled by Rissooidea, which in contrast also graze during the high tides (BANDEL & KOWALKE, 1999). The extinct family Pseudamauridae characterised the calm brackish lagoonal habitats and coastal swamps often associated with the bivalve genus *Corbicula* (KOWALKE & BANDEL, 1996; KOWALKE, 1998b). The buccinid *Suessonia*, the melongenid *Levifusus* and the fasciolariid *Dolicholatirus* were probably rare predators or scavengers of the brackish coastal swamp, comparable to modern neogastropods which marginally settle in the brackish milieu (BANDEL & KOWALKE, 1999).

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Appendix

List of the mentioned gastropod taxa of Mons

Family Neritidae RAFINESQUE, 1815

Subfamily Neritinae RAFINESQUE, 1815

? *Nerita heberti* SZÓTS, 1953

Genus *Theodoxus* MONTFORT, 1810

Theodoxus fabulus (BRIART & CORNET, 1887)

Genus *Monsneritina* n. g.

Monsneritina montensis (BRIART & CORNET, 1887)

Superfamily Rissoidae GRAY, 1847

Family Rissoidae GRAY, 1847

Genus *Alvania* RISSO, 1826

Subgenus *Arsenia* MONTESERATO, 1890

Alvania (Arsenia) craticula (BRIART & CORNET, 1887)

Alvania (Arsenia) montensis GLIBERT, 1973

Family Stenothyridae FISCHER, 1885

Genus *Stenothyrella* WENZ, 1938

Stenothyrella pupiformis (BRIART & CORNET, 1887)

Superfamily Littorinoidea GRAY, 1840

Family Littorinidae GRAY, 1840

Genus *Dissochilus* COSSMANN, 1888

Dissochilus lineatus (BRIART & CORNET, 1887)

Genus *Cavilabium* COSSMANN, 1888

Cavilabium microscopicum COSSMANN, 1924

Superfamily Cerithioidea FÉRUSAC, 1819

Genus *Krumbachiella* KOWALKE & BANDEL, 1996

Krumbachiella typica (BRIART & CORNET, 1887)

Genus *Cornetia* MUNIER-CHALMAS in FISCHER, 1885

Cornetia malaisei (BRIART & CORNET, 1870)

Family Melanopsidae H. & A. ADAMS, 1854

Genus *Melanopsis* FÉRUSAC, 1807

Melanopsis briarti COSSMANN, 1888

Family Cerithiidae FÉRUSAC, 1819

Subfamily Cerithiinae FÉRUSAC, 1819

Genus *Pseudovertagus* VIGNAL, 1904

Subgenus *Pseudaluco* CLARK & DURHAM, 1946

Pseudovertagus (Pseudaluco) dumonti (BRIART & CORNET, 1873)

Family Potamididae H. and A. ADAMS, 1854

Genus *Granulolabium* COSSMANN, 1889

Granulolabium ovalituberosum (BRIART & CORNET, 1873)

Genus *Monspotamides* n. g.

Monspotamides varians (BRIART & CORNET, 1873)

Genus *Hadraxon* OPPENHEIM, 1892

Hadraxon regularicostatum (BRIART & CORNET, 1873)

Genus *Diaatomella* CHAVAN, 1952

Diaatomella luciani (BRIART & CORNET, 1873)

Diaatomella tenuicula (BRIART & CORNET, 1877)

Family Pseudamauridae KOWALKE & BANDEL, 1996

Genus *Ampullina* BOWDICH, 1822

Ampullina montensis COSSMANN, 1915

Genus *Amaurellina* FISCHER, 1884

Amaurellina julei (BRIART & CORNET, 1873)

Superfamily Buccinoidea RAFINESQUE, 1815

Family Buccinidae RAFINESQUE, 1815

Genus *Suessonia* COSSMANN, 1899

Suessonia montensis (BRIART & CORNET, 1870)

Family Melongenidae GILL, 1871

Genus *Levifusus* CONRAD, 1865

Levifusus amplus (BRIART & CORNET, 1870)

Superfamily Columbelloidea SWAINSON, 1840

Family Fascioliidae GRAY, 1855

Genus *Dolicholatus* BELLARDI, 1884

Dolicholatus striatulus (BRIART & CORNET, 1870)

Superfamily Ellobioidea H. & A. ADAMS, 1855

Family Ellobiidae H. & A. ADAMS, 1855

Genus *Ellobium* RÖDING, 1798

Ellobium olivaeformis (BRIART & CORNET, 1873)

Genus *Auriculastra* MARTENS, 1880

Auriculastra ovata (BRIART & CORNET, 1887)

Genus *Semiauricula* COSSMANN, 1889

Semiauricula granda (BRIART & CORNET, 1887)

Explanations of Plates

All figured specimens are deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB FI 6404 – IRSNB FI 6421).

PLATE 1

- Figs. 1-4 — *Theodoxus fabulus* (BRIART & CORNET, 1887)
 1 = juvenile specimen (IRSNB FI 6404) in apertural view; the shell measures 3.42 mm in width.
 2 = apical view of the same specimen as in fig. 1; the shell measures 3.3 mm in maximum diameter.
 3 = apex of the same specimen as in fig. 1 in lateral view showing sculptural details of the embryonic shell; the first whorl measures 0.44 mm in height (in the visible part).
 4 = apex of the same specimen as in fig. 1 in apical view; the first whorl measures 0.47 mm in maximum diameter.
- Figs. 5-7 — *Monsneritina montensis* (BRIART & CORNET, 1887)
 5 = juvenile specimen (IRSNB FI 6405) in apertural view; the shell measures 2.2 mm in width.
 6 = apex of the same specimen as in fig. 5 in apical view showing the transition from the protoconch to the teleoconch; the protoconch measures 0.5 mm in maximum diameter.
 7 = apex of the same specimen as in fig. 5 in lateral view; larval whorls are partly covered by the succeeding ones; the protoconch measures 0.36 mm in maximum width (in the visible part).

PLATE 2

- Figs. 1-2 — *Cavilabium microscopicum* COSSMANN, 1924
 1 = specimen (IRSNB FI 6408) in apertural view; the shell measures 1.66 mm in height.
 2 = apex of the same specimen as in fig. 1; the smooth protoconch measures 0.57 mm in maximum diameter.
- Figs. 3-5 — *Alvania (Arsenia) craticula* (BRIART & CORNET, 1887)
 3 = juvenile specimen (IRSNB FI 6406) in apertural view; the shell measures 2.87 mm in height.
 4 = apex of the same specimen as in fig. 3 in lateral view; the protoconch comprises 2.3 whorls, it measures 0.34 mm in height.
 5 = apex of the same specimen as in fig. 3 in apical view; the protoconch measures 0.36 mm in maximum diameter.
- Figs. 6-8 — *Stenothyrella pupiformis* (BRIART & CORNET, 1873)
 6 = specimen (IRSNB FI 6407) in apertural view; the shell measures 1.28 mm in height.
 7 = apex of the same specimen as in fig. 6 in lateral view; the onset of the teleoconch is indicated by crowded growth lines; the protoconch measures 0.2 mm in height.
 8 = apex of the same specimen as in fig. 6 in apical view; the first whorl measures 0.19 mm in maximum diameter.

PLATE 3

- Figs. 1-3 — *Pseudovertagus (Pseudaluco) dumonti* (BRIART & CORNET, 1873)
 1 = juvenile specimen (IRSNB FI 6410) in apertural view with gradual loss of teleoconch sculpture in the course of the ontogeny; the height of the shell amounts 8.3 mm.
 2 = juvenile specimen (IRSNB FI 6409) showing the development of the early teleoconch sculpture; the shell measures 3.2 mm in height.
 3 = apex of the same specimen as in fig. 2 in lateral view; a slightly sinuous rim is indicating the transition from the protoconch to the teleoconch; the protoconch measures 0.31 mm in height.
- Fig 4 — *Granulolabium ovalituberosum* (BRIART & CORNET, 1873)
 4 = specimen (IRSNB FI 6411) in apertural view showing the sculptural development of the teleoconch whorls; the height of the shell amounts 13.2 mm.
- Figs. 5-7 — *Monspotamides varians* (BRIART & CORNET, 1873)
 5 = juvenile specimen (IRSNB FI 6412) in apertural view; the height of the shell amounts 6.7 mm.
 6 = juvenile specimen (IRSNB FI 6413) in apertural view; the shell measures 3.65 mm in height.
 7 = apex of the same specimen as in fig. 6 in lateral view showing sculptural details of the protoconch and transition to the teleoconch; the protoconch measures 0.28 mm in height.
- Figs. 8-9 — *Hadraxon regularicostatum* (BRIART & CORNET, 1873)
 8 = juvenile specimen (IRSNB FI 6414) in apertural view; the shell measures 3.86 mm in height.
 9 = apex of a juvenile specimen (IRSNB FI 6415) in lateral view showing the thickened sinuous rim marking the transition to the teleoconch; the protoconch measures 0.27 mm (in the visible part).

PLATE 4

- Fig. 1 — *Diastomella tenuicula* (BRIART & CORNET, 1877)
1 = specimen (IRSNB FI 6417) in apertural view with strong carination of the teleoconch whorls; the shell measures 3.3 mm in height.
- Figs. 2-3 — *Diastomella luciani* (BRIART & CORNET, 1873)
2 = specimen (IRSNB FI 6416) in apertural view; the shell measures 4.36 mm in height.
3 = apex of the same specimen as in fig. 2 in apical view; the first whorl measures 0.19 mm in maximum diameter.
- Fig. 4-5 — *Ampullina montensis* COSSMANN, 1915
4 = specimen (IRSNB FI 6418) in apertural view; the shell measures 6.8 mm in height.
5 = specimen (IRSNB FI 6419) in apical view with bulbous embryonic shell; the shell measures 3.6 mm in maximum diameter.
- Figs. 6-7 — *Amaurellina julei* (BRIART & CORNET, 1873)
6 = juvenile specimen (IRSNB FI 6420) in apertural view; the shell measures 3.65 mm in height.
7 = apex of the same specimen as in fig. 6 in apical view; the first whorl measures 0.54 mm in maximum diameter.
- Figs. 8-9 — *Suessonia montensis* (BRIART & CORNET, 1870)
8 = juvenile specimen (IRSNB FI 6421) in apertural view; the shell measures 4.18 mm in height.
9 = apex of the same specimen as in fig. 8 showing the thickened sinuous rim marking the transition to the teleoconch; the protoconch measures 1.42 mm in height.

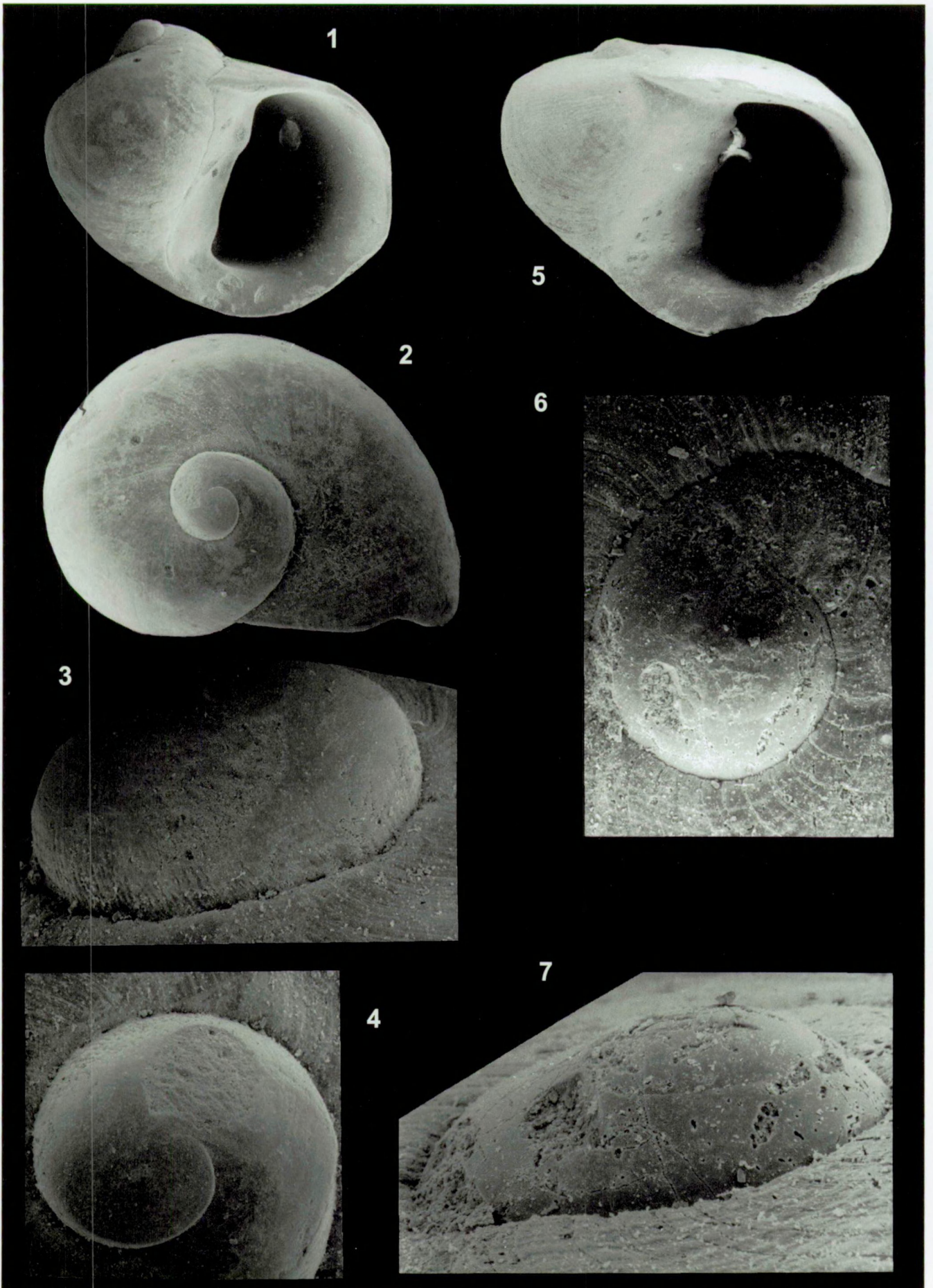


PLATE 1

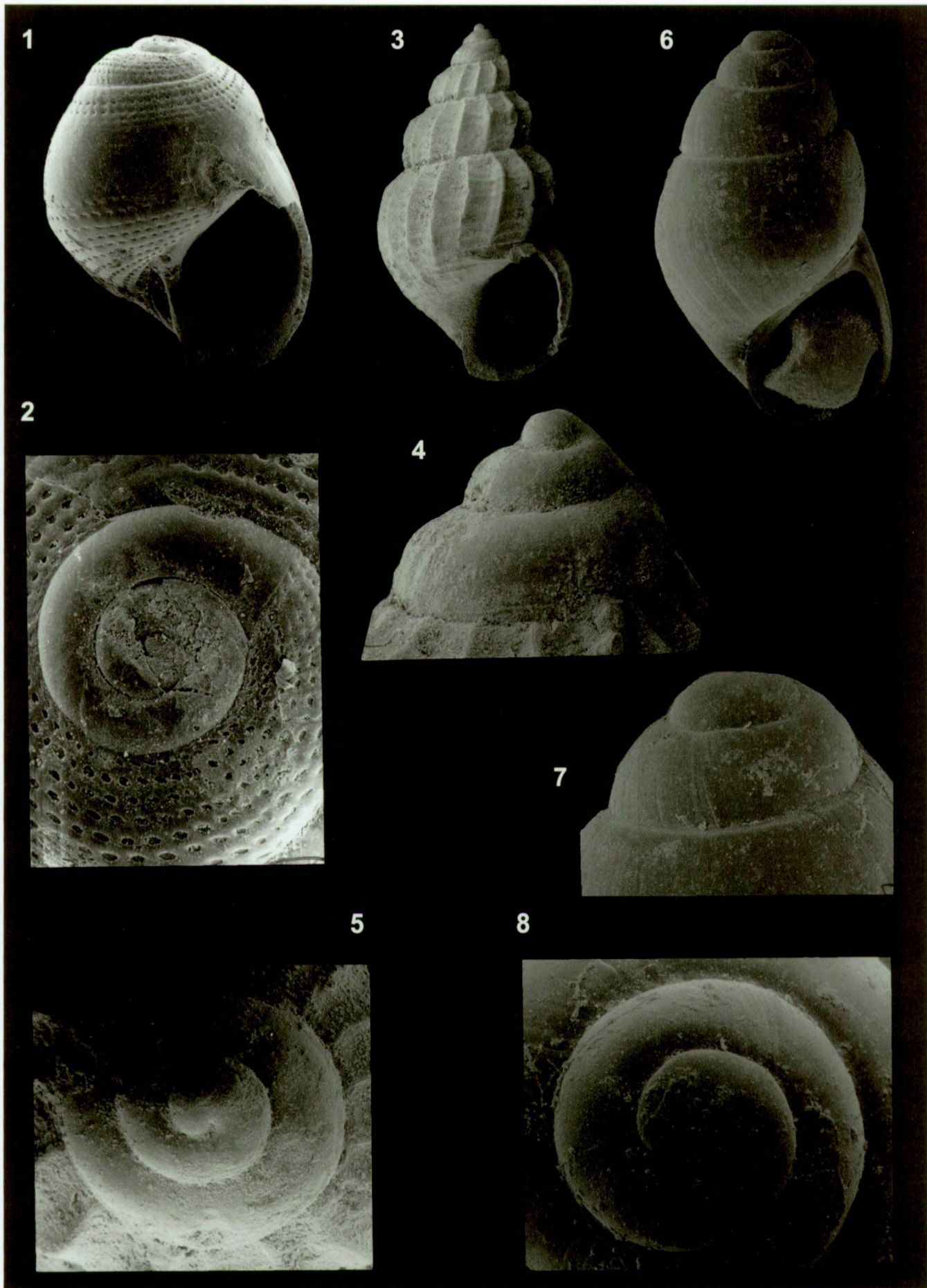


PLATE 2

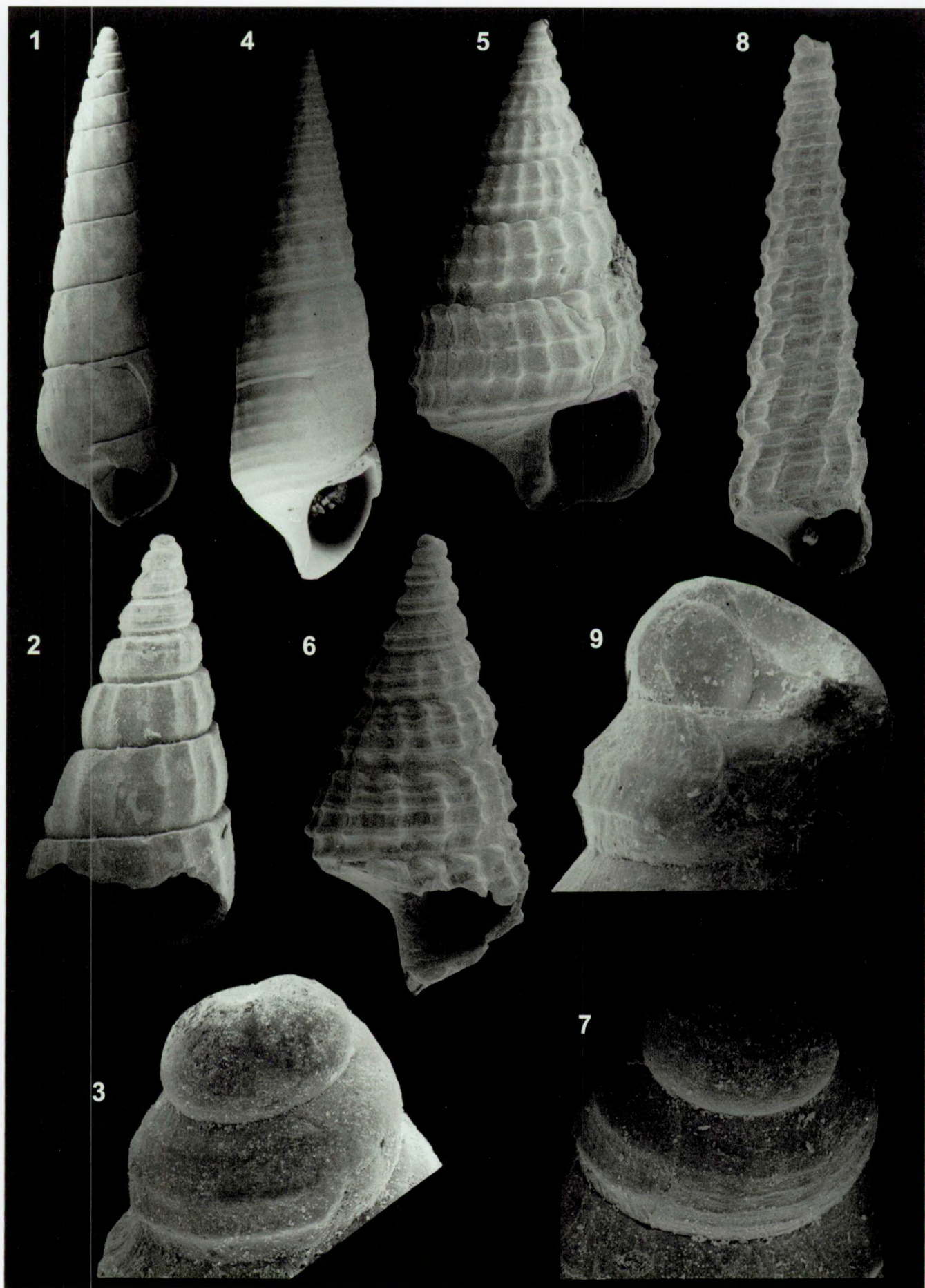


PLATE 3



PLATE 4