

# Early Pliocene heteropods and pteropods (Mollusca, Gastropoda) from Le Puget-sur-Argens (Var), France

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*'Die Ausbeutung an Ort und Stelle ist wenig lohnend und nicht jeder hat Freude an solch kleinen Schneckchen. Hat doch ein namhafter ausländischer Geologe, den ich an die Localität geführt und dem ich ein Dutzend Arten dieser kleinen aus dem Sande gesuchten Schneckchen übergeben hatte, sie mir mit der Bezeichnung "Nipps" und voller Verachtung zurückgegeben, ....'*

(H.C. Weinkauff, 1859, p. 68).

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Almost 14,000 identifiable specimens of holoplanktonic Mollusca, belonging to 23 species (Pterotracheoidea 5, Euthecosomata 15, Pseudothecosomata 3) are recorded from early Pliocene (Zanclean) rocks exposed in the Les Escavariats claypit at Le Puget-sur-Argens (France, Var department). Among the heteropods the presence of *Atlanta plana* Richter, 1972 (predominantly known from the Indo-Pacific) and a presumably undescribed species of *Protatlanta* are noteworthy. Of the Euthecosomata the species *Striolimacina imitans* (Gabb, 1873) is a first record for the Mediterranean, whereas *Heliconoides vonhachti* sp. nov. is introduced on the basis of more than a thousand specimens. *Creseis spina* (Reuss, 1867), so far only known from the late Eocene-Miocene interval, is recorded as a common species during the early Pliocene as well. The pseudothecosomatous species *Peracle reticulata* (d'Orbigny, 1834), hitherto only known from the Recent fauna and Holocene to late Pleistocene deposits, is also recorded for the first time from early Pliocene rocks.

KEY WORDS: Pterotracheoidea, Thecosomata, Pliocene, Zanclean, France, new species

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## Introduction

Pliocene Mediterranean pelagic gastropods are only incidentally recorded in papers on fossil mollusc faunas in general as in most cases heteropoda and/or pteropoda occur only sparsely in sometimes very rich benthic assemblages. Only few papers are devoted to these holoplanktonic species only. Most information is available from Italy, both in published form and in as yet unpublished collection material, partly also in private collections. In this paper a complete assemblage from a single locality in SE France is presented with an age of early Pliocene (Zanclean). All material is housed in the Naturalis Biodiversity Center, Leiden, The Netherlands (RGM registration numbers).

## Le Puget-sur-Argens

The former claypit complex Costamagna is situated in the hamlet Les Escavariats, some 1500 m S of the town

of Le Puget-sur-Argens in the French département Var (map-sheets XXXV-44 and XXXVI-44, Fréjus-Cannes, coordinates  $x = 952.350$ ;  $y = 136.500$ ) (Fig. 1). Some 20 m of greyish-blue, slightly fossiliferous clays used to be worked here for tile manufacture. Exploitation of the pit came to an end in 1983. At the time of my visits (1988, 1991) the lower 4-5 m of the pit were below water level and the former excavation fronts were for the greater part overgrown.

Fossil material from this locality is described in a number of papers (Voigt, 1979; Schwarzhans, 1980, 1981, 1986; Irr, 1984; Zheng, 1986; Zheng & Cravatte, 1986; Nolf & Cappetta, 1988; Cappetta & Nolf, 1991; Engeser *et al.*, 1993; R. Janssen, 1993). The bulk of macrofossil samples underlying these publications on the Le Puget faunas was brought together by the German non-professional collector Hans Joachim von Hacht (26 July 1923, Altona, Hamburg; †25 November 1994, Ammersbek, Germany), a WorldWar-II amputee, who for many years was fascinated by the wide variety of fossils pres-

ent in this locality and who sought to realise a 'complete' list of fossils. For this purpose he made his collected material available to specialists, subsequently pursuing the unfortunate one until his results would have appeared in printed form. In this way von Hacht succeeded to obtain a substantial list of many hundreds of fossil names. Inevitably several of the new taxa found were named after him, as e.g. the bony fish otolith species *Opisthoproctus vonhachti* Schwarzhans, 1986 and *Bythitinerum vonhachti* Nolf & Cappetta, 1988. His material was collected over many years, starting in 1972 when the clay pit was still active, and finishing in 1992. The large amount of time invested (every year von Hacht was active in the pit for at least three months!) has resulted in an extraordinary large number of fossils. Although the clay is strikingly poor in fossils, special collecting methods described below have yielded quantities of material never obtained before from comparable rocks. As an example Nolf & Cappetta (1988) studied over 60,000 bony fish otoliths from Le Puget, all collected by von Hacht: the worlds largest collection of Pliocene otoliths.

Since 1987 the complete material of heteropods and pteropods was made available to me and in doing so H.J. von Hacht enabled to study an unusually large assemblage of Pliocene heteropods and pteropods, a collection, unprecedented as far as the number of specimens is concerned (almost 14,000 identifiable specimens), but also with respect to the species composition.

An earlier paper recording pteropods from the Pliocene of SE France is Depontailier (1877), who listed *Cleodora*, *Hyalaea* and *Cuvierina astesana* from Biot (Vaugrenier) near Cannes and from Cannes, Moulin de l'Abadie (France, Alpes Maritimes). Some further Pliocene material was incidentally collected by H.J. von Hacht at Cagnes-sur-Mer (Alpes Maritimes) (*Styliola subula*, *Clio pyramidata* f. *lanceolata* and *Diacria trispinosa*) and Vences (Alpes Maritimes) (*Clio pyramidata* f. *lanceolata* and *Diacria trispinosa*). These samples are also housed in RGM. Chirli & Richard (2008) recorded two species (*Clio pyramidata* and *Cuvierina astesana*) from Pichegu Bellegarde (Gard dép., France), considering them to be of Piacenzian age.

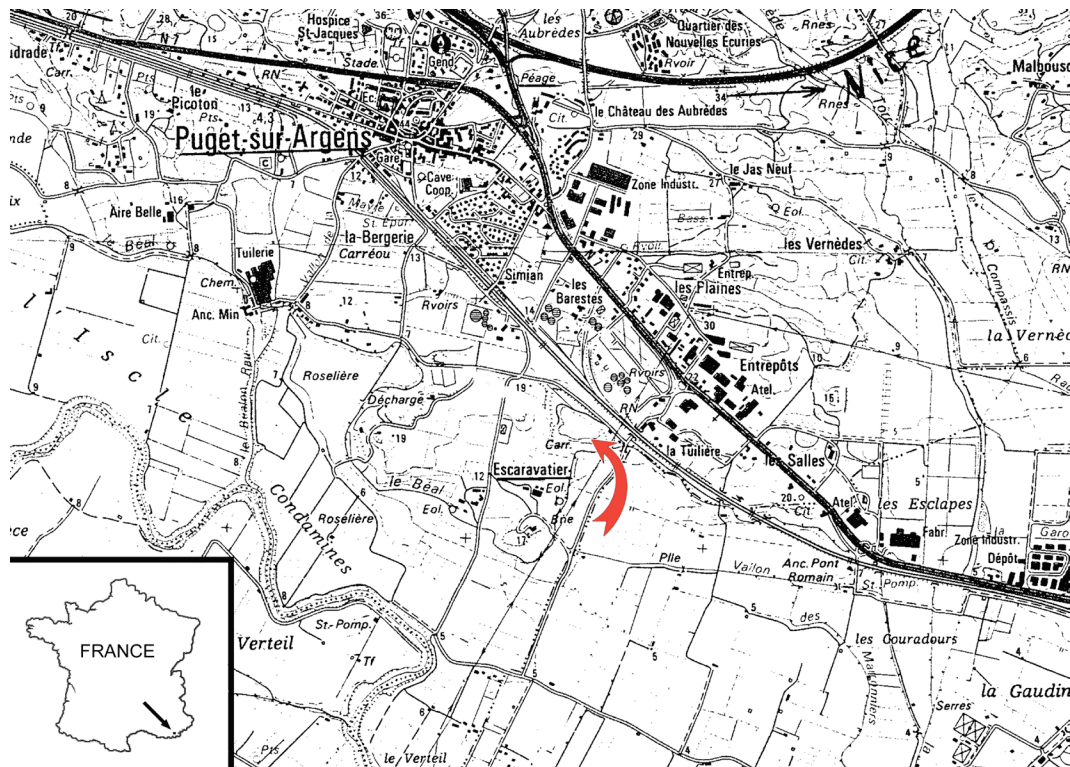


Figure 1. Location of the Costamagna clay pit (arrow) in Les Escaravatières, Le Puget-sur-Argens (France, dép. Var).

### Material and methods

The first holoplanktonic molluscs from Le Puget-sur-Argens (Fig. 1) came to my attention through Jaap van der Voort (Ostercappeln, Germany) and Klaus Bandel (Hamburg, Germany) in the second half of 1987. Subsequent contact with H.J. von Hacht started a constant and regular flow of material, which was provisionally analysed from time to time and reported in preliminary (un-

published) listings of species. The dates of these reports, with the numbers of specimens and preliminary identifications testify to his activities and to the richness of the Le Puget fauna for this group of gastropods (see Table 1). The estimated number of represented species in the last reports was 30, but the present critical revision reduced that number to 23 only and the total number of actual identifiable specimens to 13,748.

Report no.	date	total number of specimens	estimated number of species
1	00.12.1987	3,042	15
2	13.01.1988	6,537	21
3	16.02.1988	6,766	23
4	14.07.1988	8,138	26
5	18.12.1988	9,667	26
6	30.12.1988	10,227	28
7	06.10.1989	11,811	29
8	10.01.1990	13,030	30
9	07.07.1990	13,801	30
10	12.12.1990	14,031	30
11	14.02.1991	14,633	30

**Table 1.** Internal (unpublished) RGM-reports 1987-1991 on the Le Puget holoplanktonic Mollusca, showing the relation between number of identifiable specimens and number of species.

Because of their small size and fragility most holoplanktonic molluscs can hardly be expected to be found when collecting visually, which is an approved method for collecting at least the larger biota from poorly fossiliferous rocks exposed in clay pits. Even a specific search for

these fossils, by breaking pieces of fresh sediment and inspection of the surfaces with a magnifying glass, yields admittedly better preserved, but only very few specimens, and the necessary time investment is considerable. More substantial results are obtained by processing fresh rock samples, but even then specimens usually appear to occur only in low frequencies, and laborious washing of very large rock samples is obligatory to obtain a realistic idea of an assemblage.

Hans von Hacht, knowing all this by experience, developed another method, with far more substantial results. He found out that the uppermost one or two cm of slightly weathered clay, which had been exposed on near-horizontal surfaces for maybe a year or so, could easily be processed in the pit itself, yielding a residue comparatively rich in fossils. Anyway, the residues obtained by his method are distinctly more substantial than those obtained by the usual processing of fresh clay samples. This can be explained by assuming that winter rain disintegrates the upper millimeters of dry clay and washes away the fine sediment particles, during which process apparently the fossils (practically all filled with pyrite and therefore relatively heavy) are washed down the excavation slopes and are concentrated on near horizontal parts of the excavation, where they remain more or less in place. Thus, a distinct concentration of fossil material takes place, and this is one of the most important reasons that so many holoplanktonic molluscs (and other fossils) became available from Le Puget.



**Figure 2.** Hans Joachim von Hacht processing clay samples in the Les Escaravatières clay pit, Le Puget-sur-Argens; July 1991 (courtesy Ulrich von Hacht).

This method, as practiced by von Hacht, has also a severe disadvantage. Pyrite admittedly protects tiny and fragile aragonitic fossils from being destroyed during sediment processing, but residues obtained in the way as described here contain a relatively high percentage of specimens in which the pyrite is deteriorated already: several thousands of both limacinoid and cavolinoid specimens turned out to be unidentifiable. Still, the number of well-preserved specimens makes the method very worthwhile. It must be realized that the material originates from the entire overlying section.

Von Hacht's routine during the summer months of the years 1987-1990 included the daily processing of some 100 kg of dry clay, scraped from more or less horizontal clay surfaces. He soaked the clay inside nylon stockings (c. 0.5 mm mesh) in a bucket of water to disintegrate, which took half an hour on the average (Fig. 2). As electricity was not available in the clay pit a small motor pump was applied, the battery of which had to be recharged daily at his summer residence, which was a Le Puget camping site. With the pump hose put inside the stockings the disintegrated sediment was washed out, until a clean residue remained. The samples obtained in this primitive but very successful way, were dried and

fractionated immediately, and picked every evening, after which the remaining unfossiliferous, mainly pyritic leftovers flew out of his caravan window. Picked fossils were roughly separated by group and from time to time shipped by post to the various specialists. The Le Puget residents observed Hans von Hacht coming back year after year to the desolate clay pit and watched his incomprehensible activities, wondering what he was doing. He told me, with a big smile, that they honoured him with the nickname '*Le fou dans le trou*'.

The fortunate fact that several times notes were made on the quantities of processed sediment enables a rough estimate of the frequency of occurrence of holoplanktonic gastropods related to the quantity of sediment. During the years 1987 to 1989 von Hacht worked in the clay pit each year for about 100 days, processing on average 100 kg of dry sediment per day, totalling roughly 30 tons. In 1990 about 8 tons were processed. From the residues (> c. 0.5 mm) of these 38.000 kg of clay 13.748 recognizable planktonic gastropods were isolated, which means an average number of 0.362 specimen per kg dry sediment. If we calculate these numbers for the various groups of planktonic gastropods the following figures are obtained (Tab. 2).

	total number of specimens found in 1987-1990	number of specimens per kg dry clay	% of total
Heteropoda	218	0.0057	1.59
Euthecosomata	13.447	0.3539	97.81
Pseudothecosomata	83	0.0022	0.60
total	13.748	0.3618	100,00

**Table 2.** Numbers of identifiable holoplanktonic Gastropoda (> c. 0.5 mm) obtained from ~ 38,000 kg of dry sediment.

These figures mean that euthecosome pteropods occur in these sediments with a single specimen per 2.83 kg clay. To find one heteropod specimen 174 kg of sediment have to be processed and 458 kg will be necessary to obtain a single pseudothecosomatous specimen. Here we obviously have found the reason why these groups are so poorly known from the Pliocene fossil record. The natural process of fossil concentration in the washed sediment, as described above, is disregarded in this calculation, so the figures given in Table 2 are still much lower for fresh clay samples. Several thousands of unidentifiable specimens are left out of consideration here.

#### Stratigraphical and palaeoecological notes

The bluish-grey marls that used to be exploited at Le Puget are situated in one of a series of well-known Pliocene palaeocanyon fills along the Mediterranean coast of SE France (see fig. 2 in Nolf & Cappetta, 1988). These fills are lithostratigraphically indicated with the name

'Poudingues et Marnes du Var'. Strong erosion during the evaporitic Messinian regression had led to deep erosion valleys of the rivers Var, Siagne, Argens and Roya. During the Pliocene transgression these valleys, accentuated by tectonical movements, became submarine, deep canyons that rapidly filled up with clastics. At Le Puget the base of these Pliocene deposits is yet unknown, but a thickness of 300 metres does not seem unrealistic (Irr, 1975, 1984; Irr in Demarcq & Perriaux, 1984). The microfauna belongs to the *Globorotalia margaritae* Zone = Zone N19 of Blow (1969) = Zone B of Spaak (1983), indicating an age of early Pliocene, Zanclean.

The depositional environment of the Le Puget rocks, as indicated by the sediment and its biota, may be described as an open marine setting, with 'near to normal' chloride contents. Nolf & Cappetta (1988, p. 226) analyzed the bony fish otolith assemblage of Le Puget and concluded on a water depth between 200 and 500 m. Among the numerous benthic mollusc species, however, there are several indicating shallower water and even some terrestrial gastropods (*Carychium*, *Vitrea*), which because of

their pyrite filling cannot be contamination from the Recent fauna. These phenomena point to a certain degree of slumping along the comparatively steep canyon walls. Similar Pliocene deposits from deep water are known to occur along the adjacent Ligurian coast as ‘Argille di Lugagnano’.

In June 1988 a complete set of rock samples of 1 m each was collected from the accessible section by Ronald Janssen (Senckenberg Museum, Frankfurt am Main, Germany) and the present author. Thanks to the cooperation of the local authorities Mr von Hacht subsequently succeeded in having the water level brought down by 4 m during our second visit in July 1991, which occasion was used to sample the sediments further downwards. Finally, when it became clear that further pumping out of the water could not be realized because of technical and financial problems, von Hacht had a further series of sediment samples collected below water level by means of a big shovel. The depths of this latter series of samples could only roughly be estimated. From 2001 onward (Chirly & Richard, 2008, fig. on p. 8) the claypit is completely under water level. The same authors (also on p. 8) estimated the original depth of the pit erroneously at ‘une centaine de mètres’.

These three collecting activities resulted in a complete set of samples of the excavated part of the section, vertical thickness of about 20 metres. The sediment samples were processed, mainly at Leiden, through a 0.3 mm mesh. All this work, however, turned out to be unsuccessful, as the residues yielded only very few fossils, and did not lead to any conclusion on biostratigraphy. The few pteropods from this section are in RGM, the benthic molluscs, together with most (if not all) benthic molluscs collected by H.J. von Hacht, are housed in the Senckenberg Museum.

### Systematic palaeontology

Mollusca Linnaeus, 1758  
 Gastropoda Cuvier, 1797  
 Littorinimorpha Golikov & Starobogatov, 1975  
 Pterotracheoidea Rafinesque, 1814 (= ‘Heteropoda’)  
 Atlantidae Rang, 1829  
*Atlanta* Lesueur, 1817

*Type species* – ‘*Atlanta Peronii*’ (by subsequent designation, de Blainville, 1825, p. 493) = *Atlanta peronii* Lesueur, 1817 (Recent).

#### *Atlanta plana* Richter, 1972

Pl. 1, figs 1-3; Pl. 5, figs 1-2

- \* 1972 *Atlanta plana* Richter, p. 90, figs 6, 8.
- v. 2004 *Atlanta* sp. – Janssen, p. 108, figs 2, 3.
- v. 2007 *Atlanta plana* Richter, 1972 – Janssen, p. 46, pl. 12, figs 4, 5; pl. 13, fig. 1 (with further synonymy).
- . 2011 *Atlanta plana* Richter, 1972 – Seapy, Tree of Life website, 12 figs.

*Description* – See Richter (1972) and Seapy (2011). The species is, apart from its lenticular *Atlanta*-shape, characterized by a conical protoconch of 3½ convex whorls and the 4th whorl widening rapidly. A very fine spiral ornament is present on the 2nd and 3rd protoconch whorl. In one of the larger specimens (Pl. 1, fig. 2) the body whorl separates slightly from the preceding whorl.

*Material* – RGM 776 717/1 (Pl. 5, fig. 1); RGM 776 718/8; RGM 776 719/1 (Pl. 5, fig. 2a-b); RGM 776 720/1 (Pl. 1, fig. 1a-c); RGM 776 721/65 (cf); RGM 776 722/1 (cf, Pl. 1, fig. 2a-c); RGM 776 723/1 (cf, Pl. 1, fig. 3a-c).

*Discussion* – Only in a restricted number of specimens in the available material is the actual shell preserved. Most specimens are represented as pyritic internal moulds, and are frequently deformed or otherwise damaged. However, as far as can be observed, all specimens have the same shape and the same number of protoconch whorls, which means that there is no reason to assume that more than one species is present. As no surface ornament can be seen in pyritic internal moulds those specimens are included in the collection as *Atlanta* cf. *plana*.

In the Recent fauna this species is exclusively distributed in the Indo-Pacific basin, which makes its occurrence in the present material remarkable. Still, the specimens described and illustrated as *Atlanta* sp. in Janssen (2004, p. 108, figs 2, 3) from the Piacenzian of Estepona (Spain) are also now considered to belong to *A. plana*. Those specimens are larger than the present ones and the body whorl does not detach from the foregoing. It cannot be excluded that these specimens belong to another, conchologically indistinguishable ‘cryptic’ species, but soft tissue and/or molecular testing to acknowledge this is impossible.

As a fossil this species was recorded furthermore from the Pliocene (Piacenzian) of the Philippines (Janssen, 2007) and from the late Miocene-early Pliocene of the Fiji Archipelago (Janssen & Grebneff, 2012).

#### *Oxygyrus* Benson, 1835

*Type species* – *Oxygyrus inflatus* Benson, 1835 (by monotypy) (Recent).

#### *Oxygyrus inflatus* Benson, 1835

Pl. 1, fig. 4; Pl. 5, fig. 3

- non 1817 *A[tlanta] Keraudrenii*, Lesueur, p. 391 (= *Atlanta peronii* Lesueur, 1817).
- 1827 *Atlanta Keraudrenii*. Lesueur – Rang, p. 380, pl. 9, figs 4-6, 8 (*non* Lesueur).
- \* 1835 *Oxygyrus inflatus*, Benson, p. 176.
- . 1976 *Oxygyrus keraudreni* (Lesueur, 1817) – van der Spoel, p. 137, fig. 133 (*non* Lesueur) (with extensive synonymy).
- . 2011 *Oxygyrus keraudreni* Benson 1835 [*sic*] – Seapy, Tree of Life website.
- v. 2012a *Oxygyrus inflatus* Benson, 1835 – Janssen, p. 16, figs 42E-H, 43A, B (with further synonymy).

*Description* – See Seapy (2011).

*Material* – RGM 776 724/1 (Pl. 5, fig. 3); RGM 776 725/1 (Pl. 1, fig. 4a-c), RGM 776 726/1.

*Discussion* – This is a well-known species in the Recent fauna, where it is generally referred to with the name *Oxygyrus keraudrenii* (Lesueur, 1817). See Janssen (2012a) for a discussion concerning the correct name of this species. The species is widely distributed in tropical/subtropical basins.

From the fossil record *Oxygyrus inflatus* is known from the Pliocene (Zanclean) of Tabiano Bagni (Italy, Parma), Santa Maria Island (Portugal, Azores) and from the Pliocene (Piacenzian) of Estepona (Spain), Jamaica and the Philippines (RGM collections). Furthermore the species was found in numerous late Quaternary to Holocene bottom samples.

*Protatlanta* Tesch, 1908

*Type species* – Original designation by Tesch (1908, p. 8): ‘The type of this new genus is “*Atlanta lamanoni*” of Souleyet, which name has been altered by E.A. Smith in “*Atlanta souleyeti*” as the term, used by Souleyet, had been already applied, long before, by Costa to another species’ [= *Protatlanta souleyeti* (Smith, 1888)] (Recent).

***Protatlanta rotundata* (Gabb, 1873)**

Pl. 1, figs 5-8; Pl. 5, figs 4-5; Pl. 6, figs 1-2

- non 1867 *Atlanta rotundata* [sic] d’Orb. – Reuss, p. 146 [= ‘*Allanta*’ *rotunda* d’Orbigny, 1834 = *Limacina helicina* (Phipps, 1774) forma *rangii* (d’Orbigny, 1834)].
- \* v 1873a *Atlanta rotundata* Gabb, p. 201.
- v. 1922 *Atlanta rotundata* Gabb – Pilsbry, p. 314, fig. 15.
- v. 1928 *Atlanta (Atlantidea) lissa* Woodring, p. 134, pl. 2, figs 26-27.
- v 1979 *Protatlanta* sp. – D’Alessandro *et al.*, p. 78, pl. 15, fig. 4.
- . 1984 *Protatlanta kakegawaensis* Shibata, p. 75, pl. 23, figs 1-3.
- v. 1998 *Protatlanta lissa* (Woodring, 1928) – Janssen, p. 98, pl. 1, figs 4-5.
- v. 1999a *Protatlanta rotundata* (Gabb, 1873) – Janssen, p. 12, pl. 2, figs 3-4.
- v. 1999b *Protatlanta rotundata* (Gabb, 1873) – Janssen, fig. 1a-c.
- v. 2004 *Protatlanta rotundata* (Gabb, 1873) – Janssen, p. 107, pl. 2, fig. 2a-b.
- v. 2007 *Protatlanta rotundata* (Gabb, 1873) – Janssen, p. 53, pl. 1, fig. 1; pl. 17, figs 1-3.
- . 2008 *Protatlanta kakegawaensis* Shibata, 1984 – Shibata & Ujihara, p. 3, figs 3/3-4.
- v? 2010 *Protatlanta rotundata* (Gabb, 1873) – Janssen & Little, p. 1114, pl. 5, figs 2, 3.
- v. 2012b *Protatlanta rotundata* (Gabb, 1873) – Janssen, p. 277, pl. 21, figs 8-10.

*Description* – See Janssen (1999a). Several specimens from Le Puget are in aragonitic preservation and demonstrate clearly the spiral ornament of the early whorls (Pl. 5, fig. 4a). In some other specimens, also in perfect shell preservation, this ornament, however, is reduced to even virtually absent (Pl. 6, fig. 1a-b). The shape of the early whorls, as well of larger specimens, agrees completely with *Protatlanta rotundata*. The greater part of the material, as usual, is in internal pyrite preservation, which makes the identification difficult, for which reason these objects are indicated as *P. cf. rotundata* in the collection.

*Material* – RGM 776 727-728/2 (Pl. 5, figs 4a-b, 5a-b); RM 776 729/1 (Pl. 1, fig. 6a-d); RGM 776 730/15; RGM 776 727/1 (Pl. 5, fig. 4a-b); RGM 776 728/1 (Pl. 1, fig. 6; Pl. 5, fig. 5a-b); RGM 776 729/1 (Pl. 1, fig. 5; Pl. 6, fig. 2); RGM 776 731/1 (Pl. 1, fig. 8); RGM 776 732/13 (cf.); RGM 776 733/1 (Pl. 1, fig. 7; Pl. 6, fig. 1a-b).

*Discussion* – *Protatlanta rotundata* is recorded from the ‘late Miocene’ of the Dominican Republic (Gabb, 1873a; Janssen, 1999a), from the Langhian and Serravallian of the Maltese archipelago (Janssen, 2012b), from the Langhian of Gargano, Italy, D’Alessandro *et al.*, 1979; as *Protatlanta* sp.), from the Tortonian of Sicily (Janssen, 1999b), from the Pliocene (Piacenzian) of Bowden, Jamaica (Janssen, 1998), Spain (Janssen, 2004) and the Philippines (Janssen, 2007), and from the Plio/Pleistocene of Japan (Shibata, 1984; Shibata & Ujihara, 2008, as *P. kakegawaensis*). From the Miocene (Langhian) of Cyprus Janssen & Little (2010) recorded a number of specimens as *P. rotundata*, which, however, are too poorly preserved (not showing their initial whorls) to be certain of their identification

***Protatlanta* sp.**

Pl. 2, figs 1-3

*Description* – A number of juvenile specimens have the general shape of *Protatlanta rotundata*, but differ in the shape of the protoconch whorls, together forming a regularly elevated cone much higher than in *P. rotundata*, with whorls separated by a distinct suture. In one of the larger, but still juvenile specimens a remnant of spiral ornament is visible on the terminal protoconch whorl. Earlier whorls seem to be smooth.

*Material* – RGM 776 734/6; RGM 776 735a-b/2 (Pl. 2, figs 1, 2a-c); RGM 776 735c/1 (Pl. 2, fig. 3).

*Discussion* – The specimens show a striking resemblance to a species described from the Langhian of Malta and Italy, *Proatlanta kbiraensis* Janssen, 2012b (p. 275, pl. 1, figs 4, 5; pl. 21, figs 11-13) and might indeed represent the same species. Considering the restricted number of well-preserved specimens and their juvenile state, as well as the clear difference in age I prefer to record them in open nomenclature until more adult specimens might confirm their identity.

Carinariidae de Blainville, 1818  
*Carinaria* Lamarck, 1801

*Type species* – *Carinaria vitrea* auct. non Gmelin, 1791 [= *Carinaria cristata* (Linné, 1767)] (by monotypy) (Recent).

***Carinaria lamarckii* de Blainville, 1817**

Pl. 2, fig. 4; Pl. 6, figs 3, 4

- 1810 Carinaire Lamarck – Péron & Lesueur, p. 69, pl. 2, fig. 15.
- \* 1817 La Carinaire de Lamarck, *C. Lamarkii* [sic] Péron et Lesueur; de Blainville, p. 107.
- 1824 Carinaire de la Méditerranée, *Carinaria mediterranea* de Blainville, p. 283.
- 2011 *Carinaria lamarcki* Péron and Lesueur 1810 – Seapy, Tree of Life website, 9 figs.
- v. 2012a *Carinaria lamarckii* de Blainville, 1817 – Janssen, p. 22, fig. 45A-G (with further synonymy)
- v. 2012 *Carinaria lamarckii* de Blainville, 1817 – Janssen & Grebneff, p. 19, fig. 5.

*Description* – See Seapy (2011, several SEM images) and Janssen (2012a, fig. 45A-G). Exclusively larval shells are present. These are easily recognized by their wider than high shell shape in which the largest diameter is situated above the horizontal midline. Such protoconchs seem to be entirely unornamented, apart from a very narrow spiral against the upper sutures, when seen in normal light microscopy. In SEM imaging, however, two faint spirals appear to be present on the upper two whorls. The base of these small shells is narrowly umbilicate, sometimes with a number of radial crests (Pl. 6, fig. 4) around it.

*Material* – Only protoconchs: RGM 776 736a-b/2 (Pl. 6, figs 3, 4); RGM 776 737/35; RGM 776 738/35; RGM 776 739/1 (Pl. 2, fig. 4a-d).

*Discussion* – In spite of the relatively abundant occurrence of juvenile specimens not a single specimen or fragment of the adult shell was found (or recognized). The available material closely resembles late Pleistocene to Holocene specimens sometimes commonly present in Mediterranean bottom samples as specified in Janssen (2012a).

Thecosomata de Blainville, 1824  
 Limacinoidea J.E. Gray, 1847  
 Limacinidae J.E. Gray, 1847  
*Heliconoides* d’Orbigny, 1835

*Type species* – *Atlanta inflata* d’Orb. (by subsequent designation, Hermannsen, 1846, p. 514) = *Heliconoides inflata* (d’Orbigny, 1834) (Recent).

***Heliconoides inflata* (d’Orbigny, 1834)**

Fig. 8a-c; Pl. 2, fig. 5; Pl. 6, fig. 5

- \* 1834 *A[llanta] [sic] inflata* d’Orbigny, pl. 12, figs 16-19.
- 1835 *Atlanta (Heliconoides) inflata* d’Orbigny, p. 174.
- 1967 *Limacina (Thilea) inflata* (Orbigny) – van der Spoel, p. 50, figs 17, 18 (with extensive synonymy of Recent occurrences).
- v. 1990 *Limacina inflata* (d’Orbigny) – Janssen, p. 14, pl. 2, figs 5-7, pl. 3, fig. 11, pl. 10, fig. 2.
- v. 1999a *Limacina (Heliconoides) inflata* (d’Orbigny) – Janssen, p. 14, pl. 2, figs 10, 11.
- v. 2004 *Heliconoides inflata* (d’Orbigny) – Janssen, p. 110, pl. 1, figs 1-6.
- v. 2012a *Heliconoides inflata* (d’Orbigny, 1834) – Janssen, p. 25, fig. 46A, B (with further synonymy).

*Description* – See van der Spoel (1967) and Janssen (2004). Specimens from Le Puget are all juvenile. As far as can be decided all of them belong to the form A, as described in Janssen (2004). The subperipheral belt on the body whorl is externally visible in several specimens by a difference in colour or transparency of the shell wall and in a single specimen (Pl. 2, fig. 5) with an incompletely filled aperture on the inner shell wall.

*Material* – RGM 776 740/228; RGM 776 741/1 (Figure 8a-c); RGM 776 742/1 (Pl. 2, fig. 5); RGM 776 743/1 (Pl. 6, fig. 5).

*Discussion* – In the Le Puget assemblage, although not at all rare, this species is far less abundant than the, at first glance very similar, *Striolimacina imitans*. Specimens with shell preserved can be recognized rather easily, but pyritic internal moulds are more difficult to identify with certainty, especially when not fully grown. See *S. imitans* below and Fig. 8 for the differences. Presumably more specimens of this species are present in a rather large sample of unidentifiable Limacinidae.

***Heliconoides vonhachti* sp. nov.**

Pl. 3, figs 1-4; Pl. 7, fig. 1

*Holotype* – RGM 776 744 (Pl. 3, fig. 1a-c; Pl. 7, fig. 1).

*Type locality* – Le Puget-sur-Argens, Les Escaravatières, Costamagna clay pit (France, Var). See introduction for details.

*Stratum typicum* – ‘Poudingues et Marnes du Var’ (Pliocene, Zanclean).

*Etymology* – The new species is named after the late Hans Joachim von Hacht, who accumulated all of the Le Puget material covered by the present paper.

*Paratypes* – From the type locality: RGM 776 745/200; RGM 766 747/10; RGM 776 748/1 (Pl. 1, fig. 2a-b); RGM 776 749/1 (Pl. 3, fig. 3a-c); RGM 776 750/1 (Pl. 3, fig. 4a-d). Twenty specimens in the Senckenberg Museum, Frankfurt am Main (Germany) (SMF 339725/20). Bra (Italy, Piemonte, Cuneo), Monte Capriolo, abandoned claypit near railway; bluish grey marl from basal

part of exposed section (Pliocene, late Zanclean); RGM 396 120/40 specimens (mainly juveniles), leg. A.W. Janssen, 14 May 1994.

Quattro Castella (Italy, Reggio Emilia), Monticelli, active claypit, grey clay, pyritic level, *c.* 6 m above base of section (Pliocene, late Zanclean); RGM 541 226/65 (juveniles); leg/don. L. Bertolaso, January 1990; RGM 541 241/*c.* 95 specimens (mainly juveniles); leg. A.W. Janssen, 21 September 1993.

Isola d'Asti (Italy, Piemonte, Asti), abandoned claypit, Argille Azzurre Formation (ex Argille di Lugagnano) (Pliocene, Zanclean); RGM 541 272/1 specimen; leg. A.W. Janssen, 16 May 1994.

*Additional material* – From the type locality: RGM 776 746/> 1000 juveniles.

Quattro Castella (data as above); RGM 429 656/150 specimens (severely damaged in silicone oil); leg. A.W. Janssen, 21 September 1993. Many specimens in L. Bertolaso collection (Correggio, Italy) (seen 2007).

San Nicomede, between Salsomaggiore and Fidenza (Italy, Parma), outcrop in streambed of Torrente Stirone; grey clays (Pliocene, Zanclean/Piacenzian), 1 specimen, B.G. Roest collection (Silvolde, The Netherlands) nr 22227P, leg. 19 October 1992 (seen 1997).

Castell'Arquato (Italy, Piacenza), Argille di Lugagnano (Pliocene, Zanclean), 1 adult and 2 juvenile specimens, B.G. Roest collection (Silvolde, The Netherlands) nr 18541F, leg. 4 August 1988 (seen 1997).

*Diagnosis* – *Heliconoides* species of conical to slightly pupoidal shape, somewhat higher than wide, with convex tangents along rather convex whorls. Juveniles wider than high. Aperture slightly more than half shell height. There are 4½ whorls very gradually increasing in diameter, body whorl occupying 4/5th of the entire shell height. Aperture relatively small, about half shell height. Apertural reinforcement consisting of a weak, somewhat sigmoid fold preceding the actual apertural margin.

*Description* – Small sinistral shell (holotype H = 1.02 mm, W = 0.92 mm) of *c.* 4½ whorls, very slowly and gradually increasing in width (apical view, Pl. 3, fig. 1a). General shell form conical but tangents along the whorls slightly convex, giving the shell a somewhat pupoidal shape. The whorls are convex, separated by incised sutures. The body whorl is large, occupying *c.* 4/5th of the entire shell height. As usual in limacinids the protoconch is not separated: the nucleus has a diameter of *c.* 0.1 mm. The aperture is relatively small, half as high as the shell height or very slightly more. Apertural reinforcement consists of a rather weak, somewhat sigmoid fold running vertically just preceding the apertural margin, only developed in few specimens. The base of the shell is gradually rounded and has a narrow umbilicus that is clearly wider in juvenile specimens that also appear slightly wider than high (Pl. 3, fig. 4a-d).

*Discussion* – For a long time I have been considering that these limacinids possibly represent *Spirialis globulosa* Seguenza, 1867. Janssen (2012a, p. 30) discussed

this matter and concluded that the status of that taxon still is enigmatic (see also Janssen, 1995, p. 28) and that the discovery of supposed syntypic specimens of *S. globulosa* in the collections of the Museo di Geologia e Paleontologia dell'Università, Florence (Italy) by Bertolaso & Palazzi (2000, p. 22, figs 176-177) has not yet solved its true systematic position. Of 28 supposed syntypic specimens, ranging in size from 0.6 to 2.2 mm, these authors illustrated a relatively small specimen (height 0.9 mm) that is clearly higher than wide. The original illustration in Seguenza (1876, fig. 12), on the contrary, shows a specimen that is wider than high, but the dimensions given ('*Lunghezza 1,<sup>mm</sup>3, Larghezza 1,<sup>mm</sup>2*') are again contradictory to the illustration. The specimens in the Florence collection are labeled '*Spirialis globosus* Seg.' (instead of *globulosa*), which Bertolaso & Palazzi (2000) considered '*evidentemente per lapsus*'. Also the indication of the locality ('*Astiano presso Messina*') does not give the original localities mentioned in Seguenza (1867) as '*Pagliarino (nel calcare)*'; Rometta, S. Filippo, Trapani (*nelle marne*)'.

These inconsistencies make me strongly reluctant to accept these specimens as syntypes of *S. globulosa* and I cannot acknowledge Bertolaso & Palazzi's suggestion that the taxon might be included in the range of variability of *Limacina retroversa* (Fleming, 1823). It would be necessary to see the sample myself, but a request for a loan to the Florence museum was not granted. I still consider the name *S. globulosa* a *nomen dubium*.

The present new species differs from *Limacina retroversa*, only known from the Quaternary and Recent, by its smaller size, the convex tangents along the whorls and by the presence of apertural reinforcements in fully grown specimens.

*Limacina* Bosc, 1817

*Type species* – *Clio helicina* Phipps, 1774 (by monotypy) = *Limacina helicina* (Phipps, 1774), (Recent).

### ***Limacina atlanta* (Mörch, 1874)**

Figs 3-6; Pl. 2, figs 6, 7; Pl. 7, figs 2, 3

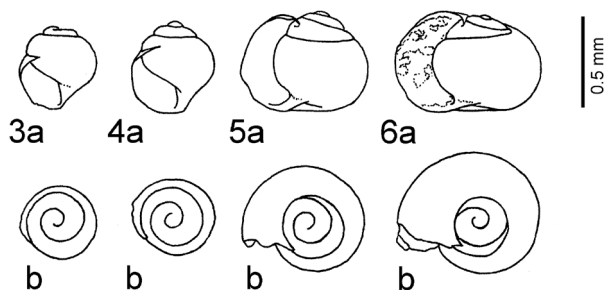
- 1842 ... a very minute sinistral shell... – Wood, p. 462, pl. 5, fig. 12.
- \* 1874 *Valvatina atlanta* Mörch, p. 286, 298.
- 1882 *Spirialis atlanta* Mörch sp. – Von Koenen, p. 359 (*partim*, specimens from Sylt only, *non* pl. 7, fig. 16a-d = *Limacina ingradae* Janssen, 1989).
- . 1907 *Valvatina atlanta* Mörch – Ravn, p. 248, 249, 369 [*partim*, specimens from 'Sild' only, *non* pl. 8, fig. 16a-c = *Heliconoides inflata* f. *mirostralis* (Kautsky, 1925)].
- v. 1956 *Spiratella atlanta* (Mörch, 1874) – Rasmussen, p. 105, 109, 117, 151 (*partim*, only the specimens from Gram and Morsum Kliff; *non* pl. 10, fig. 7a-c = *Limacina wilhelminae* Janssen, 1989).
- non* 1964 *Spiratella atlanta* (Mörch, 1874) – Anderson, p. 337, pl. 52, fig. 305a, b [= *Limacina valvatina* (Reuss, 1867)].



- v. 1964 *Spiratella* sp. (? nov.) – van Regteren Altena, Bloklander & Pouderoyen, p. 7, pl. 22, fig. 212 (age incorrectly indicated as early Pleistocene).
- v. 1968 *Spiratella atlanta* (Mörch 1874) – Rasmussen, p. 243, pl. 27, figs 8-10 (*partim*, includes various other *Limacina* species).
- v. 1969 *Limacina* C – Boekschoten, p. 44, 45, pl. 3, fig. 5a-b.
- v. 1988 *Limacina atlanta* – Janssen & King, p. 366.
- . 1998 *Limacina atlanta* (Mörch, 1874) – Marquet, p. 223, 2 figs.
- v. 1989 *Limacina atlanta* (Mörch) – Janssen, p. 121, pl. 6, figs 3-5.
- v. 1995 *Limacina atlanta* (Mörch, 1874) – Janssen, p. 21, pl. 1, fig. 5.
- 1997 *Limacina* sp. – Zorn, p. 34, text-fig. 2b, pl. 1, fig. 1.
- v. 2001 *Limacina atlanta* (Mörch, 1874) – Janssen, p. 346, pl. 1, fig. 4a, b.
- v. 2010 *Limacina atlanta* (Mörch, 1874) – Janssen, p. 62, 2 figs.
- . 2012 *Limacina atlanta* (Mörch, 1874) – Moerdijk, p. 5, figs b1, b2).

*Description* – Shell discoidal, almost twice as wide as high in adult specimens, but higher than wide in very juvenile individuals. The two to three initial whorls form together an elevated spiral, but the subsequent whorls become more and more planorboid, for a large part enveloping the preceding whorls during growth. In this way the apical side of the adult shell becomes more or less concave, with a somewhat protruding apex in the centre, which in fully adult specimens is not visible in an apertural view.

The whorls increase gradually and regularly in diameter but coiling is irregular: in apical view the last part of the second and the first part of the third whorl are covered by the subsequent volution, resulting in an irregular spiral of the suture line. This curious feature can be studied nicely in very juvenile specimens (Figs 3-6). The ‘disappearance’ of the whorl is caused by the fact that at this stage of growth the upper junction of the apertural lip skips the preceding whorl and attaches gradually one whorl higher for about half a whorl after which the outer lip slowly retakes its position on the penultimate whorl from whereon the coiling remains regular.



**Figures 3-6.** *Limacina atlanta* (Mörch, 1874), juvenile specimens demonstrating irregular whorl development. Sylt (Schleswig-Holstein, Germany), Morsum Kliff, Mica Clay, Level GliS2, *Aporrhais* Bed (Miocene, ‘Sylvian’ = Messinian), RGM 229 251-254; a: apertural views, b: apical views.

All whorls are convex, the body whorl has a very regularly curved periphery and a gradual transition to the base of the shell. The umbilicus is wide and shallow, occupying about two fifths of the shell diameter. More than one to almost two preceding whorls are visible in the umbilicus, depending on the size of the specimen. The aperture is regularly reniform, with a gradually convex abaxial margin and a columellar side indented by the preceding whorl. In typical specimens the parts of the aperture protruding beyond the upper and lower levels of the preceding whorl are almost equally large, but occasionally (Gram Clay) the basal part is larger. If this is the case, then simultaneously the umbilicus is less superficial, but distinctly deepened. The apertural margin is simple (not widened or reinforced), and hence damaged in all available specimens.

The surface of the shells is smooth, with sometimes the growth lines faintly visible. These run slightly backward from the upper suture and gradually turn in a forward direction on the periphery and the base. They reach the umbilicus at an angle of about 80°.

*Material* – RGM 776 751/56; RGM 776 752/1 (Pl. 2, fig. 6); RGM 776 753/1 (Pl. 2, fig. 7); RGM 776 754/1 (Pl. 7, figs 3a, b); RGM 776 755/1 (Pl. 7, fig. 2).

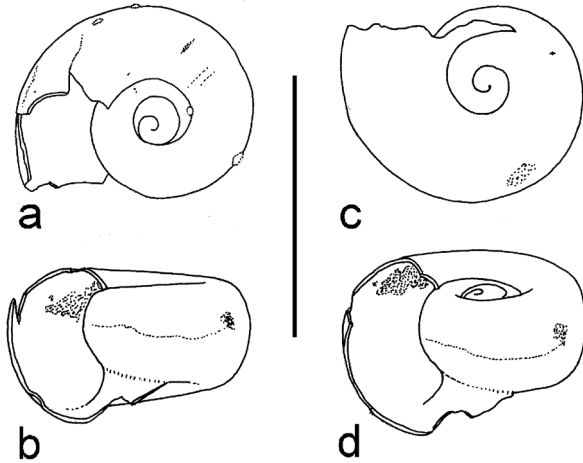
*Discussion* – *Limacina atlanta* was introduced (Mörch, 1874: 206) from ‘Sild’ (most probably the Morsum Cliff section on the island of Sylt, Schleswig-Holstein, Germany) from the so-called ‘Glimmerleret’ = Mica Clay (tmisG or tmisP, Hinsch, 1984, p. 232); Miocene, Sylvian (= Tortonian/Messinian). Ravn (1907, p. 165) reported the presence of two syntypes in the Zoological Museum of Copenhagen, although Mörch (1874, p. 286) mentioned only one. Rasmussen (1956, p. 105) stated: ‘Mörch’s type is in the MM’ (= Mineralogical Museum, Copenhagen) where, however, I was unable to trace it. The present whereabouts of this specimen and its condition (it was almost certainly a shell filled with pyrite or an internal pyritic mould) is not known.

In the North Sea Basin *Limacina atlanta* was recorded from the Gram Clay Formation (Tortonian) in Denmark and northern Germany, from the Mica Clay (Tortonian/Messinian) of Sylt, from the Coralline Crag (Zanclean ?) in East Anglia (UK) and from the Kattendijk and Lillo formations in Belgium (Zanclean/Piacenzian). It was also collected from sediment preserved in reworked larger gastropods of Pliocene age, washed ashore or sucker-dredged in the province of Zeeland (The Netherlands) (van Regteren Altena *et al.*, 1964; Moerdijk, 2012).

From the Mediterranean area *Limacina atlanta* is known from late Miocene (Tortonian/Messinian) deposits in northern Italy and Crete (Janssen, 1995; Zorn, 1997) and from various Pliocene (Zanclean and Piacenzian) occurrences in northern Italy and Spain (Janssen, 2010; RGM collections).

*Note* – The peculiar mode of coiling of the early whorls in *Limacina atlanta*, as a result of which parts of the

second and third whorls are hiding below the subsequent whorl, is also known from a late Eocene species, namely '*Planaria nitens* Lea, 1833. Although not clear from the original publication (Lea, 1833, p. 124, pl. 4, fig. 113) a study of the holotype (Fig. 7a-d, seen April 1987) made clear that this species indeed shows a very similar irregular coiling.



**Figure 7.** Holotype of '*Planaria nitens* Lea, 1833 = *Heliconoides nitens* (Lea, 1833), from Claiborne, Alabama (USA) Gosport Sand, Bartonian (Hodgkinson *et al.*, 1992, text-fig. 1), Eocene). Collection Academy of Natural Sciences, Philadelphia ANSP 5635; a: apical, b: apertural, c: umbilical, d: oblique apertural views. Bar = 1 mm.

Also Hodgkinson *et al.* (1992, p. 22, pl. 6, figs 5-10) recorded this species and studied what remains of the holotype and likewise concluded that '... the nuclear and mature whorls are exactly like ...' specimens they illustrated from the Gosport Sand. They recorded this species (as *Skaptotion nitens*) from a number of further localities belonging to the NP16 to NP21 interval (late Lutetian to Priabonian). Their illustrated specimens show the irregular coiling clearly. Hodgkinson *et al.* synonymized this species with *Skaptotion bartonense* Curry, 1965. Curry included Lea's name in his taxon with a query and illustrated in his fig. 13a-b a paratype from Claiborne, Alabama, clearly showing the irregular coiling. However, in the holotype of *Skaptotion bartonense* Curry (1965, fig. 11a-c) the coiling is completely regular. That specimen originates from the lower Barton Clay Formation (Bed A3), whereas specimens with irregular coiling are commonly represented in higher beds at Barton (RGM collection). For that reason I do not accept the synonymy suggested by Hodgkinson *et al.* As both Eocene species are furthermore characterized by well-developed apertural reinforcements I include them in the genus *Heliconoides* and accept the presence of both *H. nitens* and *H. bartonensis* in the late Eocene of the North Sea Basin. Their detailed occurrences and ranges still have to be investigated.

***Limacina bulimoides* (d'Orbigny, 1836)**  
Pl. 2, figs 8, 9; Pl. 7, figs 4, 5

Selected synonyms:

- \* 1834 *A[llanta] [sic] bulimoides* d'Orbigny, pl. 12, figs 36-38.
- . 1836 *Atlanta (Heliconoides) bulimoides* d'Orb. – d'Orbigny, p. 179.
- . 1967 *Limacina (Munthea) bulimoides* (Orbigny, 1836) – van der Spoel, p. 53, fig. 21 (with extensive synonymy).
- . 1977 *Limacina bulimoides* (d'Orbigny) – Bé & Gilmer, p. 764, pl. 3, fig. 4a-d.
- . 1983 *Limacina bulimoides* (d'Orbigny) – Shibata & Ujihara, p. 158, pl. 43, figs 3, 4.
- v. 1998 *Limacina bulimoides* (d'Orbigny) – Janssen, p. 99, pl. 1, figs 6-8.
- v. 2007a *Limacina bulimoides* (d'Orbigny, 1836) – Janssen, p. 151, pl. 15, figs 3-5.
- v. 2007b *Limacina bulimoides* (d'Orbigny, 1836) – Janssen, p. 62, pl. 1, figs 8, 9, pl. 22, figs 2, 3.
- v. 2010 *Limacina bulimoides* (d'Orbigny, 1834) – Cahuzac & Janssen, p. 43, pl. 3, fig. 5; pl. 10, fig. 4-5
- v. 2012a *Limacina bulimoides* (d'Orbigny, 1834) – Janssen, p. 27, figs 8A-E, 46C-F.

*Description* – See van der Spoel (1967), Bé & Gilmer (1977).

*Material* – RGM 776 756/16; RGM 776 757-758/2 (Pl. 7, figs 4, 5a-b); RGM 776 759/1 (Pl. 2, fig. 8a-c); RGM 776 760/1 (Pl. 2, fig. 9a-c).

*Discussion* – *Limacina bulimoides* is widely distributed in the late Quaternary and Recent fauna of tropical and subtropical basins. Pliocene (Zanclean, Piacenzian) specimens from the Caribbean, the Mediterranean and the Philippines agree more closely with the Recent form than the Miocene (Burdigalian) specimens from France, recorded by Cahuzac & Janssen (2010). The Le Puget specimens have a similar microornament on their early whorls as in Quaternary and Recent specimens (Pl. 7, fig. 5b).

*Striolimacina* Janssen, 1999a (= *Planorbella* Gabb, 1873a non Haldemann, 1843 (Mollusca).

*Type species* – *Limacina imitans* (Gabb, 1873a) (by original designation) (late Miocene).

***Striolimacina imitans* (Gabb, 1873)**

Figs 8a-d, 9d-e; Pl. 2, figs 10-12; Pl. 8, fig. 1

- \*v 1873a *Planorbella imitans* Gabb, p. 201.
- . 1873b *Planorbella imitans* – Gabb, p. 270, pl. 11, fig. 2.
- v 1922 *Limacina inflata* (Orbigny) – Pilsbry, p. 308, text-fig. 1 (non d'Orbigny).
- v 1934 *Limacina elevata* Collins, p. 181, pl. 7, figs 9-11.
- v 1934 *Limacina inflata* (d'Orbigny) – Collins, p. 179, pl. 7, figs 6-8 (partim, non d'Orbigny, non pl. 7, figs 3-5 = *Heliconoides inflata?*).
- . 1970 *Spiratella inflata elevata* (Collins) – Woodring, p. 320, 324, 427, pl. 66, figs 5, 7, 9.

- v 1974 *Spiratella inflata elevata* (Collins) – Perrilliat, p. 34.
- v 1990 *Planorbella imitans* Gabb, 1873 – Janssen, p. 16.
- v 1999a *Limacina (Striolimacina) imitans* (Gabb, 1873) – Janssen, p. 13, pl. 1, fig. la-f; pl. 2, figs 6-9 (with further synonymy).

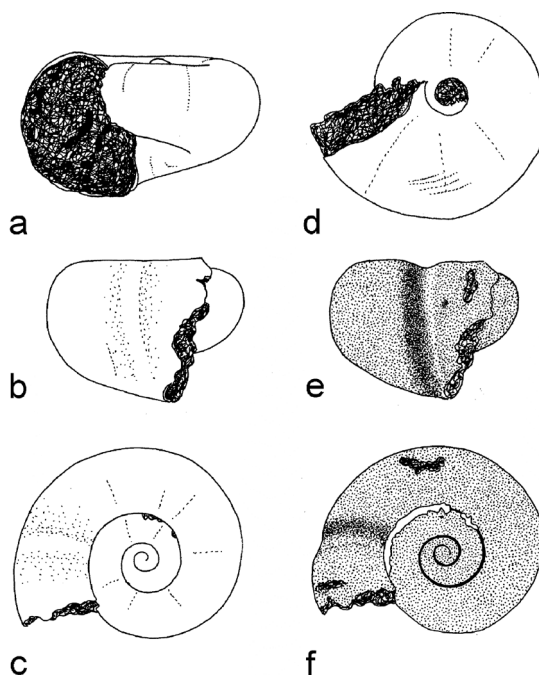
*Description* – See Collins (1934) and Janssen (1999a).

*Material* – RGM 776 761/c. 350; RGM 776 762/1 (Pl. 8, fig. 1); RGM 776 763/1 (Pl. 2, fig. 10); RGM 776 764/1 (Pl. 2, fig. 11a-e); RGM 776 765/1 (Pl. 2, fig. 12a-e); RGM 776 766/1 (Figure 9d-f); RGM 766 767/1 (Fig. 8a-f).

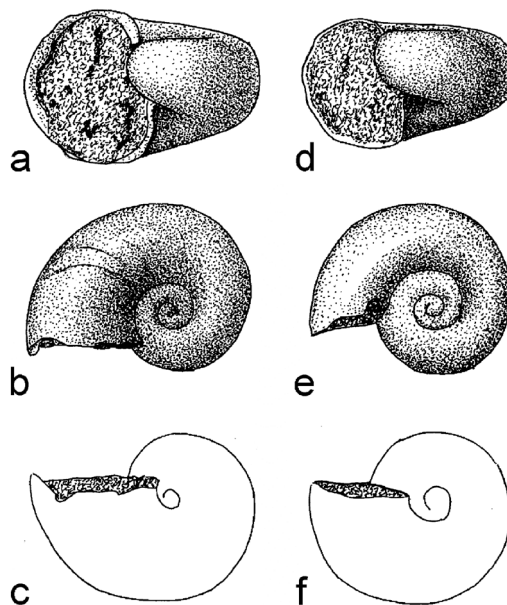
*Discussion* – This species was for a very long time interpreted as a junior synonym of *Heliconoides inflata* (see Janssen, 1990, p. 16). After publication of that paper I had the opportunity to study the remaining type material of ‘*Planorbella imitans*’ and there appear to be very clear differences. This species was introduced from the late Miocene of Santo Domingo. For further details, inclusive of the designation of a lectotype, the reader is referred to Janssen (1999a). In that paper *Striolimacina* was introduced as a taxon of subgeneric level, later (Janssen, 2003, p. 168) raised to genus level.

From the study of the type material it is clear that especially the peculiar microornament (visible at a magnification of c. 50 x) in adult and near-adult specimens of *Striolimacina imitans* distinguishes both taxa. In *Heliconoides inflata* the shell’s surface is smooth, apart from growth lines, whereas in *S. imitans* the shell is furnished with superficially incised grooves, horizontal on the periphery but diverging backwards above and below it (schematically indicated in Pl. 2, figs 11 and 12). In juvenile specimens this microornament is not yet developed. The abundant specimens from Le Puget confirmed a further difference, namely the presence of an internal apertural reinforcement. Although in the Le Puget specimens a study of the apertural reinforcements is difficult as all specimens in shell preservation are filled with pyrite, in some of the largest specimens an internal radial thickening close to the apertural margin seems to be present (Fig. 8b, c). This thickening, however, is not visible externally, except by a different colour or transparency of the aragonite. I decided to test this by drawing a specimen in shell preservation (Fig. 8a-d). After finishing those drawings the aragonite shell wall of the specimen was removed with hydrochloric acid, revealing the clean pyritic and undisturbed internal mould (Fig. 8e, f). As is obvious from these drawings an internal radial riblet, not just a fold, and only very vaguely visible from outside, indeed is convincingly present in this species, just behind the actual apertural margin.

Further, but less obvious characteristics distinguishing these two species are a somewhat tighter apical spiral with the whorls more rapidly increasing in diameter in *Heliconoides inflata* and therefore also a narrower umbilicus and a relatively higher value for the H/W-ratio, a higher position of the upper apertural margin and a clearly more concave apical plane (compare Fig. 9a-c and d-e).



**Figure 8.** Full grown specimen of *Striolimacina imitans* (Gabb, 1873a) before (a-d) and after (e, f) removal of the shell in HCl, revealing the presence of a distinct internal preapertural riblet on the pyritic mould. Le Puget-sur-Argens (RGM 776 767). Bar is 1 mm.



**Figure 9.** Proportional differences of *Heliconoides inflata* (d’Orbigny, 1834) (a-c; RGM 776 741) and *Striolimacina imitans* (Gabb, 1873a) (d-f; RGM 776 766). Not completely full grown specimens from Le Puget-sur-Argens. Bar = 1 mm.

*Striolimacina* species are more closely related to *Heliconoides* than to *Limacina*, indicated by the presence of apertural reinforcements in adult specimens. A second species, *Striolimacina andaensis* Janssen, 2007a, differ-

ing by a slightly conical spire and an externally visible apertural rim was described from the Pliocene (Piacenzian) of Pangasinan, Philippines and from the late Miocene/early Pliocene of the Fiji archipelago (Janssen & Grebneff, 2012).

*Incertae familiae*

**Limacinidae? sp.**

Pl. 3, fig. 5

*Description* – A single pyritic internal mould of a very small (H = 0.80 mm, W = 1.20 mm), sinistral gastropod is available. Its initial whorl with the nucleus is missing, almost 1½ subsequent rapidly widening whorls are strongly carinated in their upper part. Above this carina a wide concave zone is formed against the upper suture. Below the carina the body whorl is gradually convex and rounded, the base of the shell is widely umbilicated. The aperture is very large, apparently wider than high, occupying almost the entire shell height, but its lower margin is damaged.

*Material* – RGM 776 769/1 (Pl. 3, fig. 5a-c).

*Discussion* – This is a really remarkable specimen, unlike any other pteropod species. Similarly carinated limacinids are very rare and in fact only known from the late Rupelian *Limacina acutimarginata* Korobkov, 1966, which is related to and most probably a successor species of the uncarinated *Limacina umbilicata* (Bornemann, 1855), very different in shape from the present specimen. Similar forms of Pliocene age have not yet been reported.

Cavolinioidea J.E. Gray, 1850

Creseidae Rampal, 1973

*Bowdenathea* Collins, 1934

*Type species* – *Bowdenathea jamaicensis* Collins, 1934 (by monotypy) (Pliocene).

***Bowdenathea jamaicensis* Collins, 1934**

Pl. 3, figs 6, 7

- \* 1934 *Bowdenathea jamaicensis* Collins, p. 221, pl. 13, figs 13-15.
- . 1959 *Bowdenathea jamaicensis* R.L. Collins – Zilch, p. 51, fig. 171.
- 1980 *Bowdenathea jamaicensis* Collins – Shibata, p. 64.
- 1982 *Bowdenathea jamaicensis* (Collins) [sic] – Lozouet & Maestraeti, p. 184.
- 1982 *Bowdenathea jamaicensis* Collins – Bernasconi & Robba, p. 218.
- 1983 *Bowdenathea jamaicensis* Collins – Shibata, p. 80.
- v. 1995 Creseinae sp. ? nov. – Janssen, p. 30, pl. 2, fig. 3a-d.

- ? 1996 *Bowdenathea?* sp. – Ujihara, p. 780, fig. 5/43-49.
- . 1997 *Bowdenathea jamaicensis* Collins, 1934 – Zorn, p. 35, pl. 4, fig. 1-4.
- v. 1998 *Bowdenathea jamaicensis* Collins – Janssen, p. 100, pl. 1, figs 14-15.
- v. 2008 *Bowdenathea jamaicensis* Collins, 1934 – Janssen *et al.*, p. 360, pl. 1, figs 7a-c, 8a-d.

*Description* – Creseid species of conical shape with initially a circular transverse section, but especially adaperturally a slight dorso-ventral flattening. Protoconch and initial teleoconch shed and still unknown, opening closed with a septum. In some specimens, also in the holotype illustrated by Collins (1934), the shell widens more or less abruptly a short distance after the septum. Lengthwise the shell is slightly curved (ventrally convex, dorsally straight or somewhat concave). Growth lines are curved adaperturally on the dorsal side, almost straight on the ventral, meeting laterally in a v-shape, sometimes accentuated by a very faint angularity, not a real carina. Dorsal apertural margin higher than the ventral one.

*Material* – RGM 776 772/1; RGM 776 773a-b/2 (Pl. 3, figs 6a-d, 7a-d).

*Discussion* – In the Le Puget material this species strongly resembles the abundant compressed specimens of *Creseis spina* (see below). Absence of lateral cracks in the shell and presence of a septum enabled a certain identification of three specimens, each of them representing early shell parts retaining the septum, but not yet showing the dorso-ventral flattening.

Specimens from the Messinian of Crete, illustrated by Zorn (1997, pl. 4, figs 1-4) are poorly preserved as moulds in matrix, but seem to have retained the protoconch. Still, growth lines visible in at least one of the illustrated specimens (pl. 4, fig. 2) are clearly curved adaperturally, strongly recalling the present species.

*Creseis* Rang, 1828

*Type species* – Janssen (2012a) stated that it is not clear who was the first to designate a type species for the genus *Creseis*. In the meantime, however, Philippe Bouchet (pers. comm.) discovered a type designation of ‘*Creseis acicula*, Rang’ by Pelseneer (1888, p. 45), who based himself on Fol (1875, pp. 177-178), who mentioned the same taxon as an example of *Creseis*, but did not explicitly refer to it as the type species. Therefore I accept ‘*Creseis acicula*’ = *Creseis clava* (Rang, 1828) as type species of *Creseis*, as subsequently designated by Pelseneer (1888).

***Creseis clava* (Rang, 1828)**

Pl. 3, figs 8-10

Selected synonyms:

- \* v 1828 *C[leodora (Creseis)] clava* Rang, p. 317, pl. 17, fig. 5.

- v. 1828 *C[leodora (Creseis)] acicula* Rang, p. 318, pl. 17, fig. 6.
- 1829 *Creseis acus* Eschscholtz, p. 17, pl. 15, fig. 2.
- 1834 *Hyalæa aciculata [sic]* – d’Orbigny, p. 123, pl. 8, figs 29-31.
- . 1967 *Creseis acicula* (Rang, 1828) forma *acicula* (Rang, 1828) – van der Spoel, p. 58, figs 22-27, 30 (with many earlier synonyms).
- . 1967 *Creseis acicula* (Rang, 1828) forma *clava* (Rang, 1828) – van der Spoel, p. 59, figs 28, 29 (with earlier synonyms).
- . 1976 *Creseis acicula* forma *acicula* Rang – van der Spoel, p. 189 (with lectotype designation).
- v. 1976 *Creseis acicula* forma *clava* Rang – van der Spoel, p. 189 (with lectotype designation).
- . 1977 *Creseis acicula* (Rang) – Bé & Gilmer, p. 777, 20, pl. 5, fig. 11a, b.
- v. 2007b *Creseis clava* (Rang, 1828) – Janssen, p. 68, text-fig. 7b-d; pl. 2, figs 9, 10; pl. 23, figs 7, 8.
- v. 2012a *Creseis clava* (Rang, 1828) – Janssen, p. 32, fig. 12 (with further synonymy).
- 5, figs 1-6, 13-18, 21; pl. 12, fig. 2 (with further Paratethys references).
- . 1992 *Creseis hastata* (Meyer) – Hodgkinson *et al.*, p. 27, pl. 9, figs 1-3 (with further New World synonymy).
- v. 1993 *Creseis spina* (Reuss, 1867) – Janssen & Zorn, p. 190, pl. 6, figs 5-7; pl. 7, figs 2-4.
- . 1995 *Creseis spina* (Reuss, 1867) – Nikolov, p. 72, fig. 3-5.
- v. 2010 *Creseis spina* (Reuss, 1867) – Janssen, in Cahuzac & Janssen, p. 59, pl. 14, figs 7-9, 13, 14; pl. 15, figs 1-16.
- v. 2012b *Creseis spina* (Reuss, 1867) – Janssen, p. 312, fig. 42b; pl. 4, fig. 16; pl. 23, figs 4-9.

*Description* – See Bé & Gilmer (1977), Janssen (2007b).

*Material* – RGM 776 770/22 fragments; RGM 776 771a-c/3 (Pl. 3, figs 8-10).

*Discussion* – Among the available material from Le Puget unfortunately not one specimen has retained its protoconch. These were apparently all lost through the 0.5 mm sieving mesh. Therefore one could doubt whether these specimens indeed represent pteropods, as they closely resemble, for instance, certain small scaphopods with straight, unornamented shells. The shell wall of the specimens, however, is much thinner and certainly comparable with that of Recent specimens of *Creseis clava*; also the shell demonstrates similar small but unmistakable irregularities in growth. Furthermore *C. clava* is recorded with certainty in sediments of Pliocene age in northern Italy (Quattro Castella, Reggio Emilia, and Campore near Salsomaggiore, Parma; RGM coll.). Therefore I do not hesitate to refer the present incomplete specimens to this species. The samples mentioned here represent the oldest known occurrences of *C. clava*.

### ***Creseis spina* (Reuss, 1867)**

Pl. 3, figs 11-15; Pl. 8, figs 2-6

- \*v 1867 *Cleodora (Creseis) spina* Reuss, p. 145, pl. 6, fig. 9.
- . 1886 *Styliola hastata* Meyer, p. 78, pl. 3, fig. 11.
- non 1921 *Clio (Creseis) spina* Reuss – Checchia-Rispoli, p. 8, fig. 2.2a (= *Vaginella lapugyensis* Kittl, 1886).
- v non 1979 *Creseis spina* Reuss, 1867 – D’Alessandro *et al.*, p. 84, pl. 16, figs 1-4 (= *Vaginella lapugyensis*).
- v. 1982 *Creseis hastata* (Meyer 1886) – Lozouet & Maestrati, p. 183, fig. 8.
- v. 1984 *Cleodora (Creseis) spina* Reuss, 186 – Janssen, p. 66, pl. 1, figs 1-2 (with lectotype designation).
- . 1991 *Creseis spina* (Reuss, 1867) – Zorn, p. 110, pl.

*Description* – See Zorn (1991) and Janssen (2012b). The sample from Le Puget includes numerous protoconchs, but also more adult specimens, some of which have their protoconchs preserved. Striking is the fact that most larger specimens demonstrate a faint dorso-ventral curvature (Pl. 3, fig. 12), once more acknowledging the conspecificity with the late Eocene-Oligocene *Creseis hastata*, as illustrated by Hodgkinson *et al.* (1992, pl. 9, figs 1-3). The protoconchs in the available material generally agree quite well with specimens illustrated in the literature referred to, but some are markedly more slender (Pl. 3, fig. 13; Pl. 8, fig. 6). It cannot be excluded that protoconchs of *Bowdenathea jamaicensis*, currently unknown, are also present in this sample. Protoconchs of *Creseis* species may strongly resemble those of *Styliola* but can be distinguished by the possession of a rounded tip, whereas this shell part in *Styliola* is pointed. See also the notes below under *Cuvierina astesana*.

*Material* – RGM 776 774/c. 550; RGM 776 775a-c/3 (Pl. 3, figs 12-14); RGM 776 776/1; RGM 776 777/1 (Pl. 3, fig. 15a-e); RGM 776 778-782/5 (Pl. 8, figs 2-6).

*Discussion* – The abundant presence of this species in the Le Puget assemblage is really a surprise, as Pliocene specimens of this species have not been recorded before. It makes *Creseis spina* to one of the very long-ranging pteropod species: Bartonian to Rupelian of the United States (Hodgkinson *et al.*, 1992); Rupelian to Serravalian of the Aquitaine Basin (Lozouet & Maestrati, 1982; Cahuzac & Janssen, 2010), Chattian-Langhian of Malta (Janssen, 2012b); Langhian of the Central Paratethys (Reuss, 1867; Zorn, 1991; Janssen & Zorn, 1993; Bohn-Havas & Zorn, 1994; Nikolov, 1995).

The Le Puget sample also includes adult and near-adult specimens of this species, but most of the larger specimens are compressed during diagenesis (Pl. 3, figs 11, 15) and therefore superficially resemble *Bowdenathea jamaicensis*. In the present species, however, shedding of the protoconch does not occur and therefore a septum sealing the shell is absent. The growth lines (only rarely clearly visible) do not differ in curvature on ventral and dorsal sides. The blunt lateral angularities present in *B. jamaicensis* are absent in *Creseis spina*, which has a near-circular transverse section, although the frequent dorso-ventral compression of the shell may easily cause a similar appearance.

*Styliola* Gray, 1850

*Type species* – ‘Styliole’ *recta* Blainville, 1827 (by original designation) = *Styliola subula* (Quoy & Gaimard, 1827).

***Styliola subula* (Quoy & Gaimard, 1827)**

Fig. 10; Pl. 8, figs 7, 8; Pl. 9, figs 1-3

- \* 1827 *Cleodora subula* Quoy & Gaimard, p. 233, pl. 8, figs D1-D3.
- . 1967 *Styliola subula* (Quoy & Gaimard, 1827) – van der Spoel, p. 63, figs 43-45 (with earlier synonymy of Recent occurrences).
- v. 1999a *Styliola subula* (Quoy and Gaimard, 1827) – Janssen, p. 18, text-fig. 3, pl. 3, figs 7-9 (with neotype designation).
- v. 2012b *Styliola subula* (Quoy & Gaimard, 1827) – Janssen, p. 317, pl. 5, fig. 4; pl. 23, fig. 11 (with extensive synonymy).

*Description* – Material of this species agrees completely with Recent specimens. See synonyms for descriptions.

*Material* – RGM 776 783/many (Fig. 10); RGM 776 784/many juveniles; RGM 776 785-789/5 (Pl. 8, figs 7, 8; Pl. 9, figs 1, 2a-b, 3); RGM 776 790/2 (with shell repair). Altogether *c.* 7000 specimens, which is about half

the total number of identifiable holoplanktonic gastropods from Le Puget.

*Discussion* – In the extensive available material of this species some specimens show repair after shell damage, presumably caused by predation (Pl. 9, fig. 1). Some specimens demonstrate an apparent microornament of longitudinal striation (Pl. 9, fig. 2a), but seen in SEM at larger magnification (Pl. 9, fig. 2b) this appears to be no ornament, but rather a curious type of shell surface erosion. A few specimens are slightly curved apically (Pl. 9, fig. 3).

Late Oligocene-Miocene of the North Sea, Aquitaine and the Mediterranean basins; Miocene of the central Paratethys, Australia, Indonesia *etc.*, Pliocene and younger: widespread. Nowadays this species has a large distributional area covering tropical and subtropical seas.

Cuvierinidae Gray, 1847 (as Cuvieridae)

*Cuvierina* Boas, 1886 [= *Cuvieria* Rang, 1827 *non* Lesueur & Petit (1807) *nec* Cuvier, 1817] = *Triptera auct. non* Quoy & Gaimard, 1825.

*Cuvierina s. str.*

*Type species* – *Cuvierina columnella* (Rang, 1827) (by monotypy) (Recent) (redefined by neotype designation, Janssen, 2005, p. 45, fig. 10a-c).



**Figure 10.** Small part of *Styliola subula* sample RGM 776 783 from Le Puget-sur-Argens. Grid of background is 10 mm.

***Cuvierina (Cuvierina) astesana* (Rang, 1829)**

Pl. 4, fig. 1; Pl. 9, figs 8, 9; Pl. 10, figs 1, 2

- \* 1829 *Cuvieria Astesana* Rang, p. 498, pl. 19, fig. 2a-e.
- 1855 *Triptera astesana*, Rang – Pictet, p. 319, pl. 70, fig. 19.

1859 *Cuvieria astesana*, Rang – Chenu, p. 111, fig. 477.

v. 1873 *Cuvieria astesana* Rang – Bellardi, p. 36, pl. 3, fig. 19.

? 1876 *Vaginella Calandrelli* Michtti – Ponzi, p. 946, pl. 3, fig. 7 (non Michelotti ?).

- 1876 *Cuvieria Astesana* Rang – Ponzi, p. 24, pl. 3, fig. 8.  
 1877 *Cuvieria astesana* – Depontailier, p. 782.  
 1976 *Cuvierina astesana* (Rang) – Pavia, p. 115, pl. 12, figs 14, 15.  
 1979 *Cuvierina astesana* (Rang) – Pavia & Robba, pp. 559, 561, 562, text-fig. 2, pl. 54, figs 5a-c; pl. 55, figs la-c, 2a-c.  
 1982 *Cuvierina astesana* (Rang, 1827) [*sic*] – Martinnell, p. 232, pl. 1, fig. 30.  
 1982 *Cuvierina astesana* (Rang, 1829) – Grecchi, p. 726, pl. 54, fig. 6.  
 v. 1995 *Cuvierina astesana* (Rang, 1829) – Janssen, p. 31, pl. 2, figs 4-13 (with additional synonymy).  
 v. 2004 *Cuvierina (Cuvierina) astesana* (Rang, 1829) – Janssen, p. 112, pl. 2, figs 6a-c, 7a-c.  
 v. 2006 *Cuvierina (Cuvierina) astesana* (Rang, 1829) – Janssen, p. 87ff, fig. 3a-c.  
 2008 *Cuvierina astesana* Rang, 1829 [*sic*] – Chirli & Richard, p. 84, pl. 17, fig. 3.

*Description* – See Janssen (1995, 2004, 2006).

*Material* – RGM 776 791/97 (complete specimens); RGM 776 792/c. 300 (more or less damaged specimens); RGM 776 793/12 (partly retaining larval shell); RGM 776 794/c. 200 (incomplete larval shells); RGM 776 795/c. 115 (protoconchs); RGM 776 796/1 (juvenile, with early septum, Pl. 4, fig. 1); RGM 776 797-801/5 (Pl. 9, figs 4-7); RGM 776 802-805/4 (Pl. 9, figs 8a-b, 9; Pl. 10, figs 1, 2a-b).

*Discussion* – Protoconchs of *Cuvierina astesana* have hitherto not been described. Considering the common occurrence of this species in the Le Puget assemblage their presence could be expected. However, it appeared to be quite difficult to isolate them in the extensive material of embryonic shells of *Creseis spina* and/or *Styliola subula*. A solution came from juvenile specimens shed during metamorphosis preserving the initial shell part. Some of them also show an impression of the septum, as a shallow concave cavity in their aperture that distinctly identifies them with *C. astesana*, as the septum is constructed anticipating shedding of the larval shell. Once several such specimens (Pl. 9, figs 6, 7) were found also smaller specimens without a trace of the septum could be recognized. From *Styliola* they differ markedly in having a rounded tip of the protoconch, which in *Styliola* is pointed (but only visible in well-preserved specimens). Distinguishing them from *Creseis spina* was more difficult and may not always have been successful. In the *Cuvierina astesana* larval shell a junction of protoconch-1 and -2 is less clear and the apical angle is slightly wider. In other *Cuvierina* species like the Recent *C. pacifica* Janssen, 2005 and the Miocene *C. paronai* Checchia-Rispoli, 1921 (see Janssen, 2012b, pl. 5, fig. 9) a division between protoconchs-1 and 2 is virtually absent.

Exceptionally in this species, shedding of the larval shell happens twice, as is demonstrated by a single specimen of a larval shell in which the actual protoconch is broken and replaced by an early septum (Pl. 4, fig. 1), maybe a result of premature damage to the post-embryonic shell.

Cliidae Jeffreys, 1869

*Clio* Linné, 1767

Type species – ‘*Clio pyramidata*’ (by subsequent designation, J.E. Gray, 1847, p. 203) [= *Clio (Clio) pyramidata* Linné, 1767] (Recent).

*Balantium* Children, 1823

Type species – ‘*Balantium recurvum*’ (by original designation, Children, 1823, p. 220) = *Clio (Balantium) recurva* (Children, 1823) (Recent).

***Clio (Balantium) guidottii* Simonelli, 1896?**

Pl. 4, fig. 2; Pl. 10, fig. 6

? 1896 *Clio (Clio) Guidottii* Simonelli, p. 186, fig. 1a-c.

*Description* – Only early shell parts are available consisting of a very slightly curved to almost straight conical shell of which the dorso-ventral diameter considerably exceeds the shell width (Pl. 4, fig. 2a). Blunt lateral angularities indicate the development of carinae in more fully grown specimens. The protoconch is clearly separated from the early teleoconch by a constriction. Its shape is elliptical, rather inflated, a short apical spine is present. All specimens demonstrate clear wrinkles on the sides of the early teleoconch (Pl. 4, fig. 2c) as a result of shell deformation during metamorphosis.

*Material* – RGM 776 811/12 (all juveniles or apical shell parts); RGM 776 812/1 (Pl. 4, fig. 2a-c); RGM 776 813/1 (apical shell part with protoconch, Pl. 10, fig. 6a-b).

*Discussion* – Only some protoconchs and early shell parts are available that do not agree with corresponding shell parts of either *Clio braidensis* (Bellardi, 1873) or *C. cuspidata* (Bosc, 1802) of which at least the former could be expected to occur in the Le Puget fauna. From these two species the available specimens differ by an elliptical rather than spherical shape of the protoconch. Also in the species mentioned, the dorso-ventral diameter of the early teleoconch is not so large, the lateral, much more strongly developed carinae start earlier, and their early teleoconch is more curved. After careful comparisons it was found that the specimens show a remarkable resemblance to comparable shell parts of *Clio (Balantium) recurva*, a species, however, only known from the Recent fauna. Three further species belonging to the subgenus *Balantium* have occurred during the Pliocene, two of which are only known from the Pacific (Japan). From the Mediterranean Pliocene only the species *Clio (Balantium) guidottii* was recorded (e.g. Janssen & Peijnenburg, in press, fig. 14). Of that species, some specimens of which are available in the RGM collections from the type locality (Sivizzano, Parma, Italy; Zanclean), protoconch and earliest shell parts are unfortunately as yet unknown. Therefore identification has to remain with a query.

*Clio s. str.*

***Clio (Clio) pyramidata* Linné, 1767 forma *lanceolata* (Lesueur, 1813)**

Pl. 10, figs 3-5

- \* 1813 *Hyalea lanceolata* Lesueur, p. 284, pl. 5, fig. 3A, B (*mala*).
- . 1967 *Clio pyramidata* Linnaeus, 1767 forma *lanceolata* (Lesueur, 1813) – van der Spoel, p. 68, figs 50-54, 60 (with extensive synonymy).
- . 1977 *Clio pyramidata lanceolata* – Bé & Gilmer, p. 766, pl. 7, fig. 21a-c.
- . 2008 *Clio pyramidata* Linné, 1758 [*sic*] – Chirli & Richard, p. 83, pl. 17, figs 1, 2.
- v. 2012a *Clio (Clio) pyramidata* Linné, 1767 f. *lanceolata* (Lesueur, 1813) – Janssen, p. 44, figs 16A-D, 17A-F, 49J-L (with additional synonyms).

**Description** – See van der Spoel (1967), Bé & Gilmer (1977). Characteristic juvenile and subadult specimens of this very abundant form are illustrated Pl. 10, figs 3-5. Concave profiles of the larger specimens demonstrate that they belong to the f. *lanceolata*.

**Material** – RGM 776 806/c. 1700 (mainly apical shell parts); RGM 776 807/> 1000 (protoconchs); RGM 776 808-810/3 (Pl. 10, figs 3-5).

**Discussion** – *Clio pyramidata* f. *lanceolata* occurs from the Serravallian onwards (Robba, 1977, p. 601) and is a very widespread pteropod in the Recent fauna, occurring worldwide in tropical and subtropical seas, including the Mediterranean (= type locality of forma *lanceolata*). Typical *C. pyramidata* is restricted to colder waters of the northern Atlantic and is not yet known to occur earlier than Holocene.

Cavoliniidae J.E. Gray, 1850  
*Cavolinia* Abildgaard, 1791

Type species – *Cavolinia natans* Abildgaard, 1791 (by monotypy) = *C. tridentata* (Forskål, 1775) (Recent).

***Cavolinia* sp. indet.**

Pl. 4, fig. 3; Pl. 11, figs 1, 2

**Description** – Exclusively larval specimens in pre-metamorphosis stage are found. They are triangular in dorsal and ventral views and have a very small dorso-ventral diameter. These tiny shells are strongly curved, with their dorsal side concave, the ventral convex. The apex is gradually pointed but the extreme tip is rounded. Adult specimens or even fragments were not encountered.

**Material** – RGM 776 814/70 (all juveniles); RGM 776 815/1 (Pl. 4, fig. 3a, b); RGM 776 816-817/2 (Pl. 11, figs 1a-c, 2a-b).

**Discussion** – Juvenile *Cavolinia* as found in the present material cannot (yet?) be identified to species. Their strong curvature, however, indicates that they do not belong to either *C. tridentata* or *C. grandis* (Bellardi, 1873), as in these species the protoconch is much less strongly curved. Several *Cavolinia* species are known to occur in deposits of similar age, but adult specimens are necessary for a reliable identification.

*Diacria* J.E. Gray, 1847

Type species – ‘*Hyalea trispinosa*’ (by original designation, J.E. Gray, 1847, p. 203) = *Diacria trispinosa* (de Blainville, 1821) (Recent).

***Diacria trispinosa* (de Blainville, 1821)**

Pl. 4, fig. 4; Pl. 11, figs 3, 4

- \* 1821 Hyale à trois pointes; *Hyalea trispinosa* Lesueur, de Blainville, p. 82.
- . 1967 *Diacria trispinosa* (ms. Lesueur) (Blainville, 1821) forma *trispinosa* (ms. Lesueur) (Blainville, 1821) – van der Spoel, p. 85, figs 76-78 (with extensive synonymy).
- . 1977 *Diacria trispinosa* (de Blainville) – Bé & Gilmer, p. 785, fig. 28; pl. 7, fig. 23a-d.
- v. 1995 *Diacria trispinosa* (de Blainville, 1821) – Janssen, p. 107, pl. 9, fig. 3-5 (with many additional synonyms for fossil occurrences)
- v. 2012a *Diacria trispinosa* (de Blainville, 1821) – Janssen, p. 58, fig. 50E-H.

**Description** – See van der Spoel (1967), Bé & Gilmer (1977).

**Material** – RGM 776 818/115 (protoconchs); RGM 776 819-820/2 (protoconchs, Pl. 11, figs 3a-b, 4); RGM 776 821/28 (more or less damaged adult specimens); RGM 776 822/1 (Pl. 4, fig. 4a, b); RGM 776 823/c. 310 (mainly apical shell parts).

**Discussion** – Considering the number of fragments this species was rather common in the Le Puget assemblage but more or less complete specimens are rare, all of them mutilated or internal pyritic moulds with shell remnants. Janssen (2012a, p. 59) discussed this species as follows: ‘The taxonomy of the *Diacria trispinosa*-group was repeatedly discussed during the last half century (e.g. van der Spoel, 1967; Dupont, 1979; Hilgersom & van der Spoel, 1987; Bleeker & van der Spoel, 1988; Bontes & van der Spoel, 1998; Rampal, 2002), various formae were raised to species level and new species were introduced. For a discussion of these see Janssen (2004). For the time being I am inclined to accept only two separate Recent species in the *D. trispinosa*-group, viz. *D. trispinosa* and *D. major* (Boas, 1886), whereas the validity of all other names can only be demonstrated by molecular techniques’.

*Diacria major* in fact is the only taxon distinguished from *D. trispinosa* by shell- morphological characteristics (i.e. larger size and lateral spines distinctly curved



downwards), all other currently recognized taxa are based on differences in colour patterns of the shell. The Le Puget specimens are too poorly preserved to reliably recognize differences between *D. trispinosa* and *D. major*, but the latter has not yet been recorded as a fossil.

Cymbulioidea J.E. Gray, 1840  
 Peraclidae Frontier, 1963  
*Peraclis* Forbes, 1844 (= *Peraclis* Pelseneer, 1888)

Type species: *Peraclis physoides* Forbes (1844, p. 186) (by monotypy) = *P. reticulata* (d'Orbigny, 1834) (Recent).

***Peraclis bispinosa* (Pelseneer, 1888)**

Pl. 4, figs 5, 6; Pl. 11, fig. 5

- \* 1888 *Peraclis bispinosa* Pelseneer, p. 36, pl. 1, figs 9, 10.
- 1897 *Peraclis diversa*, de Monterosato – Locard, p. 29, pl. 1, figs 4-6 (*non* Monterosato).
- 1976 *Peraclis bispinosa* Pelseneer, 1888 – van der Spoel, p. 29, fig. 10 (with further synonyms, but exclusive of those of *P. diversa*).
- 2001 *Peraclis bispinosa* Pelseneer, 1888 – Gofas *et al.*, p. 200.
- v. 2004 *Peraclis bispinosa* Pelseneer, 1888 – Janssen, pl. 4, figs 5a-b, 6, 7a-b (excl. synonyms of *P. diversa*).
- v. 2012a *Peraclis bispinosa* (Pelseneer, 1888) – Janssen, p. 62, fig. 33A-C.

*Description* – See van der Spoel (1976) and Janssen (2004). Only juvenile specimens were found at Le Puget, resembling closely *Peraclis reticulata* in shape, but easily distinguished by the presence of subsutural crests. These crests are rather fine on the early whorls but increase markedly in coarseness in apertural direction (Pl. 4, fig. 6a).

*Material* – RGM 776 824/6; RGM 776 825/1 (Pl. 4, fig. 5); RGM 776 826/1 (Pl. 4, fig. 6a-c); RGM 776 827/1 (Pl. 11, fig. 5).

*Discussion* – Pliocene specimens of this species were recorded for the first time from the Piacenzian of Estepona, Spain (Janssen, 2004). The few specimens from Le Puget now also document its occurrence during the Zanclean. It is a recognized bathypelagic species. The Le Puget specimens are all considerably smaller than the ones from Estepona.

***Peraclis elata* (Seguenza, 1875)**

Pl. 4, fig. 7

- \* 1875 *Embolus elatus* Seguenza, p. 148.
- . 1876 *Embolus elatus*, Seguenza – Seguenza, p. 47.
- . 1882 *Embolus triacanthus* Fischer, p. 49.
- . 1897 *Protomedea triacantha*: P. Fischer – Locard, p. 27, pl. 1, figs 1-3.
- . 1970 *Peraclis triacantha* (Fischer) – Colantoni *et al.*,

- p. 184, pl. 26, fig. 6a, b.
- . 1976 *Peraclis triacantha* (Fischer, 1882) – van der Spoel, p. 32, fig. 14.
- . 1986 *Peraclis triacantha* (Fischer, 1882) – Nofroni & Silesu, p. 6, fig.
- . 1988 *Peraclis reticulata* (D'Orbigny, 1836) – Grecchi & Bertolotti, p. 114, pl. 1, fig. 18 (*non* d'Orbigny).
- . 2000 *Embolus elatus* G. Seguenza – Bertolaso & Palazzi, p. 17, figs 110-112, 178, 179.
- v. 2004 *Peraclis triacantha* Fischer, 1882) – Janssen, p. 122, pl. 4, fig. 8.
- v. 2012a *Peraclis elata* (Seguenza, 1875) – Janssen, p. 65, fig. 35A-C.

*Description* – See van der Spoel (1976) or Janssen (2012a).

*Material* – RGM 776 828/4; RGM 776 829/1 (Pl. 4, fig. 7a, b).

*Discussion* – The synonymy of *Embolus elatus* and *E. triacanthus* is discussed by Bertolaso & Palazzi (2000) and Janssen (2012a). In the Le Puget fauna only a few juvenile specimens were found, not yet demonstrating the features of adult specimens such as apertural spines or the wide columellar membrane.

***Peraclis reticulata* (d'Orbigny, 1834)**

Pl. 4, fig. 8

- \* 1834 *A[llanta] reticulata* d'Orbigny, pl. 12, figs 32-35, 39.
- . 1836 *Atlanta (Heliconoides) reticulata*, d'Orb. – d'Orbigny, p. 178.
- . 1976 *Peraclis reticulata* (d'Orbigny, 1836) – van der Spoel, p. 28, fig. 9 (with extensive synonymy).
- v. 2012a *Peraclis reticulata* (d'Orbigny, 1834) – Janssen, p. 66, figs 36A-C, 53A, B (with additional synonymy).

*Description* – See van der Spoel (1976).

*Material* – RGM 776 830/66; RGM 776 831a-b/2 (Pl. 11, fig. 6); RGM 776 832/1 (Pl. 4, fig. 8a-b).

*Discussion* – The presence of a considerable number of specimens of the present species in the Le Puget assemblage is, to say the least, rather surprising, as the species has never before been observed in Pliocene rocks. Janssen (2012a) recorded specimens from Saalian, Eemian and Holocene age in a core from the eastern Mediterranean. This species, especially in juvenile state, resembles *Peraclis bispinosa* closely in shape, but is immediately recognizable by the absence of subsutural crests.

**Conclusions**

The holoplanktonic mollusc assemblage collected at Le Puget-sur-Argens yielded 23 species, five of which are Pterotracheoidea (four Atlantidae, one Carinariidae), 17

are Euthecosomata (five Limacinidae, four Creseidae, one Cuvierinidae, two Cliidae, two Cavoliniidae) and three are Pseudothecosomata (Peraclidae). Total number of identifiable specimens is almost 14,000, several thousands of specimens are too poorly preserved to identify with any degree of certainty. The assemblage belongs to Pteropod Zone 22 (Janssen, 2012b).

Among the Pterotracheoidea are two species of interest, viz. *Atlanta plana* Richter, 1972, a species that in the Recent fauna is restricted to the Indo-Pacific realm. Few specimens were also recorded from the Piacenzian of Estepona (Spain). The relatively common occurrence at Le Puget (78 specimens, partly with a query) is striking. Among the specimens of *Protatlanta rotundata* some have a very restricted spiral ornament on the protoconch whorls, never seen before. Some juvenile specimens, apparently of the same genus, differ by the shape of their initial whorls, and might be conspecific with a new species described from the Miocene of Malta (Janssen, 2012b).

Two species of the Limacinidae are worth mentioning. *Striolimacina imitans*, originally described from the late Miocene and Pliocene of the Dominican Republic and Mexico and already suspected to be present in the Mediterranean Basin by Janssen (1999a; 2012b) is commonly present (> 350 specimens). Another, even far more abundant species, *Heliconoides vonhachti* n. sp., is introduced, but is also known from other Mediterranean localities.

Most species of the Cavolinioidea are elements that could be expected in an early Pliocene assemblage, in view of their known distribution patterns, but the absence of full grown specimens of *Cavolinia* is curious. Considering the age of the deposit, dated as Zanclean by planktonic foraminifera, at least the species *C. grandis* (Bellardi, 1873) was expected to be present. Comparison with localities in northern Italy (such as Quattro Castella) makes it clear that *C. grandis* is present in the higher parts of Zanclean sediments, so it might be characteristic for late Zanclean only and has apparently a more restricted range than supposed hitherto. An early Zanclean age of the Le Puget assemblage is further suggested by the common presence of *Creseis spina*, a species hitherto only known from older rocks. Of the three species of Pseudothecosomata only *P. reticulata* is surprising, as it has not yet been recorded from early Pliocene sediments so far.

As far as known all species but one are epipelagic, only *Peraclis bispinosa* has a bathypelagic distribution. This acknowledges the palaeoecological conclusion of Nolf & Cappetta (1988) who estimated water depth at 200-500 m on the basis of bony fish otoliths.

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**Plate 1.**

1. *Atlanta plana* Richter, 1972. RGM 776 720.
- 2-3 *Atlanta* cf. *plana* Richter, 1972. RGM 776 722-723.
4. *Oxygyrus inflatus* Benson, 1835, RGM 776 725.
5. *Protatlanta rotundata* (Gabb, 1873) (specimen lost)
- 6-8. *Protatlanta rotundata* (Gabb, 1873), RGM 776 729, 776 733 and 776 731, respectively).

All specimens from Le Puget-sur-Argens; a: apertural, b: apical, c: umbilical, d: dorsal views. Bar = 1 mm.

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All specimens from Le Puget-sur-Argens; a: apertural, b: apical, c: umbilical, d: dorsal views. Bar = 1 mm.

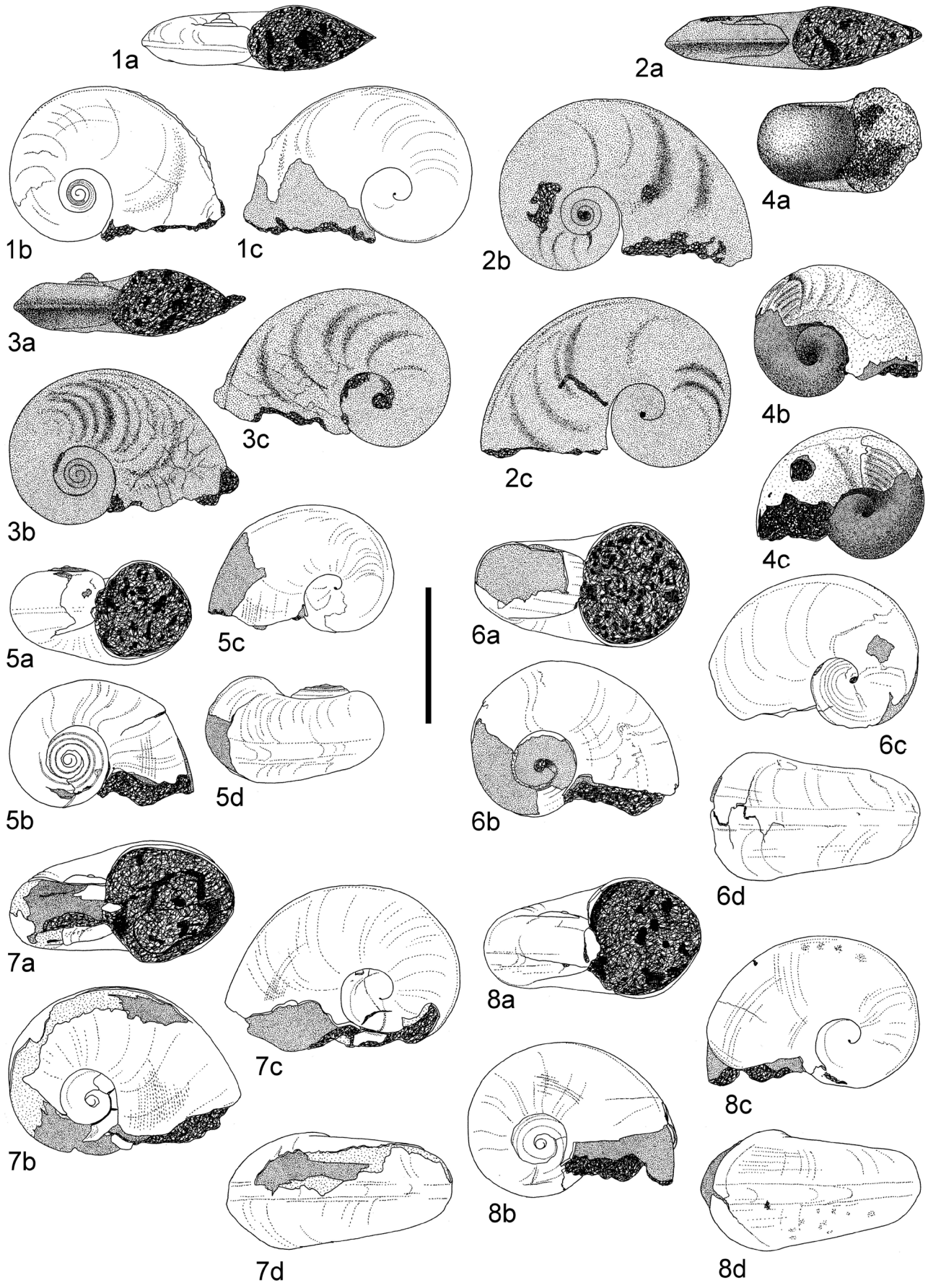


Plate 1.



**Plate 2.**

- 1-3. *Protatlanta* sp.; RGM 776 735a-c; a: apertural, b: apical, c: umbilical views.
4. *Carinaria lamarckii* de Blainville, 1817, protoconch; RGM 776 739; a: apertural, b: umbilical, c: lateral, d: apical views.
5. *Heliconoides inflata* (d'Orbigny, 1834), showing internal subperipheral belt, RGM 776 742; apertural view.
- 6-7. *Limacina atlanta* (Mörch, 1874); RGM 776 752-753; a: apertural, b: apical, c: umbilical views.
- 8-9. *Limacina bulimoides* (d'Orbigny, 1834); RGM 776 759-760; a: apical, b: apertural, c: lateral views.
- 10-12. *Striolimacina imitans* (Gabb, 1873); 10: RGM 776 763; apical view; 11-12: RGM 776 764-765; a: apertural, b: tilted apertural, c: lateral, d: apical, e: umbilical views.

All specimens from Le Puget-sur-Argens. Bar = 0.5 mm.

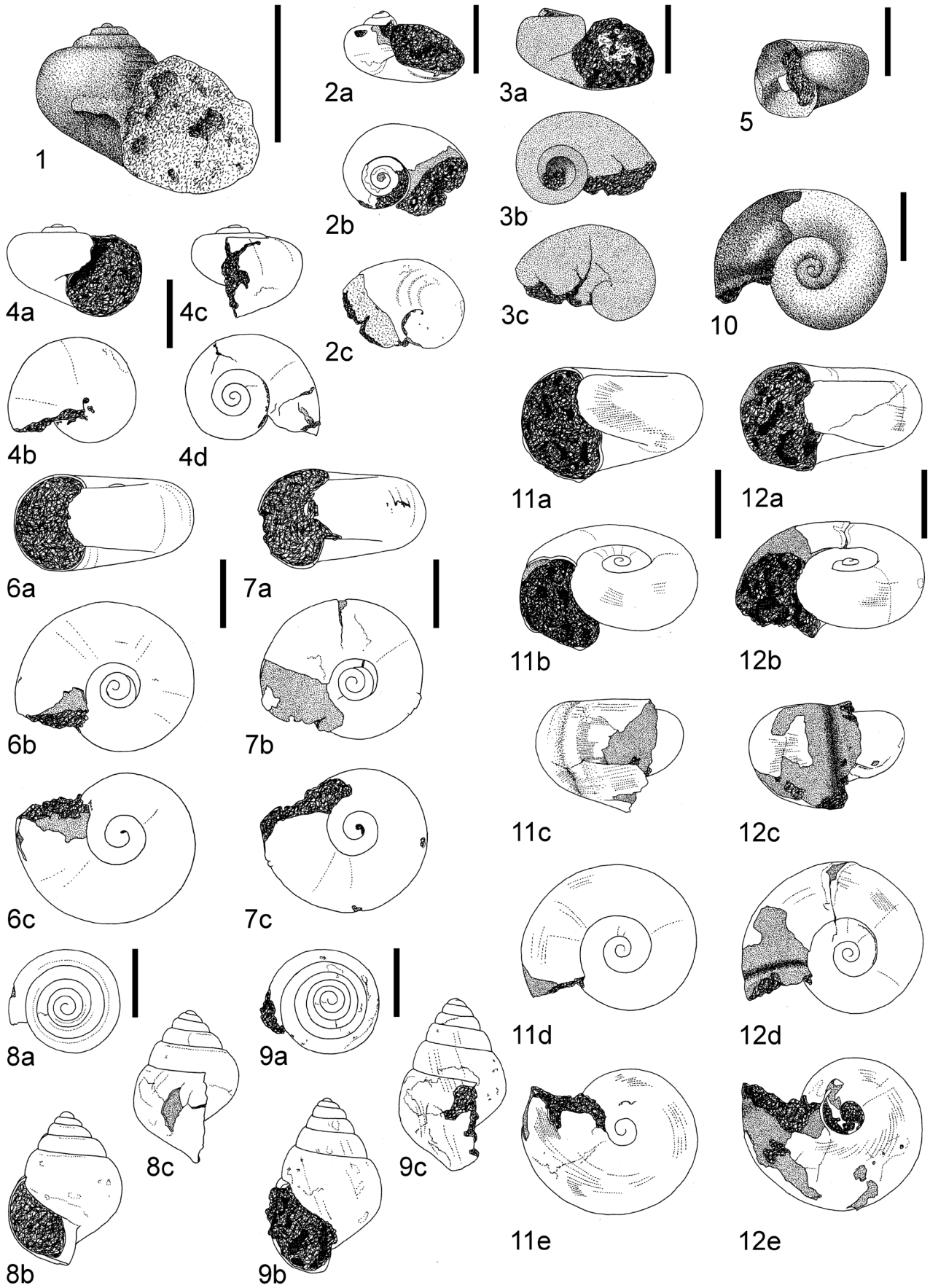


Plate 2.

**Plate 3.**

- 1-4. *Heliconoides vonhachti* sp. nov. 1: **holotype**, RGM 766 744, a: apical, b: apertural, c: lateral views; 2: **paratype**, RGM 766 748, a: apertural, b: lateral view; 3: **paratype**, RGM 776 749, a: apical, b: apertural, c: lateral views; 4: **paratype** (juvenile specimen), RGM 766 750, a: apical, b: umbilical, c: apertural, d: lateral views.
5. *Limacinidae* sp., RGM 776 769, a: apical, b: apertural, c: tilted dorsal view.
- 6-7. *Bowdenathea jamaicensis* Collins, 1934, RGM 776 773a-b; a: apertural, b: dorsal, c: left lateral, d: right lateral views.
- 8-10. *Creseis clava* (Rang, 1828), RGM 776 771a-c; a: apertural, b: frontal views.
- 11-15. *Creseis spina* (Reuss, 1867). 11. RGM 776 775b, adult, slightly compressed specimen, a: apertural, b: frontal, c: lateral views. 12. RGM 776 775a, adult specimen, protoconch missing, a: apertural, b: frontal, c: lateral views. 13-14. RGM 776 775b, 776 776, juvenile specimens, a: frontal. b: lateral views. 15. RGM 776 777, juvenile specimen, compressed, a: apertural, b: frontal, c: lateral views, d: protoconch, frontal view, magnified, d: protoconch, lateral view.

All specimens from Le Puget-sur-Argens. Bar = 0.5 mm.

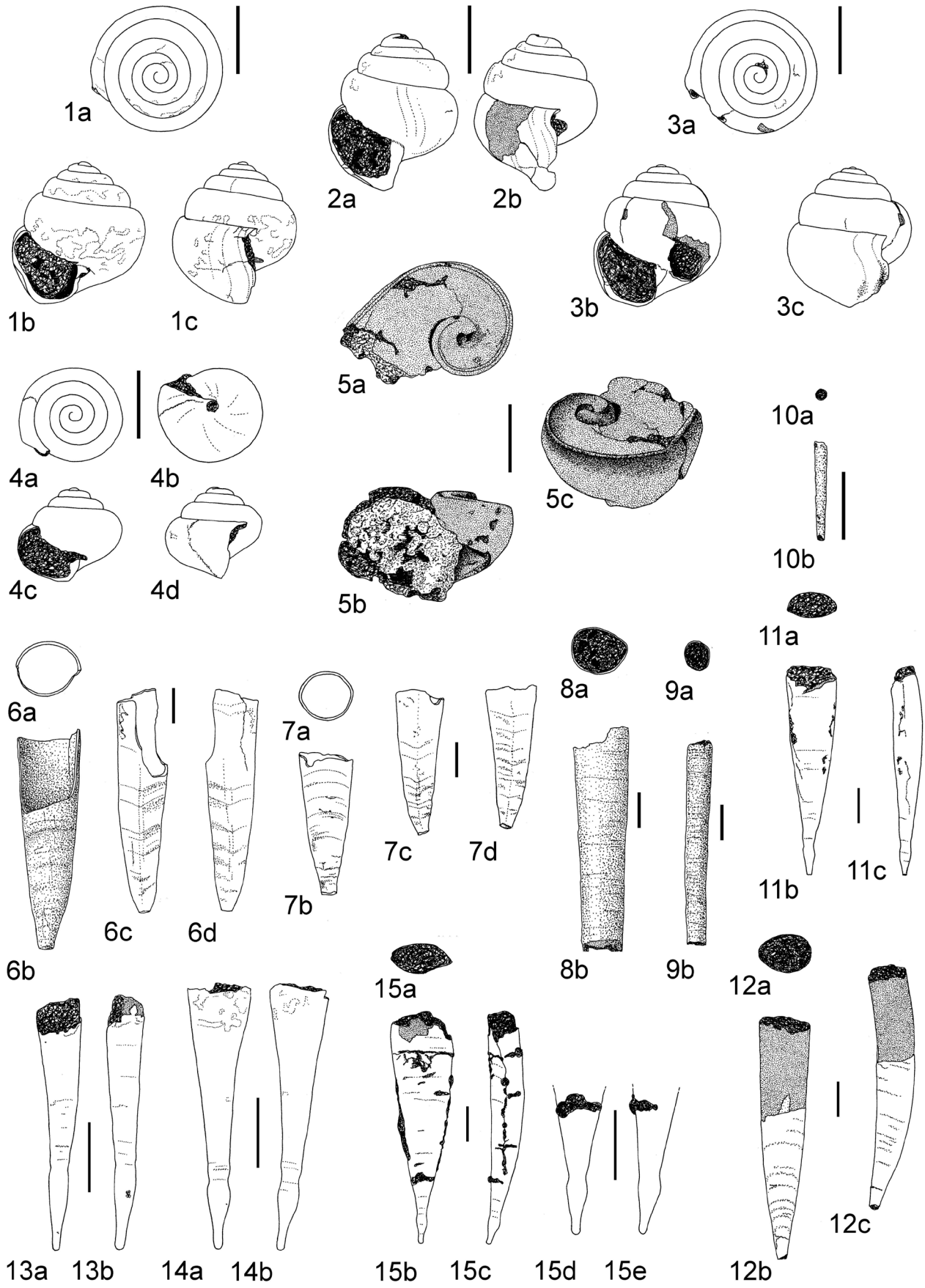


Plate 3.

**Plate 4.**

1. *Cuvierina (Cuvierina) astesana* (Rang, 1829), RGM 7756 796; larval shell with early septum; lateral view.
2. *Clio (Balantium) guidottii* Simonelli, 1896 ?, RGM 776 812, larval shell; a: apertural, b: frontal, c: lateral views.
3. *Cavolinia* sp., RGM 776 815, larval shell; a: dorsal, b: left lateral views.
4. *Diacria trispinosa* (de Blainville, 1821), RGM 776 822; a: dorsal, b: ventral view.
- 5-6. *Peracle bispinosa* (Pelseneer, 1888); 5. RGM 776 825, apertural view. 6. RGM 776 826, a: apical, b: apertural, c: dorsal views.
7. *Peracle elata* (Seguenza, 1875), RGM 776 829, a: apical, b: apertural view. 8. *Peracle reticulata* (d'Orbigny, 1834), RGM 776 832; a: apical, b: apertural view.

All specimens from Le Puget-sur-Argens. Bar = 1 mm.

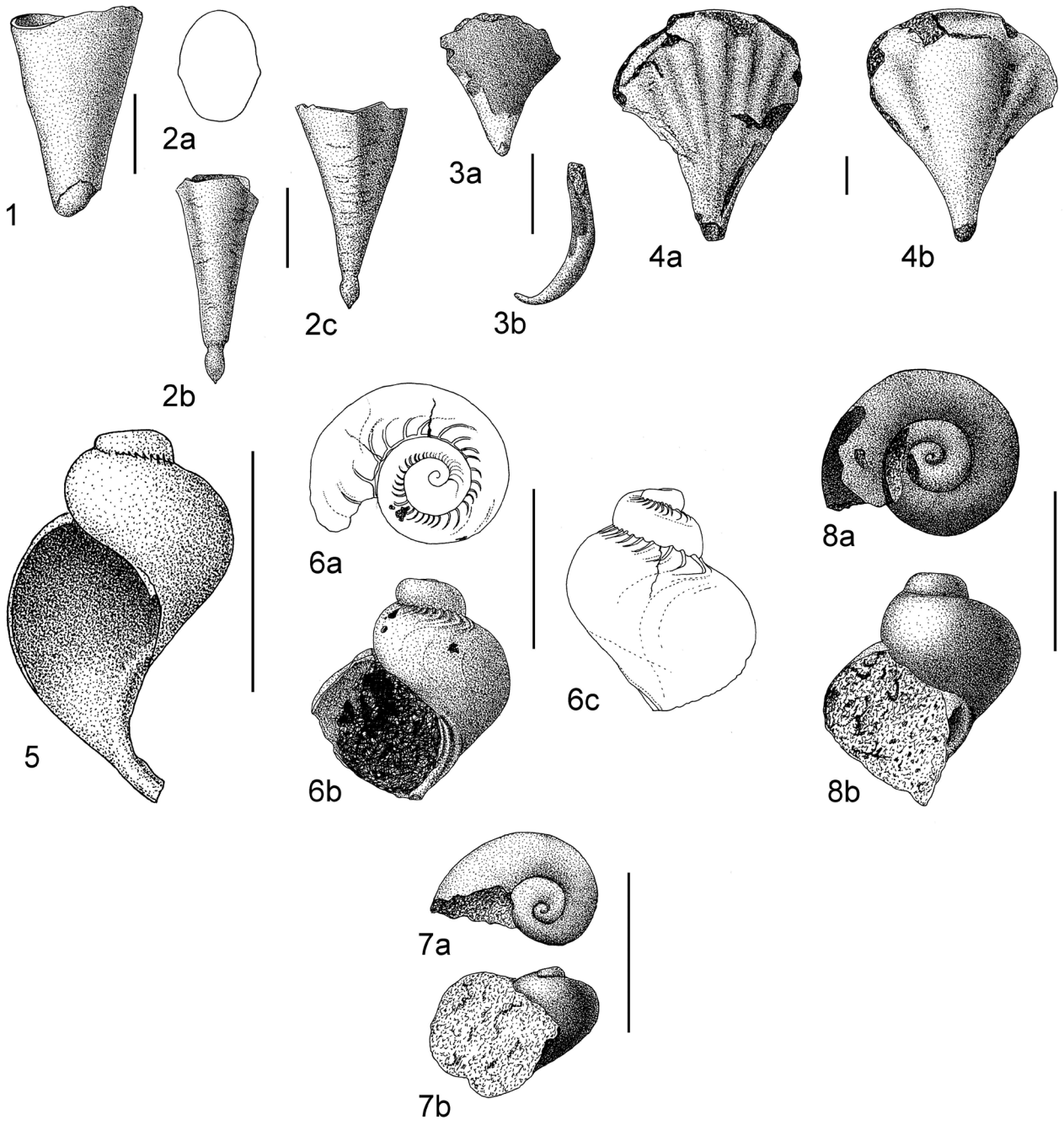


Plate 4.

**Plate 5.**

- 1-2. *Atlanta plana* Richter, 1972. 1. RGM 776 717, oblique apical view. 2. RGM 776 719, a: apical view, b: protoconch magnified.
3. *Oxygyrus inflatus* Benson, 1835. RGM 776 724; juvenile, apertural view.
- 4-5. *Protatlanta rotundata* (Gabb, 1873), RGM 776 727-728; a: apical views, b: nucleus and early protoconch whorls magnified.

All specimens from Le Puget-sur-Argens.

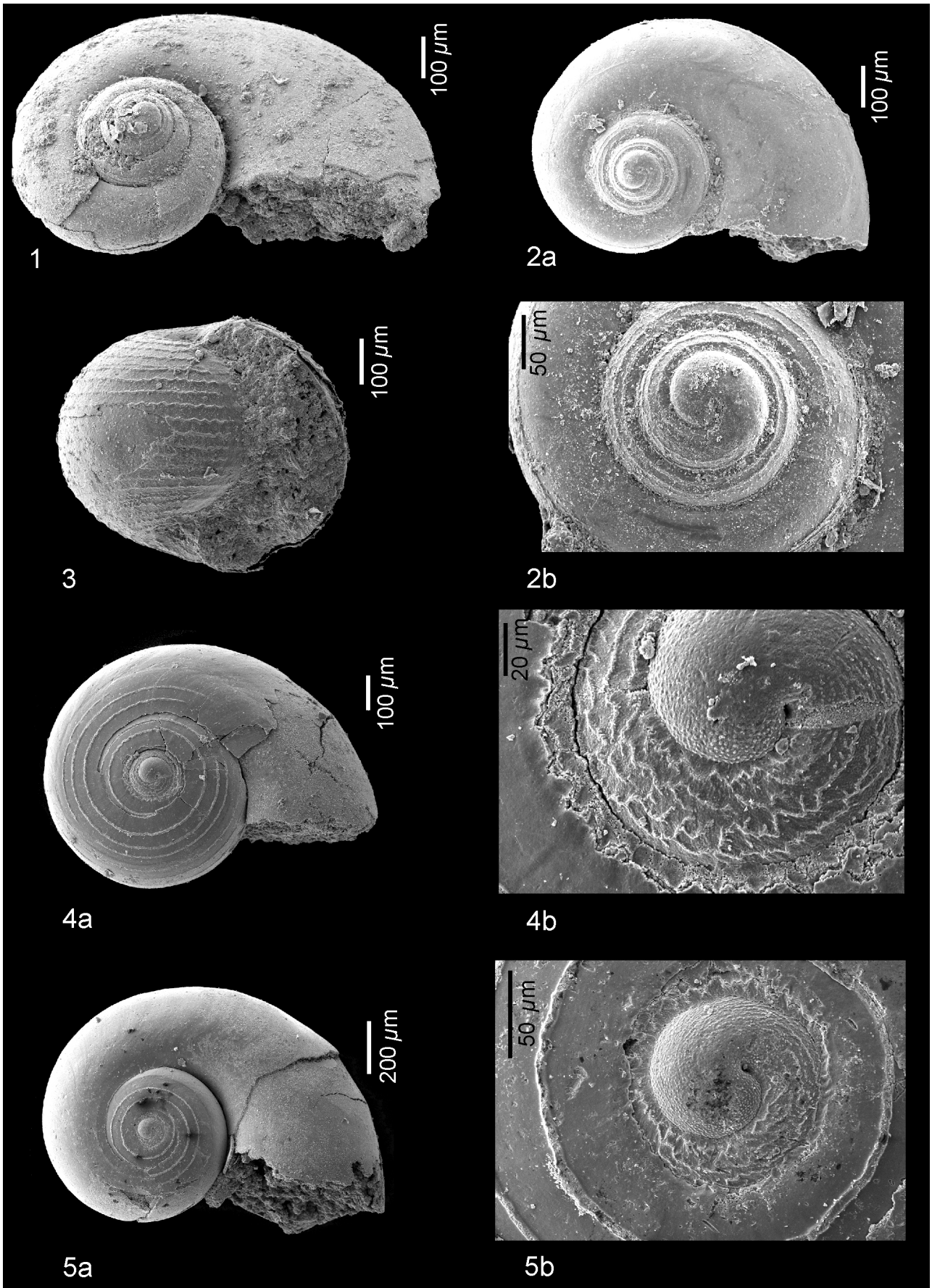


Plate 5



**Plate 6.**

- 1-2. *Protatlanta rotundata* (Gabb, 1873). 1. RGM 776 733, specimens with reduced spiral ornament on protoconch; a: apical view, b: protoconch magnified, c: nucleus magnified. 2. RGM 776 729, dorsal view.
- 3-4. *Carinaria lamarckii* de Blainville, 1817, RGM 776 736a-b. 3. Protoconch, apertural view. 4. Protoconch, umbilical view.
5. *Heliconoides inflata* (d'Orbigny, 1834), RGM 776 743, apertural view.

All specimens from Le Puget-sur-Argens.

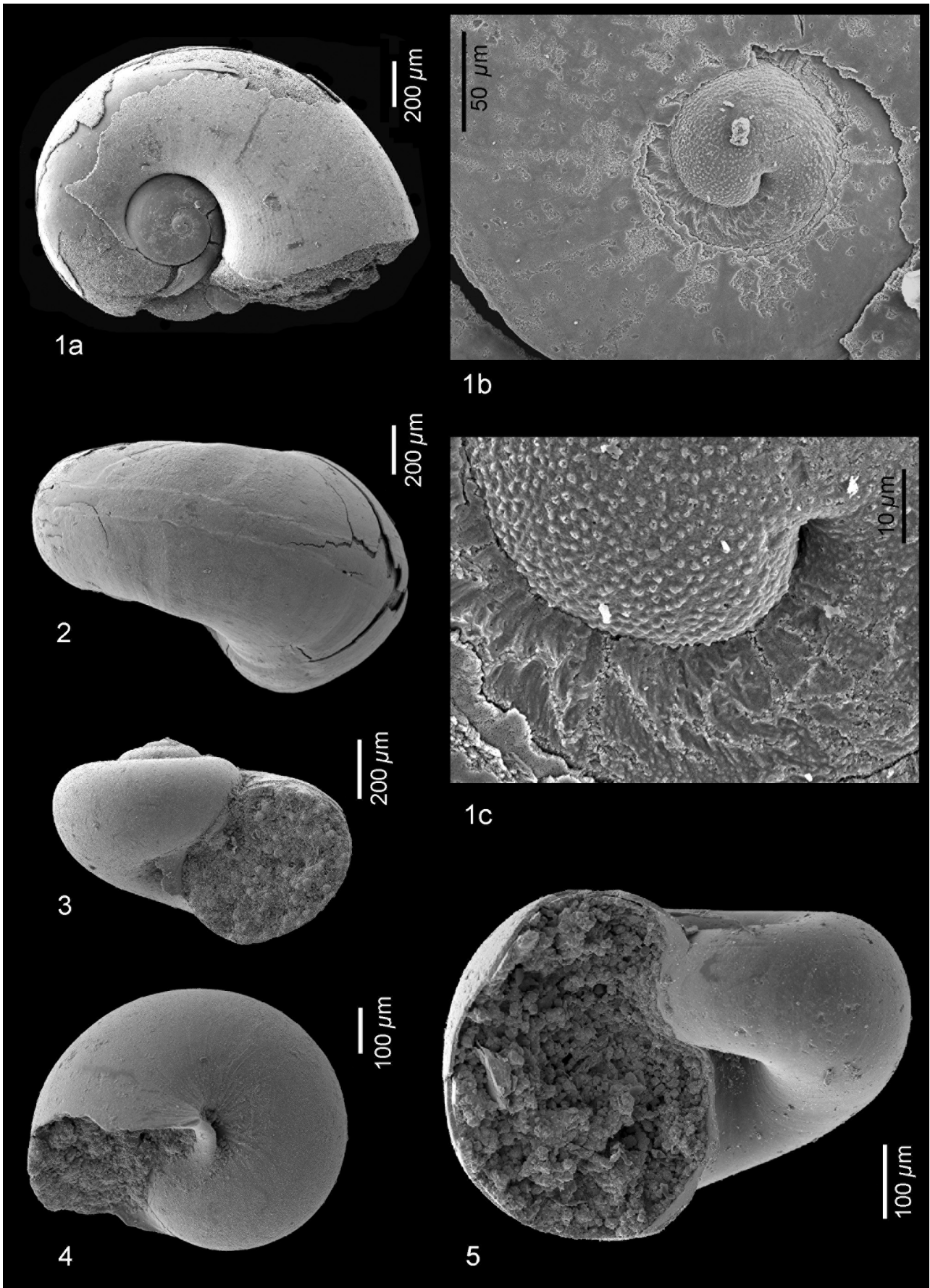


Plate 6.

**Plate 7.**

1. *Heliconoides vonhachti* sp. nov., **holotype**. RGM 766 744, lateral view.
- 2-3. *Limacina atlanta* (Mörch, 1874), 2. RGM 776 755, apical view. 3. RGM 776 754, a:: apical view, b: protoconch magnified.
- 4-5. *Limacina bulimoides* (d'Orbigny, 1834). 4. RGM 766 758, apertural view. 5. RGM 776 757; a: apertural view, b: early whorls magnified.

All specimens from Le Puget-sur-Argens.

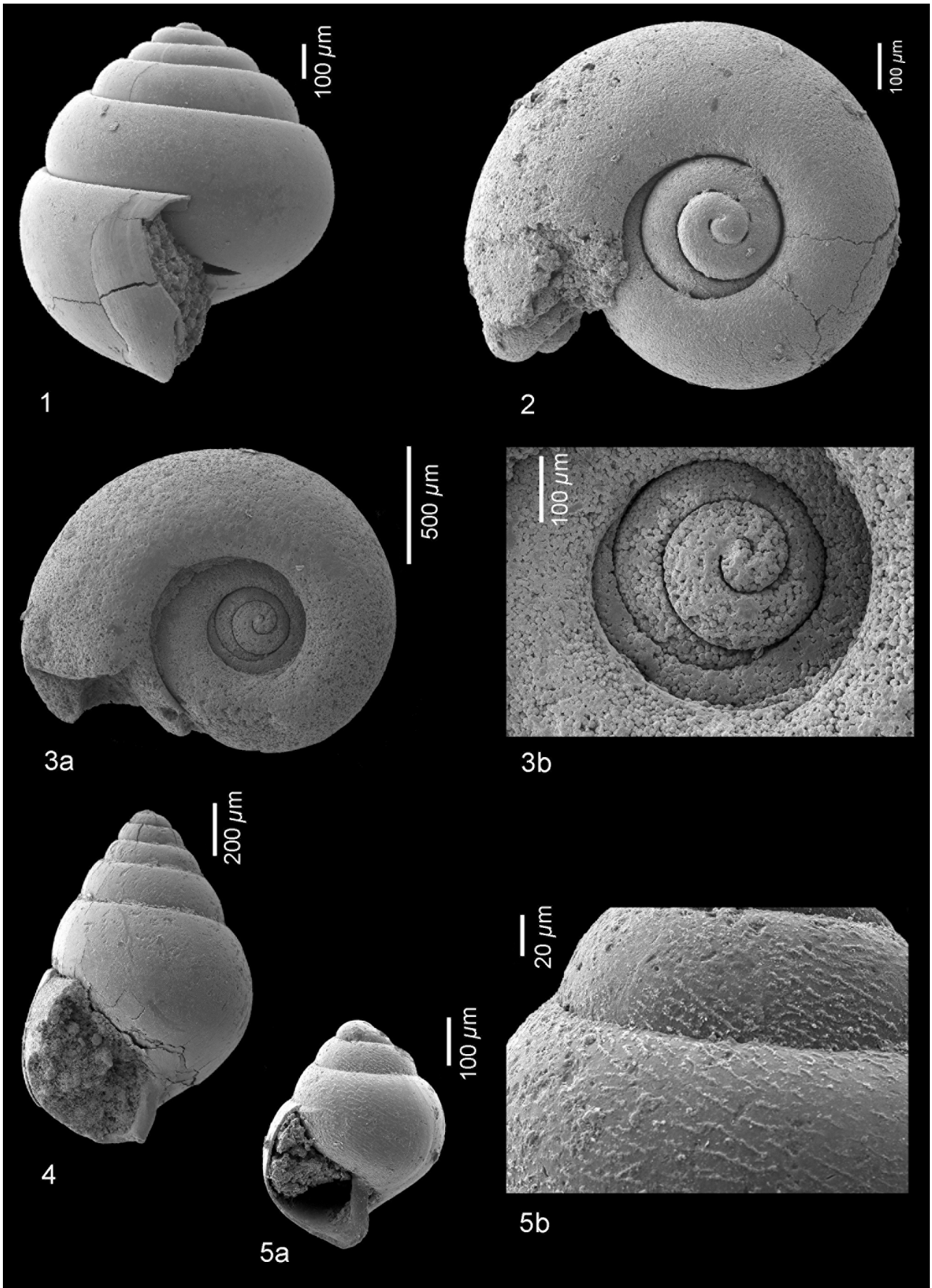


Plate 7.

**Plate 8.**

1. *Striolimacina imitans* (Gabb, 1873), RGM 776 762; apertural view.
- 2-6. *Creseis spina* (Reuss, 1867), 2. RGM 776 778, lateral view; 3. RGM 776 780, a: lateral view, b: protoconch magnified. 4. RGM 776 778, a: frontal view, b: protoconch magnified. 5. RGM 776 782, a: frontal view, b: protoconch magnified. 6. RGM 776 781, a: frontal view of specimen with slender protoconch, b: protoconch magnified.
- 7-8. *Styliola subula* (Quoy & Gaimard, 1827), RGM 776 785-786, dorsal views.

All specimens from Le Puget-sur-Argens.

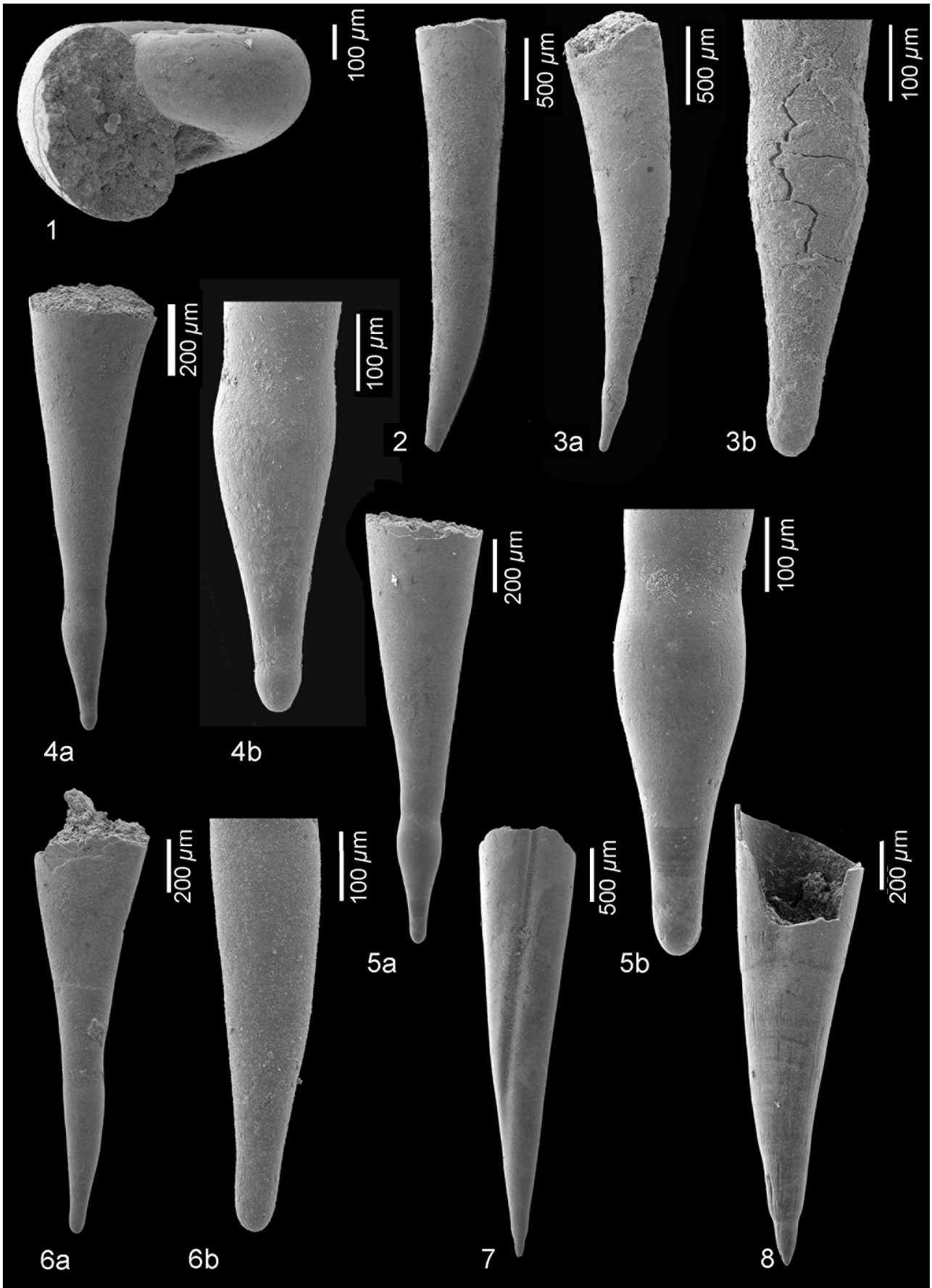


Plate 8.

**Plate 9.**

- 1-3. *Styliola subula* (Quoy & Gaimard, 1827). 1. RGM 776 787, specimens showing shell repair. 2. RGM 776 788, specimens with pseudo-microornament, a: lateral view, b: apical part magnified. 3. RGM 776 789. Specimens with curved apical part, lateral view.
- 4-9. *Cuvierina (Cuvierina) astesana* (Rang, 1829). 4. RGM 776 797, larval shell with protoconch. 5. RGM 776 798, a: larval shell with protoconch, b: protoconch magnified. 6. RGM 776 800, larval shell retaining impression of septum in aperture. 7. RGM 776 801, a: larval shell retaining impression of septum in aperture, b: protoconch magnified. 8. RGM 776 802, a: adult specimen, b: base with septum magnified, ventral views. 9. RGM 776 803, adult specimen, ventral view.

All specimens from Le Puget-sur-Argens.

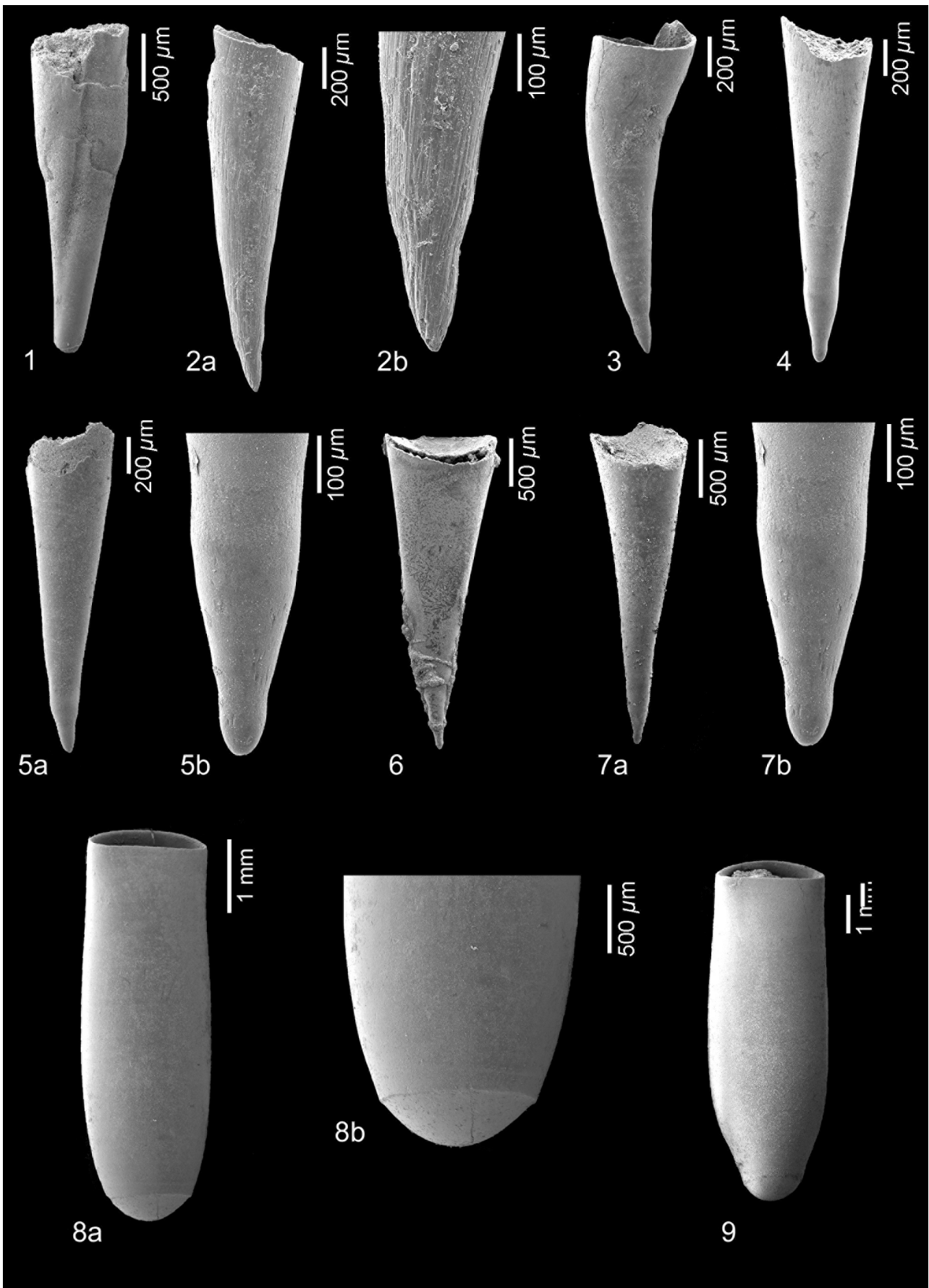


Plate 9.



**Plate 10.**

- 1-2. *Cuvierina (Cuvierina) astesana* (Rang, 1829). 1. RGM 776 804, adult specimen, ventral view. 2. RGM 776 805; a: adult specimen, left lateral view, b: septum magnified.
- 3-5. *Clio (Clio) pyramidata* L., 1767 forma *lanceolata* (Lesueur, 1813). 3. RGM 776 808; a: ventral view, b: protoconch magnified. 4. RGM 776 809; a: right lateral view, b: protoconch magnified. 5. RGM 776 810; a: dorsal view, b: protoconch magnified.
6. *Clio (Balantium) guidottii* Simonelli, 1896 ?, RGM 776 813; a: apical shell part with protoconch, b: protoconch magnified.

All specimens from Le Puget-sur-Argens.

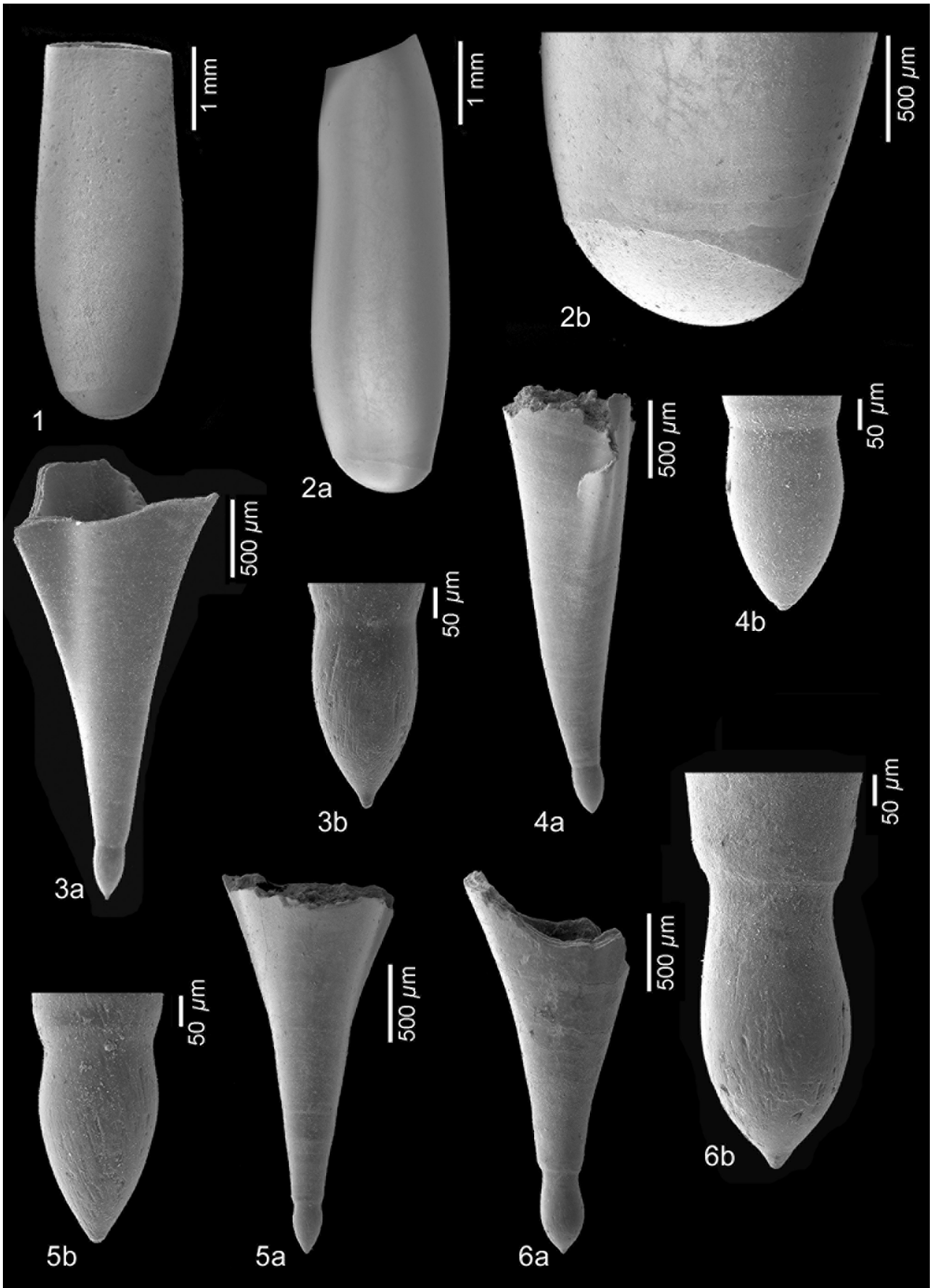


Plate 10.

**Plate 11**

- 1-2. *Cavolinia* sp. indet. RGM 776 816, juvenile specimen, a: dorsal view, b: apical part magnified, c: microornament magnified.
2. RGM 776 817, juvenile specimen, a: left lateral view, b: apical part magnified.
- 3-4. *Diacria trispinosa* (de Blainville, 1821. 3. Larval shell, a: frontal view, b: protoconch magnified. 4. Larval shell, lateral view.
5. *Peracle bispinosa* (Pelseneer, 1888), RGM 776 827, dorsal view.
6. *Peracle reticulata* (d'Orbigny, 1834), apertural view.

All specimens from Le Puget-sur-Argens.

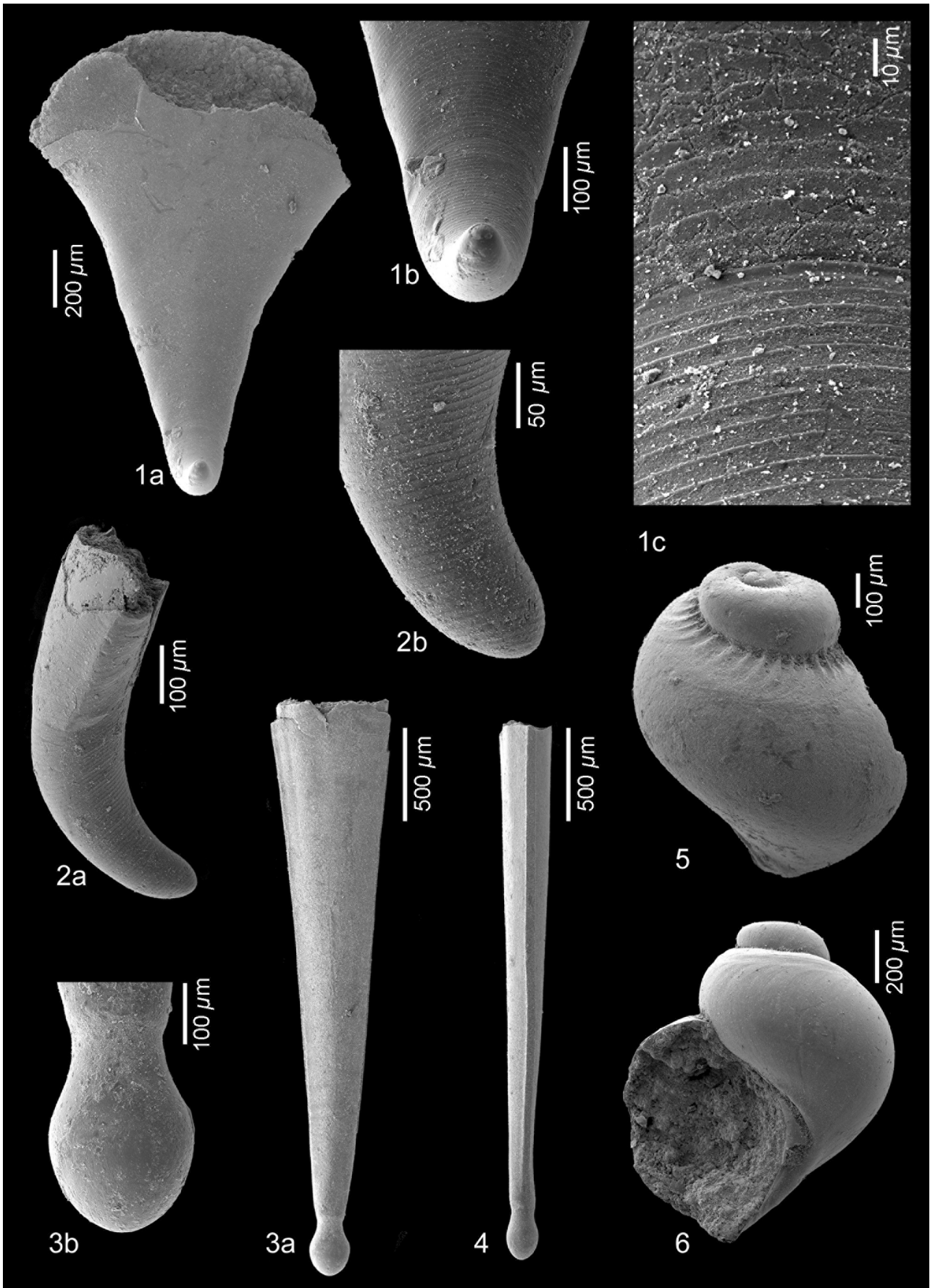


Plate 11.