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NEW PLIOCENE AND OLIGOCENE OLIVIDAE (MOLLUSCA, GASTROPODA) FROM FRANCE AND THE MEDITERRANEAN AREA

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Two olivid species, *Olivella clanzigi* n. sp. and *Amalda* cf. *obsoleta* (Brocchi, 1814), are recorded for the first time from the Mediterranean Pliocene of Tunisia and Spain, respectively. It has generally been assumed that the Olividae had disappeared from the Mediterranean area during the Late Miocene, having fallen victim to the Messinian salinity crisis. The climatic deterioration during the Pliocene would not have permitted their re-introduction into the area. In addition, a new species of *Amalda, A. abessensis*, from the Late Oligocene of France is described and illustrated. This species appears to have no match in European Cainozoic faunas and is close to *Amalda papillata* Tate, 1885, the type species of the subgenus *Alocospira* Cossmann, 1899, from the Early Miocene of Australia. In view of this, the most important Late Oligocene-Miocene Ancillinae of Europe are here illustrated; it is shown that *Gracilancilla* Thiele, 1925 (type species: *G. sumatrana* Thiele, 1925, western Indo-Pacific) is a junior synonym of *Ancillina* Bellardi, 1882 (type species: *Ancilla pusilla* Fuchs *in* Karrer, 1877, European Miocene).

Key words — Mollusca, Gastropoda, Olividae, Oligocene-Pliocene, Mediterranean area, France, new taxa.

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INTRODUCTION

Field work carried out in co-operation with Mr Sylvain Clanzig in Spain, in the counties of Maghreb (Morocco, Algeria and Tunisia) and in northern Italy from March to July of 1983 has yielded diverse molluscan faunas from the Oligocene (Italy) and the Neogene (Spain and Maghreb). This material includes an important collection from the Pliocene of northern Tunisia. This particularly fossiliferous Pliocene, described by Fékih (1975), complements our views of the Mediterranean Pliocene gleaned mainly from Italian strata. Material from Malaga (Spain) now available shows the necessity of studying in greater detail the strata in other countries as well in order to be able to describe more exhaustively the Pliocene populations of the Mediterranean area. The discovery of two olivid species from Spain and Tunisia, may serve as an illustration in this respect.

Field work carried out during nearly fifteen years in the Oligocene of Aquitaine (France) has led to the discovery of numerous new species, amongst which is the new species of *Amalda* described herein. In view of this, most of the Oligocene and Neogene Ancillinae of Europe are here illustrated.

The material described is housed in the following institutions: MNHN (Muséum National d'Histoire Naturelle de Paris, Laboratoire de Biologie des Invertébrés Marins et Malacologie) and SMF (Senckenberg Naturmuseum, Frankfurt am Main, Germany).

SYSTEMATIC DESCRIPTIONS

Genus *Amalda* H. & A. Adams, 1853

Type species — *Ancillaria tankervillii* Swainson, 1825.
Discussion — The European Oligocene and Miocene Ancillinae have traditionally been assigned to *Ancilla*

Fig. 1. Map showing location of fossil localities referred to in the text.

Lamarck, 1799 (type species: *Ancilla cinnamonea* Lamarck, 1801). This classification was adopted by Davoli (1989), who considered another genus to be valid, viz. *Ancillarina* Bellardi, 1882. However, the presence in the two principal species, *A. obsoleta* (Brocchi, 1814) and *A. glandiformis* (Lamarck, 1811), of a divided basal fasciole, a deep siphonal sinus and a strong secondary callus indicates that these should in fact be referred to *Amalda*. This interpretation is in accordance with the typical features of the genera *Amalda* and *Ancilla* as worked out by Chavan (1965) and Kilburn (1977, 1981).

A number of species have also been assigned to *Ancillus* de Montfort, 1810 (type species: *Ancilla buccinoides* Lamarck, 1805), which is occasionally considered to be a subgenus of *Ancilla*. In fact, as Kilburn (1977) has already noted, *Ancillus* is apparently most closely related to *Amalda*. The genus *Ancillus* is the oldest known representative of the Ancillinae with the species *Eoancilla acutulata* Stephenson, 1941 from the Maastrichtian (Late Cretaceous) of the United States (see Sohl, 1964, pl. 36, figs 1-7).

Finally, only *Ancillarina* (type species: *Ancilla cana-*

lifera Lamarck, 1802) is clearly a representative of *Ancilla* of which it is probably the precursor (Kilburn, 1977). *Ancillarina* comprises but few species and appears to have been in quasi-stasis during the Eocene to Late Miocene, when it became extinct.

The Ancillinae, which are so poorly represented in the Oligocene and Miocene of Europe, have apparently had the following distribution pattern:
- Six species of Ancillinae are known with certainty from the European Late Oligocene:
1 - Northern area:
Ancillus indivisus (Koch & Wiechmann, 1872) (Pl. 2, Figs 8, 9)
Ancillus karsteni (Beyrich, 1853) (Pl. 2, Figs 10, 11).
Amalda obsoleta (Brocchi, 1814) (Pl. 1, Figs 9-12)
Amalda glandiformis anomala (Schlotheim, 1820) (Pl. 1, Figs 5-8)
2 - Mesogean area:
Ancillus raulini (Peyrot, 1936) (Pl. 2, Figs 5-7)
Ancillarina subcanalifera (d'Orbigny, 1852) (Pl. 2, Figs 12, 13)
Amalda abessensis n. sp. (Pl. 1, Figs 1-4).
3 - Mesogean and Northern areas:
Amalda glandiformis anomala (Schlotheim, 1820)

Remark — *Ancillus raulini* differs principally from *Amalda glandiformis* in the weakness of the ancillid band and the absence of secondary spire callus. *A. glandiformis* is also a much larger-sized species. Saubade *et al.* (1978) did not accept *Ancillus raulini* (Peyrot) and united this taxon with a population of *Amalda glandiformis* comprising specimens of reduced size.

According to Janssen (1979) *Amalda anomala* from the North Sea Basin Oligocene differs from Miocene *A. glandiformis* in having a poorly developed spire callus, a columella with numerous small folds and in lacking spiral ridges on the parietal side. I examined specimens of *A. glandiformis* from a number of Miocene localities (Early Miocene [Burdigalian] of the Aquitaine [Saucats, Meilhan, Mimbaste], Middle Miocene of the Aquitaine [Saubrigues, St-Jean-de-Marsacq], Middle Miocene of the Loire Basin [Le Louroux], Middle Miocene of Austria [Soos, Steinabrunn], Middle Miocene of Italy [Turin hills] and Late Miocene of Italy [Stazzano]. In addition, I studied specimens of *A. glandiformis* from several Late Oligocene localities in the Aquitaine (St-Paul-lès-Dax [Abesse], St-Etienne-d'Orthe, Peyrehorade [Peyrère] and from the Late Oligocene of Germany (Wilhelmshöhe). All specimens are housed in MNHN collections, and this study has shown that the Late Oligocene *Amalda anomala* from Wilhelmshöhe differs from Late Oligocene *A. glandiformis* from the Aquitaine only in having a less well-developed spire callus. In fact, these two species cannot be separated. In the Early Miocene of Aquitaine, *A. glandiformis* frequently shows spiral ridges on the parietal region, which are unknown in Late Oligocene specimens, but a few individuals (*e.g.* from Saucats, Moulin de Lagus) show a columella with numerous small folds. *Amalda glandiformis* from the Middle and Late Miocene differs in generally having only two high columellar folds and in lacking ridges on the parietal region.

The above leads me to conclude that the presence of numerous columellar folds is an ancestral feature which permits to separate *A. glandiformis* from the Late Oligocene, in addition to the absence or presence of ridges on the parietal region. Following Glibert (1960) I therefore consider *Amalda anomala* to be an Oligocene subspecies widely distributed in Europe.

From the European Miocene (when distinctions between the Northern and Mesogean areas tend to blur) I have been able to recognise five species, viz.
Amalda glandiformis (Lamarck, 1811) (Pl. 1, Figs 5-8)
Amalda obsoleta (Brocchi, 1814) (Pl. 1, Figs 9-12)
Ancillarina subcanalifera (d'Orbigny, 1852) (Pl. 2, Figs 12, 13)
Ancillus sismondanus (d'Orbigny *in* Bellardi, 1882) (Pl. 2, Figs 2-4)
Ancillina pusilla (Fuchs *in* Karrer, 1877) (Pl. 3, Figs 8, 11).

Remark — Davoli (1989) recorded from the European Miocene two additional species of Ancillinae, viz. *Amalda patula* (Doberlein *in* Bellardi, 1882) and *Amalda sowerbyi* (Michelotti, 1847). Judging from Davoli's illustrations, the first may be but a forma of *A. glandiformis*, whereas the second appears to be conspecific with *A. obsoleta.*

Gracilancilla Thiele, 1925 was erected for *Ancilla sumatrana* Thiele, 1925 of the western Indo-Pacific; it is a junior synonym of *Ancillina* Bellardi, 1882 (type species: *A. pusilla* Fuchs, 1877). The differences between *A. pusilla* and *A. sumatrana* are less important and are at the species level. I have been able to convince myself of this by an examination of specimens of *A. pusilla* (SMF collections) and of *A. sumatrana* (MNHN, Bouchet & Triclot Collection, Musorstom II, station 106, 13°47 N - 120°30 E,

640-668 m; Pl. 3, Figs 9, 10). So far as differences in the protoconchs are concerned, in *A. sumatrana* it is much more acuminate, of brownish colour and clearly separated from the teleoconch. Chavan (1965) suggested that *Gracilancilla* be classed as a subgenus of *Ancillina*.

Amalda (Alocospira) abessensis n. sp.
Pl. 1, Figs 1-4

Stratum typicum — Late Oligocene, faluns bleu à *Miogypsinoides*.
Locus typicus — Château d'Abesse, St-Paul-lès-Dax (Landes, France).
Derivatio nominis — After the type locality.
Types — Holotype (MNHN), seven paratypes (four specimens, MNHN, Lozouet *et al.* Collection; three specimens, Lesport Collection). Additional material from the same locality comprises nine fragmentary shells (MNHN, Lozouet *et al.* Collection).
Dimensions — The holotype measures 12.2 mm (height) and 5 mm (maximum diameter).
Description — The shell is of medium size, ovate, with thick test. The number of whorls cannot be determined. The cyrtoconoid spire is relatively short, covered in a strong callus which masks the suture completely. The apex takes the form of a mamillate button. The callus extends over part of the last whorl and is continuous with the callus over the parietal part of the aperture; that of the spire is peculiar in being sectioned by 7-8 effacing spiral lirae. The last whorl represents more than two thirds of the total shell height. The aperture (damaged in the holotype) would have been lanceolate, narrower in its adapical part and forming a large siphonal notch. The convex columella is clearly twisted at the columella pillar, on which some ten oblique folds may be counted. At its base, a fairly large band (the ancillid band) envelops the neck, being delimited anteriorly and posteriorly by two grooves. The neck is entirely covered in a callus consisting of a large basal fasciolar band, which is divided into two zones, and of the dorsal columella.
Discussion — *Amalda abessensis* bears some resemblance to *A. obsoleta* in general shape, but differs in the bulbous spire apex and the spiral groove. The specimens of *A. abessensis* before me are not very well preserved and the spiral ornament may have been accentuated by erosion/abrasion. For this reason, I examined specimens of *A. obsoleta* from various localities (MNHN collections) with various states of preservation: from the Early Miocene of Aquitaine (St-Paul-lès-Dax [Cabanes]), from the Middle Miocene of Aquitaine (Saubrigues, St-Jean-de-Marsacq), from the Middle Miocene of Belgium (Edegem), from the Middle Miocene of Germany (Dingden), from the Middle Miocene of Austria (Soos, Vöslau), from the Late Miocene of the Loire Basin (St-Clément-de-la-Place) and from the Late Miocene of Italy (Montegibbio, Tortonese and Santa Agata). In a number of specimens I noted only very shallow and inconspicuous spiral grooves, not comparable with the spiral ornament seen in *A. abessensis*. There is no other species of olivid in the European Cainozoic that is likely to be confused with the present new taxon.

Amalda abessensis is referred to the subgenus *Alocospira* Cossmann, 1899 (type species: *Amalda papillata* Tate, 1885 from the Early Miocene of Australia, see Ninomiya, 1990, pl. 2, fig. 8). Extra-Australian records of this subgenus include the Early Miocene of New Zealand (*A. hebera* Hutton, 1873), and the Late Miocene of Java (*A. nitida* Wanner & Hahn, 1935). At present, *Alocospira* contains fewer than ten species distributed in the Pacific, mainly on Australian coasts (Ninomiya, 1990) but present also south of Japan (Ninomiya, 1988), in the south China Sea and near New Caledonia (Kilburn & Bouchet, 1990). *Amalda abessensis* is closely related to *A. papillata*, but is nevertheless more slender and possesses a much more clearly cyrtoconoid spire.

Michaux (1991) elevated the taxon *Alocospira* to the rank of genus and considered the spiral grooves to be an important feature in species referred to it. He also recognised three subgenera of *Amalda*, viz. *Gracilispira, Baryspira* and *Spinaspira*. The other subgenera of *Amalda*, especially those recently erected by Ninomiya (1988, 1990) are poorly defined and were not included in Michaux's paper. Michaux remarked that *A. montrouzieri* of Bouchet & Kilburn (1988) from New Caledonia was probably a mixed lot, their figures 1-6 representing *Alocospira montrouzieri* (Souverbie, 1860) and figures 7, 8 appearing to represent an *Amalda (Baryspira)* of the *mucronata* group. However, an examination of Bouchet & Kilburn's material from New Caledonia does not permit me to in fact distinguish two species and - a fortiori - two genera. Michaux's (1991) statement is confusing and in need of clarification, which is why I prefer here to accept only the genus *Amalda* for the time being.

Amalda cf. **obsoleta** (Brocchi, 1814)
Pl. 2, Fig. 1

Age and locality — Early Pliocene (F. Serrano, pers. comm.), Colonia Santa Ines (Province of Malaga, Spain).

Discussion — *Amalda obsoleta* is known with certainty from Europe from the Early Miocene onwards (Burdigalian of St-Paul-lès-Dax, Moulin de Cabanes). Rossi-Ronchetti (1955, p. 238) indicated that Brocchi's type specimen originates from the Piemont Pliocene. Davoli (1989) contested this provenance and considered it to have come from the Italian Late Miocene. This species differs from *Amalda glandiformis*, with which it has often been confused, in having a much larger basal band (ancillid band). Glibert (1952, p. 353) calculated ratios (size of the band vs. total shell height) for populations of *A. obsoleta* and *A. glandiformis*, which make the differences between these species appear clear cut as far as this feature is concerned. Glibert noted for *A. obsoleta* a mean value of 6.4 (range of variation 5.64 to 6.57) and for *A. glandiformis* forma *elongata* (Deshayes, 1832) a mean of 4.65 (range from 4.35 to 4.95). The two specimens from the Spanish Pliocene before me with values of 6.4 and 6.66 should thus be referred to *A. obsoleta.*

Saubade *et al.* (1978) did not consider the size of the basal band in their biometric study of '*Ancilla*' from the Early Miocene of Aquitaine. The result of this was that certain populations of *A. glandiformis* and *A. obsoleta* were mixed up. In this way, *A. obsoleta* from the Burdigalian of St-Paul-lès-Dax (Moulin de Cabanes, see Pl. 1, Figs 11, 12) was interpreted to be an elongate form of *A. glandiformis.*

Chavan (1951) used the name *Amalda obsoleta* var. *marcaisi* Chavan for a much more elongate form from the Pliocene of Morocco (Oued el Arjat, near Rabat). *Amalda marinhensis* (Cox, 1941) from the Pliocene of Portugal has a profile similar to that of the Malaga specimens. However, the Portuguese specimen possesses a broad ancillid band, which makes it attributable to the *A. glandiformis* group. There are thus two additional species of *Amalda* in the Pliocene of the western part of the Mediterranean area. One of these may be assigned to the *A. obsoleta* lineage, while the other is referred to the *A. glandiformis* lineage.

Genus *Olivella* Swainson, 1831

Type species — *Oliva dama* (Mawe, 1828).

Olivella clanzigi n. sp.
Pl. 3, Figs 1-4

Stratum typicum — Falun with *Potamides* (Early Pliocene).

Locus typicus — Oued el Galaa, southeast of Lac de Bizerte, Tunisia.

Derivatio nominis — Dedicated to Mr Sylvain Clanzig.

Types — Holotype (MNHN), a single paratype (MNHN, Clanzig and Lozouet Collection).

Dimensions — The holotype measures 14 mm (height) and 6 mm (maximum diameter).

Description — Shell of moderate size, with 3 1/2 cylindroconical whorls, thick test, aperture elongate, wide, conical spire short. Only 2 1/2 whorls of the spire are preserved; these are separated by a deep suture. The last whorl is ovate and occupies three quarters of the total shell height. Its elongate aperture is wide, but narrower in its adapical part where it terminates in a wide anal notch extended by the suture. The abapical part of the aperture is wider and displays a large siphonal notch in a highly asymmetrical U-form. The columella is very oblique, is near-rectilinear and terminates in a twisted columella pillar, covered in a callus forming a fairly large bulge adapically and showing some ten subparallel ridges on the columella pillar; these ridges are slightly more pronounced in the abapical part where they converge into a strong basal limbus. The lip is slightly convex, with bevelled margin, and is smooth interiorly. Protoconch unknown.

Remarks — The last whorl of the paratype specimen is better preserved and permits to enlarge upon the typical features of this species. The callus of the columella forms a fairly strong bulge in the parietal part. The columella pillar shows some ten oblique folds and terminates in a strong limbus accentuated by a groove, below which extend two folds. The callus of the base extends over *c* 1/4 of the total height of the last whorl. This callus subdivides into two fasciolar bands of equal magnitude. The first (posterior fasciolar band) differs by a narrower inductura. The second (anterior fasciolar band) attaches to the siphonal notch and growth lines may be seen. It is delimited adapically by a small bourrelet and abapically by the protuberance of the columella pillar.

Discussion — *Olivella grateloupi* (d'Orbigny, 1852) (Pl. 3, Fig. 7), the sole species of *Olivella* known to date from the European Cainozoic (Late Oligocene-

Early Miocene), is smaller and possesses but 5 to 6 columellar folds which are, however, more pronounced. This species is known from the Aquitaine Basin (Late Oligocene-Early Miocene) and from Italy (Early Miocene of the Turin hills).

Olivella clanzigi may also be compared with *O. pulchella* (Duclos, 1836) (Pl. 3, Figs 5, 6) from the Recent West African coast, of which it may be the precursor. The new species differs from specimens of *O. pulchella* from Senegal and Angola (MNHN, leg. Pin, leg. Gofas) in having an anterior fasciole with much wider inductura and a columella terminating in a much stronger fold.

Conclusions

Davoli (1989) emphasised the absence of Olividae from the Mediterranean Pliocene which he thought was attributable to climatic factors. The present-day Olividae of the North Atlantic are restricted to tropical and subtropical regions. They are held to have disappeared from the Mediterranean at the end of the Miocene, having fallen victim to the Messinian salinity crisis. The climatic conditions prevailing in the Mediterranean during the Pliocene did not permit their re-introduction.

Despite this, the Pliocene fauna of the Mediterranean comprises numerous tropical elements amongst gastropod faunas: Ficidae, Cancellariidae, Mitridae, Conidae and Terebridae (Marasti & Raffi, 1979). In addition, Olividae have been recorded from the Portuguese Pliocene (Cox, 1941) and from Morocco (Tétouan) (Gentil & Boistel, 1905). This means that the climatic conditions hypothesis does not suffice to explain the absence of Olividae from the area; the discovery of the new species described herein is in fact not surprising. Appear as they may in the Pliocene of the Mediterranean area, Olividae remain rare.

Amalda abessensis n. sp. of the Late Oligocene of Aquitaine is the sole European representative of the *A. (Alocospira) papillata* group, which at present occurs mainly in Australian waters. Its presence in European waters is fairly easily explained, as it appears prior to the principal closure of the Tethys which, judging from the faunas, occurred at the start of the Early Miocene. Quite a different story holds for *Ancillina pusilla*, which occurs commonly in the Middle Miocene of Europe. This species, or a closely related form, is not known prior to the Middle Miocene and is close to the Recent *A. sumatrana* from the west Indo-Pacific. Consequently, it appears to be yet another species that was introduced from the west Indo-Pacific at the Early/Middle Miocene boundary or during the Middle Miocene. This is in support of the view that there have in fact been intermittent communications between the Paratethys and the Indian Ocean at that time.

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PLATE 1

Figs 1-4. *Amalda (Alocospira) abessensis* n. sp., Late Oligocene, St-Paul-lès-Dax, Château d'Abesse (Landes, France). 1, 2 - holotype, height 12.2 mm; 3, 4 - paratype, height 14 mm. Lozouet & Maestrati Coll. (MNHN).

Figs 5-8. *Amalda glandiformis anomala* (Schlotheim, 1820). Late Oligocene. 5-7 from St-Paul-lès-Dax, 'Estoti' (Landes, France), height 32 mm (5, 6), height 36 mm (7); 8 from Peyrehorade, 'Peyrère' (Landes, France), height 15 mm. Lozouet & Maestrati Coll. (MNHN).

Figs 9-12. *Amalda obsoleta* (Brocchi, 1814). Early and Middle Miocene. 9, 10 from Saubrigues (Landes), Middle Miocene (Langhian), height 21 mm, Staadt Coll. (MNHN); 11, 12 from St-Paul-lès-Dax, 'Cabanes' (Landes), Early Miocene (Burdigalian), height 29 mm, Lozouet, Maestrati & Senut Coll. (MNHN).

Specimens in Figs 1-10 were coated with ammonium chloride prior to photography.

PLATE 1

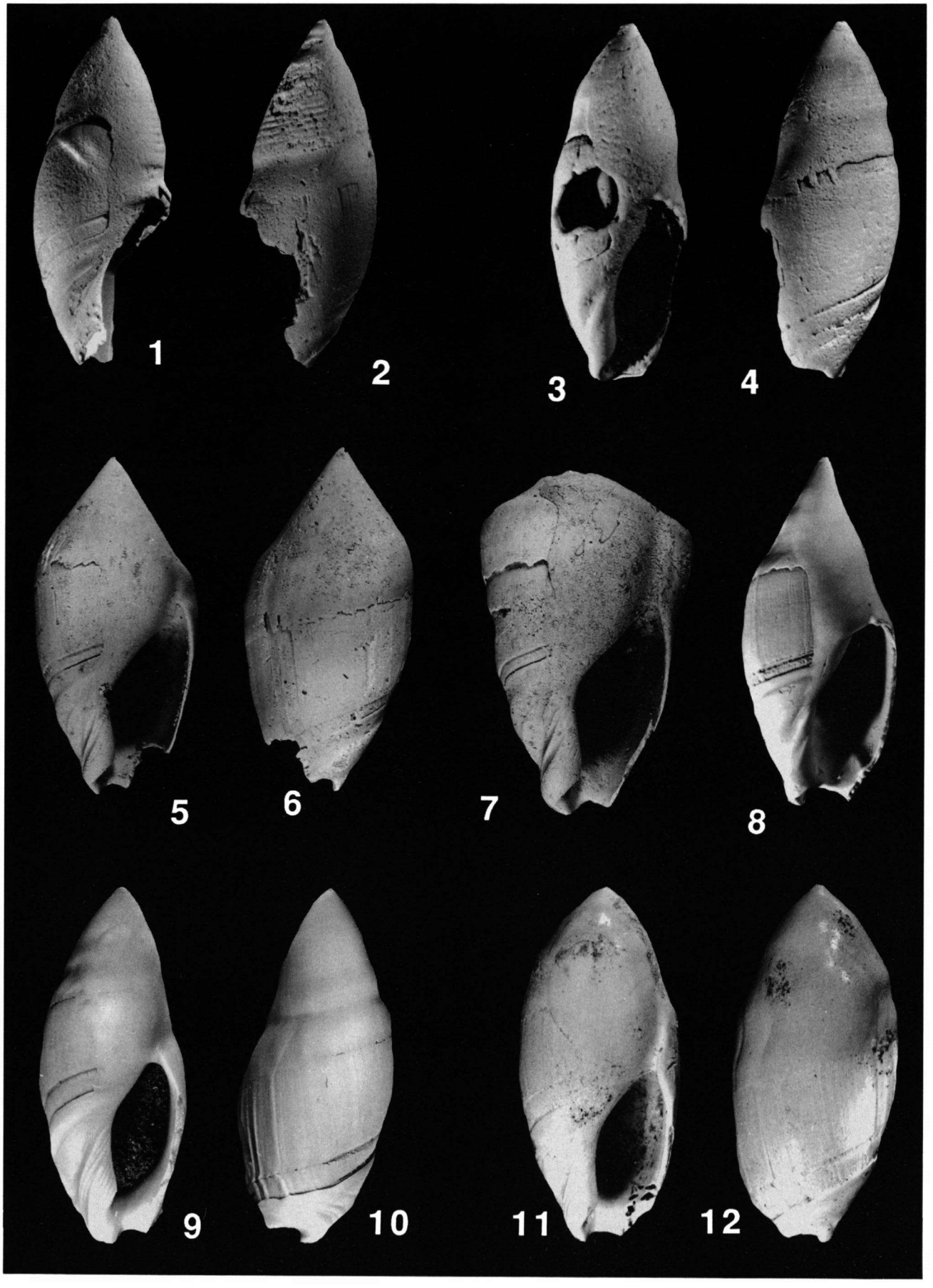

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PLATE 2

Fig. 1. *Amalda* cf. *obsoleta* (Brocchi, 1814). Early Pliocene. Colonia Santa Ines (Malaga, Spain), height 12 mm, MNHN (leg. A. Barrajon).

Figs 2-4. *Ancillus sismondanus* (d'Orbigny *in* Bellardi, 1882). Middle Miocene (Langhian), Turin hills (Italy), height 18.4 mm (2), height 20 mm (3, 4), Staadt Coll. (MNHN).

Figs 5-7. *Ancillus raulini* (Peyrot, 1936). Late Oligocene, St-Etienne-d'Orthe (Landes, France), height 16 mm (5, 6), height 15 mm (7), Lozouet & Maestrati Coll. (MNHN).

Figs 8, 9. *Ancillus indivisus* (Koch & Wiechmann, 1872). Late Oligocene (Chattian), Rumeln (Germany), height 12 mm. Görges Coll. (SMF no. 250936).

Figs 10, 11. *Ancillus karsteni* (Beyrich, 1853). Late Oligocene (Chattian), Rumeln (Germany), height 9.8 mm, SMF Coll. (no. 251543a).

Figs 12, 13. *Ancillarina subcanalifera* (d'Orbigny, 1852). Late Oligocene, St-Etienne-d'Orthe (Landes, France), height 25 mm, Lozouet & Maestrati Coll. (MNHN).

All specimens were coated with ammonium chloride prior to photography.

PLATE 2

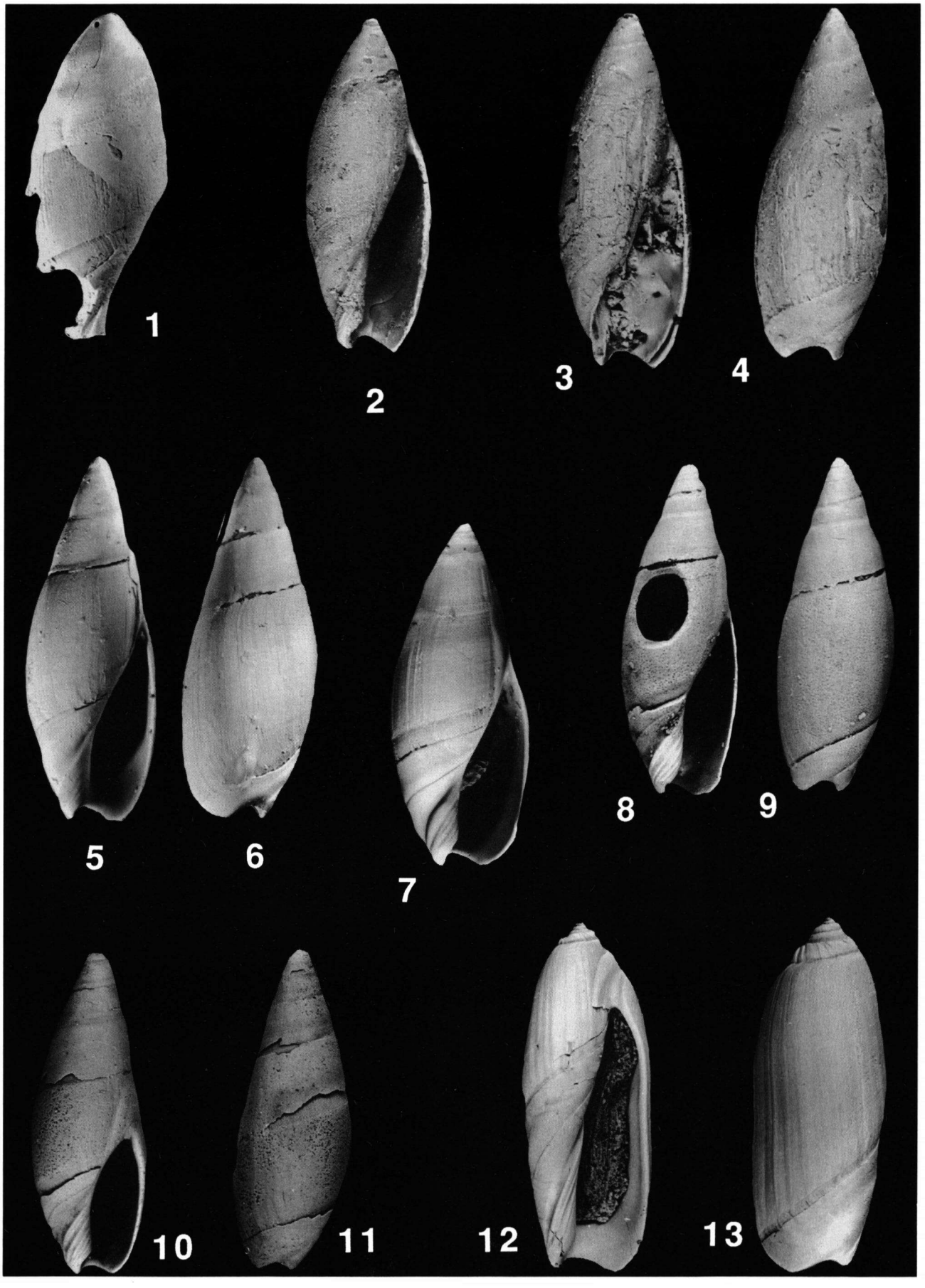

PLATE 3

Figs 1-4. *Olivella clanzigi* n. sp. Early Pliocene, southeast of Lac de Bizerte, Oued et Galaa (Tunisia), 1, 4 - holotype, height 14 mm; 2, 3 - paratype, height 15.6 mm, Clanzig & Lozouet Coll. (MNHN).

Figs 5, 6. *Olivella pulchella* (Duclos, 1836). Joal, at depth 10-20 m (Senegal), height 16 mm, MNHN (leg. Pin).

Fig. 7. *Olivella grateloupi* (d'Orbigny, 1852). Early Miocene (Burdigalian), St-Paul-lès-Dax, 'Cabanes' (Landes, France), height 11 mm, Lozouet & Maestrati Coll. (MNHN).

Figs 8, 11. *Ancillina pusilla* (Fuchs *in* Karrer, 1877). Middle Miocene, Kostej (Rumania), height 6 mm (8), height 6.5 mm (11), SMF (Boettger Coll.).

Figs 9, 10. *Ancillina sumatrana* (Thiele, 1925). Campagne Musorstom 3, station 106, 13°47 N - 120°30 E (at depth 640-668 m), Philippine Islands, height 5.6 mm, MNHN (Bouchet & Triclot Coll.).

Specimens in Figs 1-4 and 8 were coated with ammonium chloride prior to photography.

PLATE 3

Maria Tembrock's scientific work, produced under the above-mentioned circumstances, is impressive and has justly found international acclaim. The main objectives of her studies were the gastropods of the Cainozoic North Sea Basin. The basic concepts that she consistently adhered to are the following:

— the gastropod shell is to be considered an entirety and yields a lot of information on ontogenetic and phylogenetic developments.

— of especial taxonomic importance are the embryonic whorls. These were relatively conservative during evolution and thus often preserve features which may indicate relationships.

— the development of genera and groups of genera in a regional setting becomes conceivable and tangible by proper arrangement in geological time of faunas and detailed studies of features in relation to chronostratigraphical position. Maria Tembrock's papers on muricids and on the genus *Scalaspira* from the North Sea Basin exemplify this very well.

— in addition to morphological studies, keeping in mind the development in time, an analysis of conditions of life should be considered, if one is to avoid serious misinterpretations. Ecological conditions may cause far-reaching but reversible phenotypic changes, of limited taxonomic and phylogenetic value. At the other extreme, shell morphology may not be sufficient to distinguish forms living in very different environments without overlap, so that these should be considered to represent separate species.

When Maria Tembrock started her career in the 1960s, these principles were hardly matter of course amongst malacologists, but became accepted more and more. In this respect, Maria Tembrock's work was pioneering. Several extensive papers (*e.g.* one on the Dentaliidae from the North Sea Basin) had been completed for over twenty years, but were not published because of a misplaced state security policy. As soon as these restrictions dropped, Maria Tembrock updated these papers, but she unfortunately could not complete these studies.

Maria Tembrock was always prepared to pass on her own experience to others. The author of the present obituary notice will always remember with gratitude the many discussions he had with her on scientific as well as personal matters, and her unselfish helpfulness.

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List of Dr M.L. Tembrock's papers

[This list includes only those papers that have actually been published in scientific journals]

Tembrock, M.L., 1958. Einige Zahlenverhältnisse bei den häufigsten Molluskenarten des Rupeltones von Freienwalde und Joachimstal. — Ber. geol. Gesellsch. DDR, 3: 136-138.

Tembrock, M.L., 1960. Zum Problem der Determination von Gastropodenschalen. — Ber. geol. Gesellsch. DDR, 5: 365-381, 2 pls.

Tembrock, M.L., 1962. Bemerkungen zur Molluskenfauna der Bohrungen Golßen 2, Drehna 5 (Lausitz) und des Fundpunktes Söllingen (Braunschweig). — Geologie, 11: 118-123, 1 tab.

Tembrock, M.L., 1963. Muriciden aus dem Mittel- und Oberoligozän und den Vierlandschichten des Nordseebeckens. — Paläont. Abhandl., (A)1(4): 299-351, 3 tabs, 10 pls.

Tembrock, M.L., 1964a. Taxionomie des Formenkreises "Fusus multisulcatus" Nyst, 1843 (Gastropoda). — Ber. geol. Gesellsch. DDR, 9: 304-310, 3 pls.

Tembrock, M.L., 1964b. Einige Beispiele von Faziesabhängigkeit bei tertiären Gastropoden. — Ber. geol. Gesellsch. DDR, 9: 311-337, 6 pls.

Tembrock, M.L., 1965a. Erläuterungen zur Gattung Streptochetus Cossmann (Gastropoda). — Senckenb. leth. (Weiler-Festschrift), 46a: 427-439, 4 figs, 1 pl.

Tembrock, M.L., 1965b. Zur Systematik einiger problematischer Caeciden-Gattungen (Gastropoda). — Abhandl. Zentr. Geol. Inst. Berlin, 1: 81-93, 1 pl.

Tembrock, M.L., 1965c. Zum Artproblem bei Gastropoden, erläutert an den Scalaspira (al. "Aquilofusus")-Arten des norddeutschen Oligozäns und Miozäns. — Ber. geol. Gesellsch. DDR, 10: 429-438, 1 pl.

Tembrock, M.L., 1967. Book review [Die Miozän-Mediterranen Gastropoden Ungarns, by L. Strausz]. — Ber. deutsch. Gesellsch. geol. Wiss., A. Geol. Paläont., 12: 741-743.

Tembrock, M.L., 1968. Taxionomisch-stratigraphische Studie zur Scalaspira-Gruppe (Gastropoda, Tertiär). — Paläont. Abhandl., (A)3(2): 193-366, 2 figs, 2 tabs, 18 pls.

Tembrock, M.L., 1982. Eine Sammlung obereozäner, oligozäner und miozäner Mollusken aus der La-Tène-Zeit. — Z. geol. Wiss., 10: 1387-1391, 1 pl.

Tembrock, M.L., 1989. Neue Spiratella-Arten (Gastropoda, Opisthobranchier, Pteropoda). — Z. angew. Geol., 35: 242-244, 1 pl.

Strauch, F., & M.L. Tembrock, 1978. Marine Molluskenreste. In: K. Brunnacker (ed.). Geowissenschaftliche Untersuchungen in Gönnersdorf: 231-233. Wiesbaden.