

Contributions to eratoid systematics (Mollusca, Gastropoda), 1. Early Pliocene Eratoidae from the western Mediterranean

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The species-rich, Early Pliocene eratoid gastropod faunas occurring around Estepona (southern Spain) are systematically revised, a new species, *Erato globosa* n. sp., is described and illustrated, and eratoid faunas are compared with others of Neogene age elsewhere in the Mediterranean.

KEY WORDS: Mollusca, Gastropoda, Eratoidae, Zanclean, western Mediterranean, systematics.

Introduction

Few molluscan families have been viewed as controversial as the Eratoidae. Members of this family, widely distributed both geographically and stratigraphically, are all small and at first sight share closely similar morphological shell features. This has led many previous authors to treat eratoid faunas in a somewhat subjective way, often lumping them within widely polytypic species.

The same problems surround the taxonomy of the various forms from the Mediterranean Neogene, with some authors distinguishing various species (Sacco, 1894; Schilder, 1932, 1933), whilst others recognised but a single, highly polytypic taxon (Cavallo & Repetto, 1992; Caprotti, 1976; Inzani, 1985).

Franz Alfred Schilder was the first to try to instil some objectivity and order into the differentiation of the Eratoidae, using mathematical measurements of shell characteristics and tabulating his results to show the differences between the species. Schilder's criteria have been ignored by most subsequent workers, because of their 'rather complicated character, which needs time-consuming, in-depth analysis' (Cate, 1979, pp. 5, 78, 79). Nevertheless, the present authors feel Schilder's formulae form a sound, albeit somewhat complicated and visually uninviting, basis for the differentiation of a group of shells so similar that only careful attention to detail can differentiate.

Schilder (1932, 1933) distinguished a large number of species, tabulating the differences between them. Unfortunately, his descriptions are mostly incomplete, often comprising merely a comparison with another species,

and not always the most closely similar. Schilder (1932) examined the Miocene fossils from Italy in the Sacco Collection, but probably never studied the Pliocene material, his reclassification having been based on shells sent to him and on illustrations in previous publications.

In the present paper we not only describe all the characters considered important by Schilder, but our attention was drawn to the protoconch, preserved in a large number of the specimens available to us. This structure has so far not been used to distinguish eratoid species. In extant species, the protoconch is covered and obscured by callus. In contrast, in many of the specimens from Estepona taphonomic processes have removed this callus, allowing us to observe quite a variety of forms.

Geological setting

Only in recent years have the extremely rich deposits from around Estepona received attention in the literature, with the emphasis on molluscs (*e.g.*, Véra-Peláez *et al.*, 1995; Muñiz-Solis, 1995; Landau & Marquet, 1999, 2000). Molluscan diversity is high, with over 700 species of gastropod known to date (BL, pers. obs.). Sanz de Galdeano & López Garrido (1991) are here referred to for stratigraphical, tectonic and palaeogeographical data on the Málaga Basin. During the Tortonian (Miocene), an extended seaway existed between the Mediterranean (Málaga area) to the Atlantic, via the Guadalquivir and Ronda basins; during the Pliocene, this basin was much smaller, extending inland for *c.* 30 km from the Málaga-Torremolinos area. Pliocene sediments also outcrop

along the coast, southwest to Estepona; this series comprises conglomerates and sands, changing laterally into bluish grey marls and clays, topped by yellowish white sands. This series reaches a maximum thickness of c. 400 m in the easternmost areas, and the age ranges from Early/Middle to early Late Pliocene. Uppermost Pliocene and Quaternary sediments in the area are of terrestrial origin.

The present paper is based on material collected at four localities, all situated 5.5 to 9 km northeast of Estepona. Deposits here consist of a variety of different facies, from coarse-grained sands (Velerín Sands), representing nearshore or beach deposits, to fine clayey sands (Velerín Carretera, Padrón), deposited at relatively greater depths, and to a coarse conglomerate (Velerín Conglomerates). These conglomerates, which must have been deposited relatively rapidly or under storm conditions, contain the richest fauna: a curious admixture of large and small water-worn as well as pristine shells amongst rocks and lumps of mudstone of varying sizes.

Systematic palaeontology

Abbreviations — The following abbreviations are used in the text to denote the repositories of material studied:

- BLP B. Landau Colln, Albufeira;
 BS Bellardi & Sacco collections, Torino;
 CS F.A. Schilder Colln, provisionally deposited at the Naturkunde Museum der Humboldt Universität, Berlin;
 DFB D. Fehse Colln, Berlin;
 HNC Haus der Natur, Cismar.

To describe eratoid shells the following abbreviations (after Schilder, 1933, pp. 250-253) are used:

- L length of outer lip expressed in tenths of mm (10 = 1 mm)
 Sp projection of spire: average index = 100 x total length/length of outer lip
 BL relative breadth: average index = 100 x width/length of outer lip
 D ornament on dorsum:
 - smooth
 g granular on spire and posterior part
 G granular throughout
 SD dorsal sulcus:
 - absent
 v indicated by small impression behind anterior extremity
 s marked
 n deeply excavated
 pd (plicae dextrae) = absolute number of labial teeth
 ps (plicae sinistrae) = absolute number of columellar teeth

pd+ps expression of average relative density of labial and columellar teeth, e.g. hypothetical number of teeth in shells the length of outer lip of which is 5 mm. Anterior columellar ridges have been included. Of species in which the columellar teeth invariably become obsolete posteriorly, the relative density ps is replaced by a cross (+). The relative densities of teeth are found by the formula:

$$pd = 7 + [5(PD - 7)^2 / \text{length of outer lip}]^{1/2}$$

$$ps = 7 + [5(PS - 7)^2 / \text{length of outer lip}]^{1/2}$$

- PT (plicae terminalis) = terminal ridge of the columellar ridge
 A - coarse, simple bordering the outlet, the following columellar teeth are small
 B - coarse, double (split longitudinally), columellar teeth are small
 C - several oblique ridges gradually pass into columellar teeth
 D - like C, but ridges nearly transverse
 E - first ridge bordering the outlet becomes obsolete, whereas second one is coarse, oblique to transverse
 F - like C, but ridges radially convergent and often confluent along aperture
 F fossula:
 - completely absent
 v obsolete or nearly so
 s narrow, gradually sloping from the terminal ridge posteriorly
 n broad, angularly projecting anteriorly
 p very broad and concave
 d denticulate on its inner margin
 c transversely costate

psp number of shells (in per cent) in which the posterior columellar teeth are well developed so that they can be counted along the whole length of the lip.

Superfamily Trivioidea Troschel, 1863
 Family Eratoidea Schilder, 1925
 Subfamily Eratoinae Schilder, 1925
 Genus *Erato* Risso, 1826

Type species — *Voluta cypraeola* Brocchi, 1814, by monotypy.

Erato pieris De Stefani & Pantanelli, 1879

Figures 1, 3, 8, 37/1

- *1879 *Erato pieris* De Stefani & Pantanelli, p. 138.
- 1880 *Erato brevispira* Seguenza, p. 253.
- 1894 *Erato laevis* var. *brevispira* Segu. — Sacco, p. 60, pl. 3, fig. 66.
- 1925 *Erato (Erato) pieris* Stef. Pant. — Schilder, p. 59.
- 1932 *Erato (E.) cypraeola pieris* Stef. & Pant. — Schilder, p. 90.
- 1933 *Erato (Erato) pieris* Stefani & Pantanelli, 1878 — Schilder, pp. 250, 254, 259, 269, text-fig. 75.
- 1971 *Erato (Erato) pieris pieris* Stefani-Pantanelli, 1878 — Schilder & Schilder, p. 14.
- 1984 *Erato laevis* var. *brevispira* Seguenza, 1880 — Ferrero Mortara *et al.*, pp. 157, 329.

Type — The type specimen should be in the collections of the museum at Modena. No details are available.

Stratum typicum — Lower Piacenzian (Middle Pliocene).

Locus typicus — Siena (Tuscany, Italy).

Distribution — Sacco (1894, p. 60) listed Villavernia, Fontanili, Piacentino, Zinola, R. Torsero; Schilder (1932, p. 90) added Guistrigona, Podere Sant'Uliviere, Pietrafitta (all Lower Piacenzian) and Siena, Monte Mario. Upper Piacenzian of Italy and Zanclean (Velerin Conglomerates, Velerin Carretera, Estepona) of Spain.

Material studied — from the Velerin Conglomerates, 20 specimens (BLP), 4 specimens (DFB).

Description — Shell very large, solid, elongated pyriform, inflated with a relatively high, conical spire. Protoconch usually covered by callus, but visible in a single specimen; consisting of 2 1/2 rapidly expanding, elevated whorls, with a small nucleus. An axial ornament of fine, close-set, wavy lines covers the entire protoconch. Suture distinct and somewhat incised. Junction with teleoconch clearly defined. Teleoconch of about 3 weakly convex whorls, covered by callus which obscures the suture. Body whorl almost 80-90% of total height, shouldered adapically, with the maximum diameter 1/4 distance from the adapical suture, rounded below and constricted at the base. Dorsum smooth, rounded, with the dorsal sulcus reduced to a small dimple behind the anterior extremity, where the shell is strongly constricted. The shell surface is covered with a heavy, smooth, glossy callus. Aperture almost 80% of total height, straight and narrow, although slightly wider in the area of the anal canal and fossula. Outer lip very greatly thickened, smooth, with the outer margin evenly rounded, bearing 19-24 weak denticles, which extend a short distance onto the lip. The denticulate area of the outer lip tapers into the aperture. Siphonal canal relatively long, rounded and straight. Columella smooth and sinuous, bordered internally by a weak carinal ridge. The outer border usually bears a row of 9-11 denticles on the anterior portion, becoming obsolete in the mid-portion, with 4-5 weaker denticles on

the posterior portion. The most anterior 3-4 denticles are developed into folds, which run obliquely across the base. Fossula broad, concave and poorly delimited from the columella. Terminal ridge simple, short and weakly developed.

Range of variation — This is the largest species of *Erato* found at Estepona. It is fairly constant in shape and the dorsal dimple is almost always present. The height of the spire is variable. The number of teeth on the outer lip also varies, although they are always weak and poorly expanded. The dentition on the columella and number of teeth at the anterior extremity developed into folds is also variable. The weaker denticles on the posterior portion of the columella are occasionally absent.

Discussion — Schilder & Schilder (1971, p. 14) ranked *E. subalata* Sacco, 1894 as a subspecies of *E. pieris*. At Estepona, these taxa co-occur, which makes the subspecific status of the former impossible. *Erato pieris* differs in being much larger with a higher spire; it lacks the wing-like adaxial expansion of the outer lip seen in *E. subalata*. In addition, the teeth on the outer lip extend further and the area of lip tapering into the aperture is wider. In *E. subalata*, a groove runs along the posterior portion of the columella adaxially and obliquely inwards starting at the posterior extremity of the fossula. There is also a trace of a reddish colour pattern on the protoconch and on either extremity of the outer lip, which is absent in *E. pieris*. The protoconch, visible in one of the specimens, is most unusual. The axial ornament, best compared in pattern to the rootlets of a plant, we have not seen in any other eratoid species.

Erato pieris is uncommon at Estepona, occurring exclusively in the conglomerates.

Erato subalata Sacco, 1894

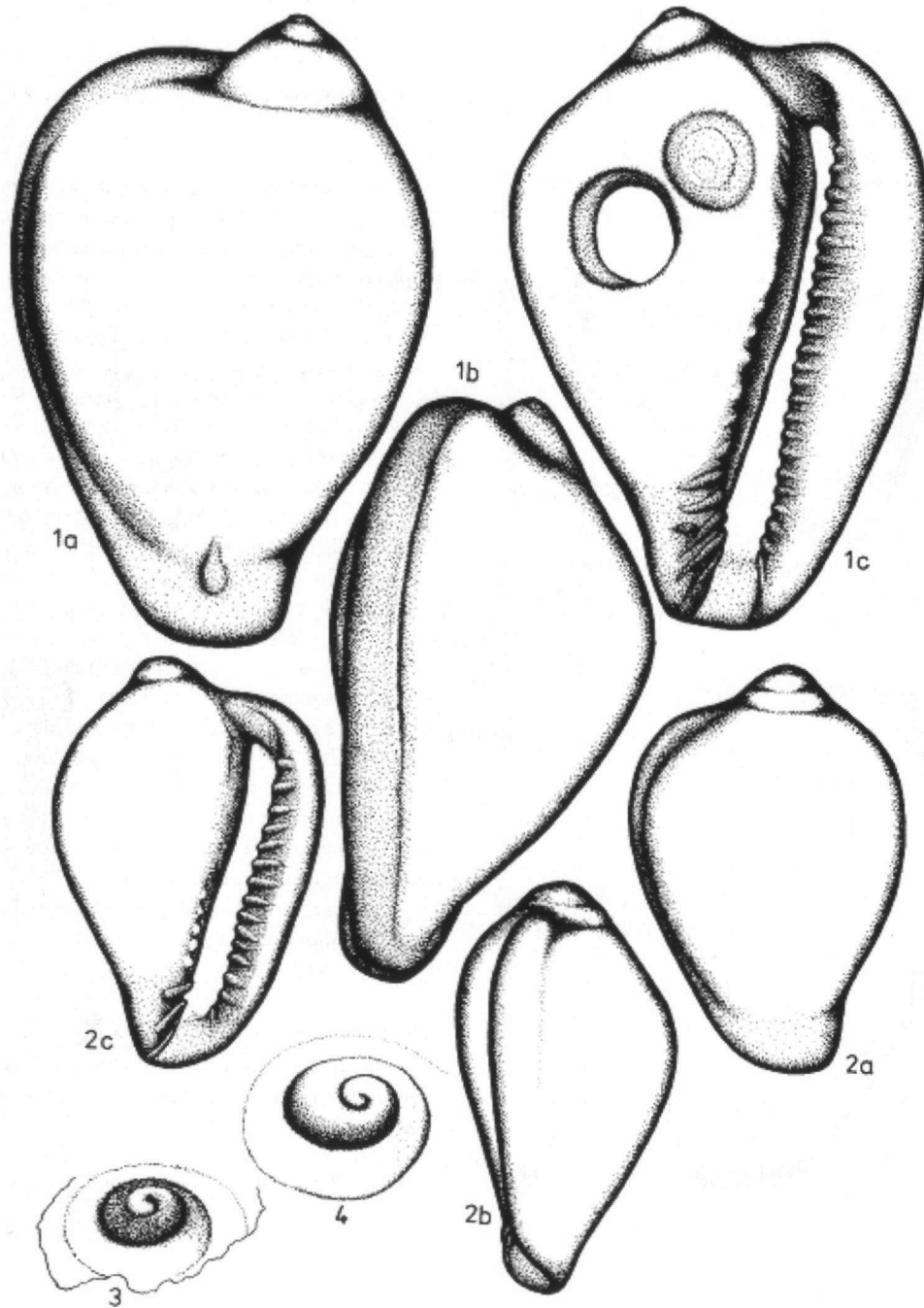
Figures 5-7, 37/2

- *1894 *Erato laevis* var. *subalata* Sacco, p. 61, pl. 3, fig. 68.
- 1932 *Erato (E.) subalata* Sacco 1894 — Schilder, p. 90.
- 1933 *Erato (Erato) subalata* Sacco, 1894 — Schilder, p. 272.
- 1971 *Erato (Erato) pieris subalata* Sacco, 1894 — Schilder & Schilder, p. 14.
- 1984 *Erato laevis* var. *subalata* Sacco, 1894 — Ferrero Mortara *et al.*, pp. 157, 329.

Type — Holotype is BS 043.15.008.

Stratum typicum — Lower Piacenzian (Middle Pliocene).

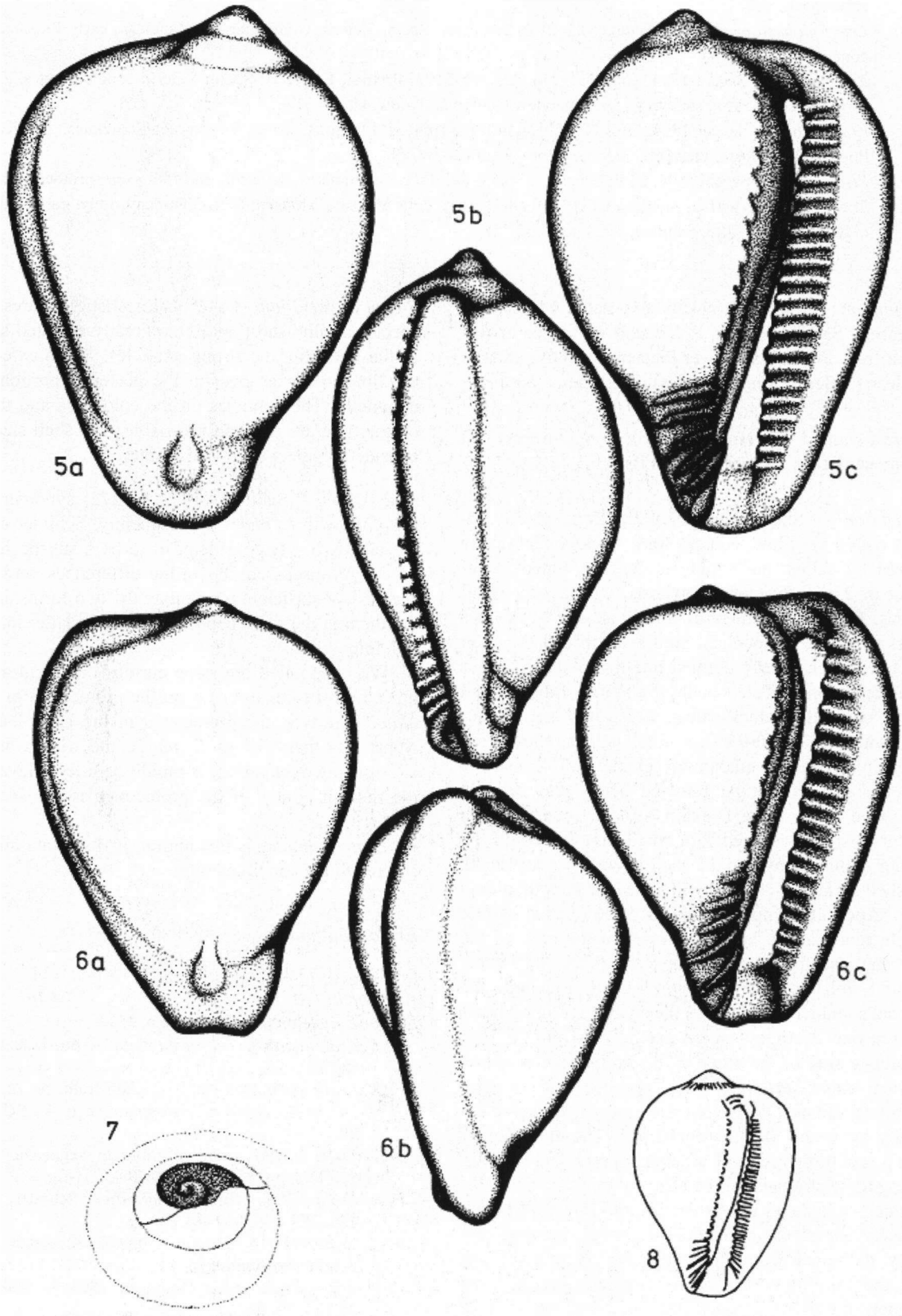
Locus typicus — Sacco (1894, p. 61) did not indicate a type locality.



(drawings by D. Fehse)

Fig. 1. *Erato pieris* De Stefani & Pantanelli, 1879, coll. DFB No. 2212A14211710[6462], Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 1a - dorsal view, 1b - side view, 1c - ventral view, x9.

Fig. 2. *Erato globosa* n. sp., (paratype 2), coll. DFB No. 2212A14211723[6467], Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 2a - dorsal view, 2b - side view, 2c - ventral view, x9.



- Fig. 3. *Erato pieris* De Stefani & Pantanelli, 1879, coll. BLP, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; protoconch, x18.
- Fig. 4. *Erato globosa* n. sp., (paratype), coll. BLP, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; protoconch, x18.
- Fig. 5. *Erato subalata* Sacco, 1894, coll. DFB No. 22I2A14211714[6464], Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 5a - dorsal view, 5b - side view, 5c - ventral view, x9.
- Fig. 6. *Erato subalata* Sacco, 1894, DFB No. 22I2A14211711[6463], Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 6a - dorsal view, 6b - side view, 6c - ventral view, x9.
- Fig. 7. *Erato subalata* Sacco, 1894, BLP, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; protoconch, x18.
- Fig. 8. *Erato pieris* De Stefani & Pantanelli, 1879 (holotype), coll. Museum Modena, Siena, Tuscany, Italy, early Piacenzian, middle Pliocene (after Schilder, 1933, text fig. 75).

Distribution — Sacco (1894, p. 61) listed Masserano, Piacentino, Savona, Zinola, R. Torsero, Bordighera; also known from Pietrafitta (Lower Piacenzian, Italy) and the Zanclean (Velerín Conglomerates) of Estepona (Spain).

Material studied — from the Velerín Conglomerates, 20 specimens (BLP), 5 specimens (DFB).

Description — Shell large, solid, pyriform, greatly inflated with a very low, conical spire. Protoconch mostly covered by callus, but visible in four specimens; consisting of 2 slightly elevated whorls, with a very small nucleus. An axial ornament of fine, close-set, wavy lines covers the entire protoconch. Suture superficial. Junction with teleoconch clearly defined due to a reddish colour on the protoconch. Teleoconch of about 3 straight-sided whorls, covered by thick callus, which obscures the suture. Body whorl 90-95% of total height, shouldered adapically, with the maximum diameter 1/4 distance from the adapical suture, rounded below and strongly constricted at the base. Dorsum smooth, rounded, with the dorsal sulcus reduced to a small dimple behind the anterior extremity, where the shell is weakly constricted. The shell surface is covered with a heavy, smooth, glossy callus. Aperture comprising almost 90% of total height, straight and narrow, although wider in the area of the anal canal and fossula. Outer lip very greatly thickened, smooth, with the outer margin evenly rounded, the adapical shoulder rising above the aperture. The lip bears 16-19 strong denticles, which extend onto the lip. The denticulate area of the outer lip tapers into the aperture. Siphonal canal relatively long, rounded and straight. Columella sinuous, or weakly so, smooth, bordered internally by a very weak carinal ridge. The outer border bears a row of denticles of varying strength and number, tending to be strongest in the abapical portion. The most anterior 3-5 denticles are developed into folds, which run obliquely across the base. Fossula broad, concave and poorly delimited from the columella. A groove runs along the posterior portion of the columella adaxially and obliquely inwards starting at the posterior extremity of the fossula. Terminal ridge simple, short and weakly developed.

Range of variation — The characteristic features of this species are the short spire, the greatly elevated shoulder of the outer lip, the strong denticles, which extend onto the lip and the groove on the posterior portion of the columella. The denticles on the columella and the folds on the base are extremely variable. The shell size varies considerably between 8 and 13 mm.

Discussion — Schilder (1933, p. 272) synonymised *E. subalata* with *E. pieris*. Subsequently, Schilder & Schilder (1971, p. 14) considered it to be a subspecies of *E. pieris*. As discussed above, the differences between the species are sufficient to separate the two forms and finding them in the same deposits makes the latter interpretation impossible.

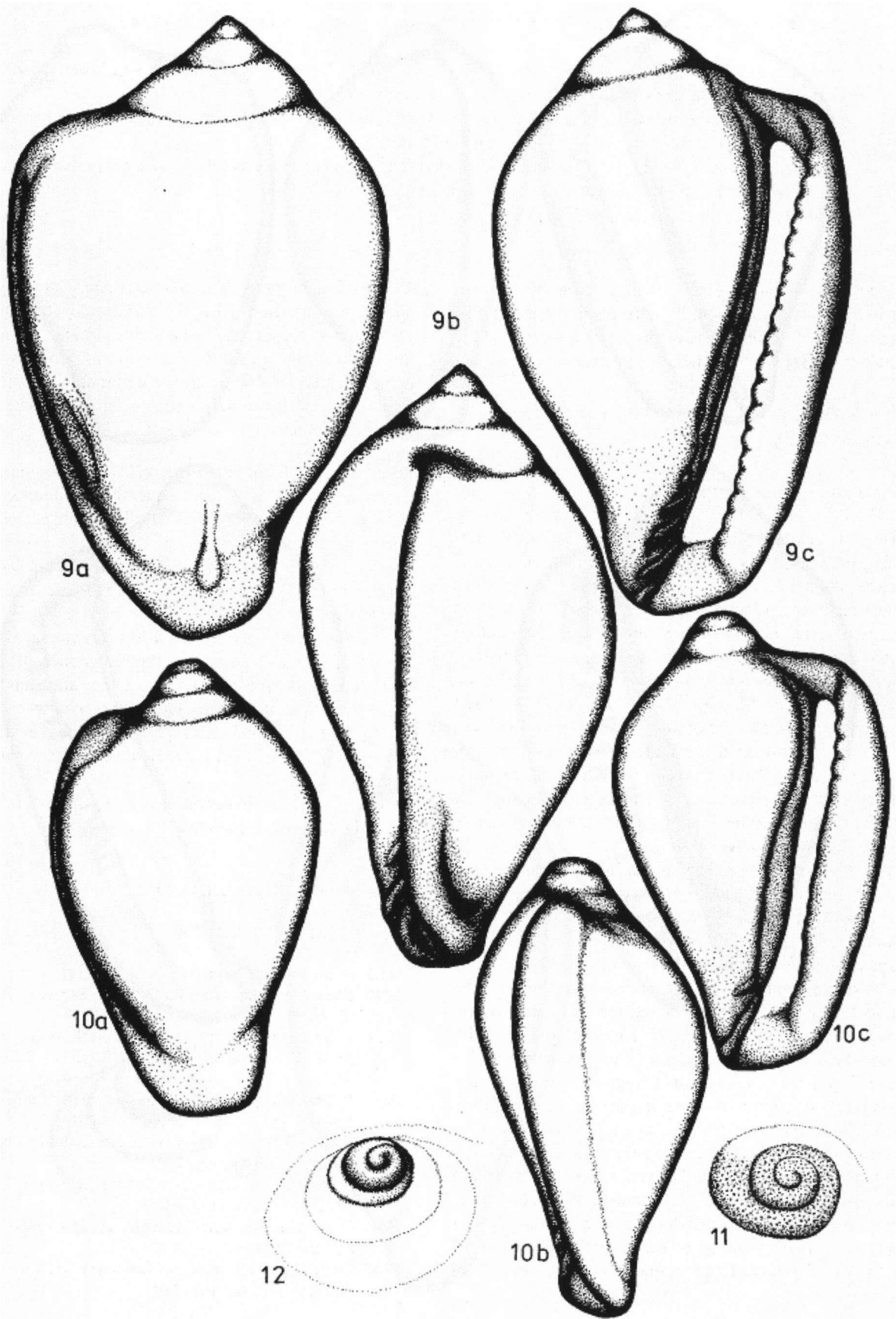
We have noted the same curious ornament as in the preceding species to occur on the protoconch of *E. subalata*. However, the protoconch of the latter has half a whorl less than that of *E. pieris*, the whorls are more closely coiled, expand less rapidly, are less elevated and the reddish colour of the protoconch is not seen in *E. pieris*.

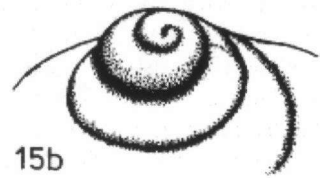
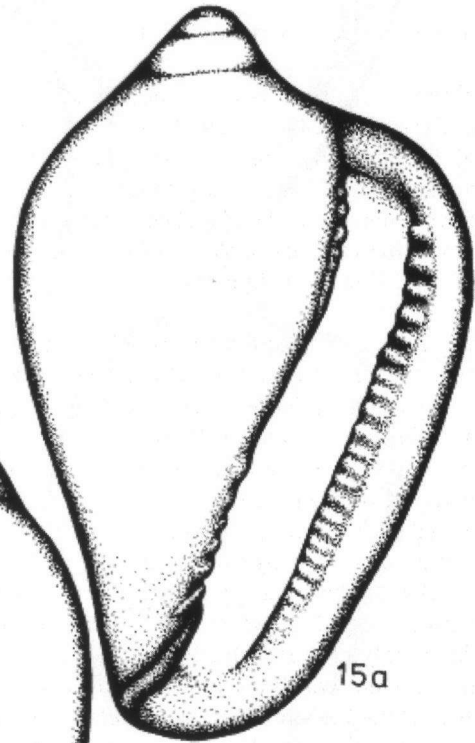
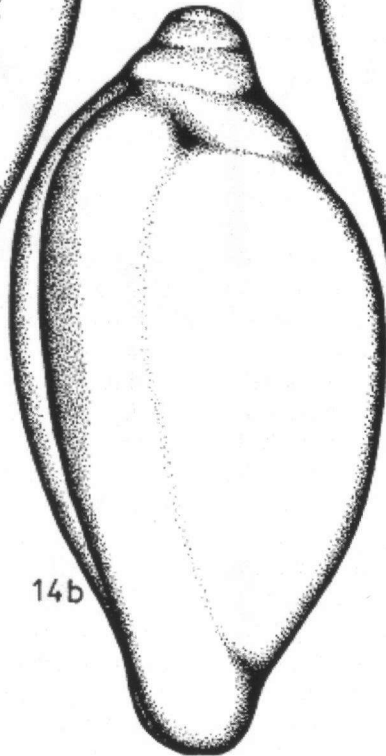
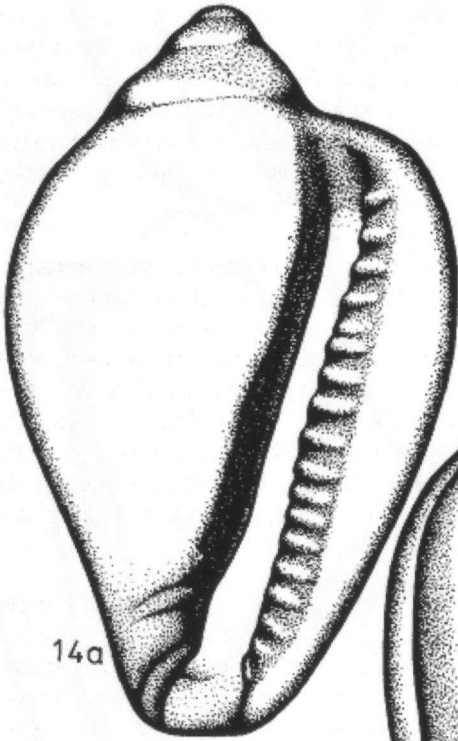
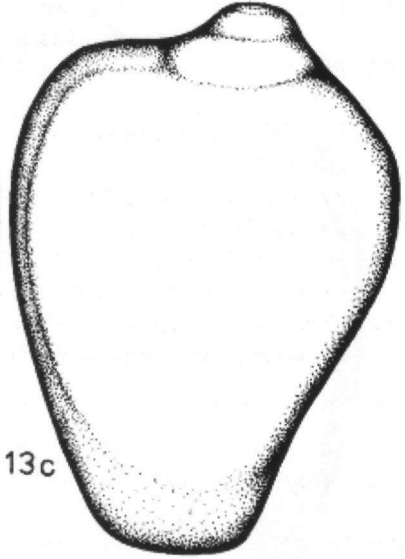
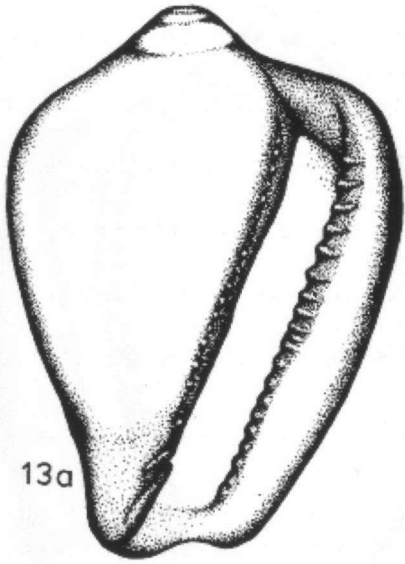
Erato subalata is uncommon in Estepona and is restricted to the conglomerates.

Erato elongata Seguenza, 1880

Figures 10, 12, 15, 28, 37/3-4

- *1880 *Erato elongata* Seguenza, p. 253.
1894 *Erato laevis* var. *elongata* Segu. — Sacco, p. 60, pl. 3, fig. 65.
1911 *Erato laevis* Don. sp. — Cerulli-Irelli, pl. 26, figs 23, 24. 1932 *Erato (E.) elongata* Segu. — Schilder, p. 90.
1933 *Erato (Erato) elongata elongata* Seguenza, 1880 — Schilder, pp. 250, 254, 259, 264, text-fig. 81.
1933 *Erato (Erato) voluta panormitana* Schilder, pp. 250, 254, 259, 269, text-fig. 83.
1971 *Erato (Erato) elongata elongata* Seguenza 1880 — Schilder & Schilder, p. 14.
1974 *Erato (Erato) voluta* (Montagu, 1803) — Malatesta, p. 247, pl. 19, fig. 6.
1984 *Erato laevis* var. *elongata* Seguenza, 1880 — Ferrero Mortara *et al.*, pp. 157, 329.





- Fig. 9. *Erato cerullii* Schilder, 1933, coll. DFB No. 22I2A14211721[6465], Estepona, Spain, Velerín Conglomerates, Zanclean, early Pliocene; 9a - dorsal view, 9b - side view, 9c - ventral view rotated to view fossular area, x9.
- Fig. 10. *Erato elongata* Seguenza, 1880, coll. DFB No. 22I2A14211722[6466], Estepona, Spain, Velerín Conglomerates, Zanclean, early Pliocene; 10a - dorsal view, 10b - side view, 10c - ventral view, x9.
- Fig. 11. *Erato cerullii* Schilder, 1933, coll. BLP, Estepona, Spain, Velerín Conglomerates, Zanclean, early Pliocene; protoconch, x18.
- Fig. 12. *Erato elongata* Seguenza, 1880, coll. BLP, Estepona, Spain, Velerín Conglomerates, Zanclean, early Pliocene; protoconch, x18.
- Fig. 13. *Hespererato cocconii* Schilder, 1933 (holotype of *Erato etrusca* Schilder, 1933), coll. CS 5118, Siena, Italy, late Piacenzian, late Pliocene; 13a - ventral view, 13b - side view, 13c - dorsal view, x9.
- Fig. 14. *Erato spiralis* Döderlein, 1862 in Sacco, 1894 (hypotype), coll. CS 5087, Monte Gibbio, Italy, Tortonian, middle Miocene; 14a - ventral view, 14b - side view, x9.
- Fig. 15. *Erato elongata* Seguenza, 1880 (holotype of *Erato panormitana* Schilder, 1933), coll. CS 5166, Monte Pellegrino, Italy, Pleistocene; 15a - ventral view, 15b - Protoconch, x18.

Type — Neotype, here designated, is CS 5109.

Stratum typicum — Upper Piacenzian (Upper Pliocene).

Locus typicus — Asti (northern Italy).

Distribution — Sacco (1894, p. 60) listed Piacentino, Savona, Zinola, Albenga,...., Bordighera; Schilder (1933, p. 250) added Sicily; also known from Rio Torsero (Lower Piacenzian) and Astigiana, Altavilla (Upper Piacenzian), Italy, and the Zanclean Arenas de Huelva Formation, Huelva (Spain), Velerín Conglomerates, Velerín Carretera (Estepona, Spain).

Material studied — from the Velerín Conglomerates, 30 specimens (BLP), 9 specimens (DFB); from Velerín Carretera, 15 specimens (BLP); from the Velerín Sands, 3 specimens (BLP), 1 specimen (DFB).

Description — Shell medium sized, relatively solid, elongated pyriform with an elevated, somewhat pointed spire. Protoconch mostly covered by callus, but visible in numerous specimens; consisting of 2½-2¾ whorls, with a small nucleus. The first protoconch whorl is tightly coiled and depressed, the second is convex, elevated and expands rapidly. Suture clearly marked and incised. Junction with teleoconch not clearly defined. Teleoconch consists of about 2½ straight-sided whorls. The first teleoconch whorl is shorter than the preceding protoconch whorl. Spire covered by very thin callus, which partly obscures the suture. Body whorl 80% of total height, shouldered adapically, with the maximum diameter 1/4 distance from the adapical suture, evenly tapered below and only slightly constricted at the base. Dorsum smooth, rounded, without any dorsal sulcus. The shell surface is covered by a very thin callus, which is only partially preserved in most specimens. Aperture comprising about 75% of total height, straight and narrow. Outer lip thickened, smooth, with the outer margin evenly rounded, bearing 14-19 weak to very weak denticles, which are subobsolete in fully-grown specimens and do not extend

onto the lip. Siphonal canal elongated, rounded and straight to recurved. Columella almost straight, with the carinal ridge developed only weakly in the fossular area. Columellar denticles present only in juvenile specimens. One or two short folds of variable strength are present on the base. Fossula indistinct, limited to a weak concave depression and poorly delimited from the columella. The inner border of the fossular area is weakly convex, extending into the aperture. Terminal ridge simple, short and weakly developed.

Range of variation — The characteristic features of this species are the high spire, elongated shape and the simplicity of the labial and columellar ornament. The denticles on both sides of the aperture are more evident in juvenile specimens, but become obsolete, or nearly so in fully-grown specimens. The siphonal canal may be straight or more elongated and recurved. The folds on the base are very variable, in some specimens obsolete, whereas in others strong and running very obliquely along the base.

Discussion — This species was not clearly defined by Seguenza (1880), whose description was merely a comparison to another species, lacking an illustration. Unfortunately, most of the Seguenza Collection was lost during an earthquake in Messina. Both Sacco (1894, pl. 3, fig. 65) and Schilder (1933, text-fig. 81) illustrated their own specimens without comparing them with the 'type'. Schilder (1933, p. 264) wrote, 'Seguenza's description may be referred to the small, slender Astian *Erato* from Italy; the shell figured by Sacco (1894) from Astigiana (Mus. Torino) represents the same species.'. Although the type is lost, all the authors seem to be referring to the same species. For this reason, we here designate neotype Schilder's specimen.

The elongated form and other characteristics mentioned above clearly distinguish *E. elongata* from *E. pieris* and *E. subalata*. The protoconch of the first-named is also quite different, less depressed with a rapidly ex-

panding, convex second whorl and devoid of ornament. The transitional area between the protoconch and adult shell is narrow in *E. elongata*, which is not seen in the other species.

This is the oldest record of *E. elongata*, which also occurs in the Middle/Upper Pliocene of Italy, and survives into the Lower Pleistocene of Monte Mario, Italy (Cerulli-Irelli, 1911, pl. 26, figs 23, 24). It is common at Estepona, in both nearshore and deeper-water deposits.

Cerulli-Irelli sent Schilder the Monte Mario Collection from the Lower Pleistocene of Italy (Schilder, 1933, p. 269, wrote, 'Type from Monte Pellegrino'). He created a new subspecies, *Erato voluta panormitana*, restricted to these Pleistocene deposits. In our opinion, this is synonymous with *E. elongata* (compare Figure 15).

Erato globosa n. sp.

Figures 2, 4, 37/6

Types — Holotype is HNC 57201; paratypes are HNC 57202, two specimens (DFB) and six specimens (BLP).

Stratum typicum — Zanclean (Lower Pliocene).

Locus typicus — Estepona, Spain.

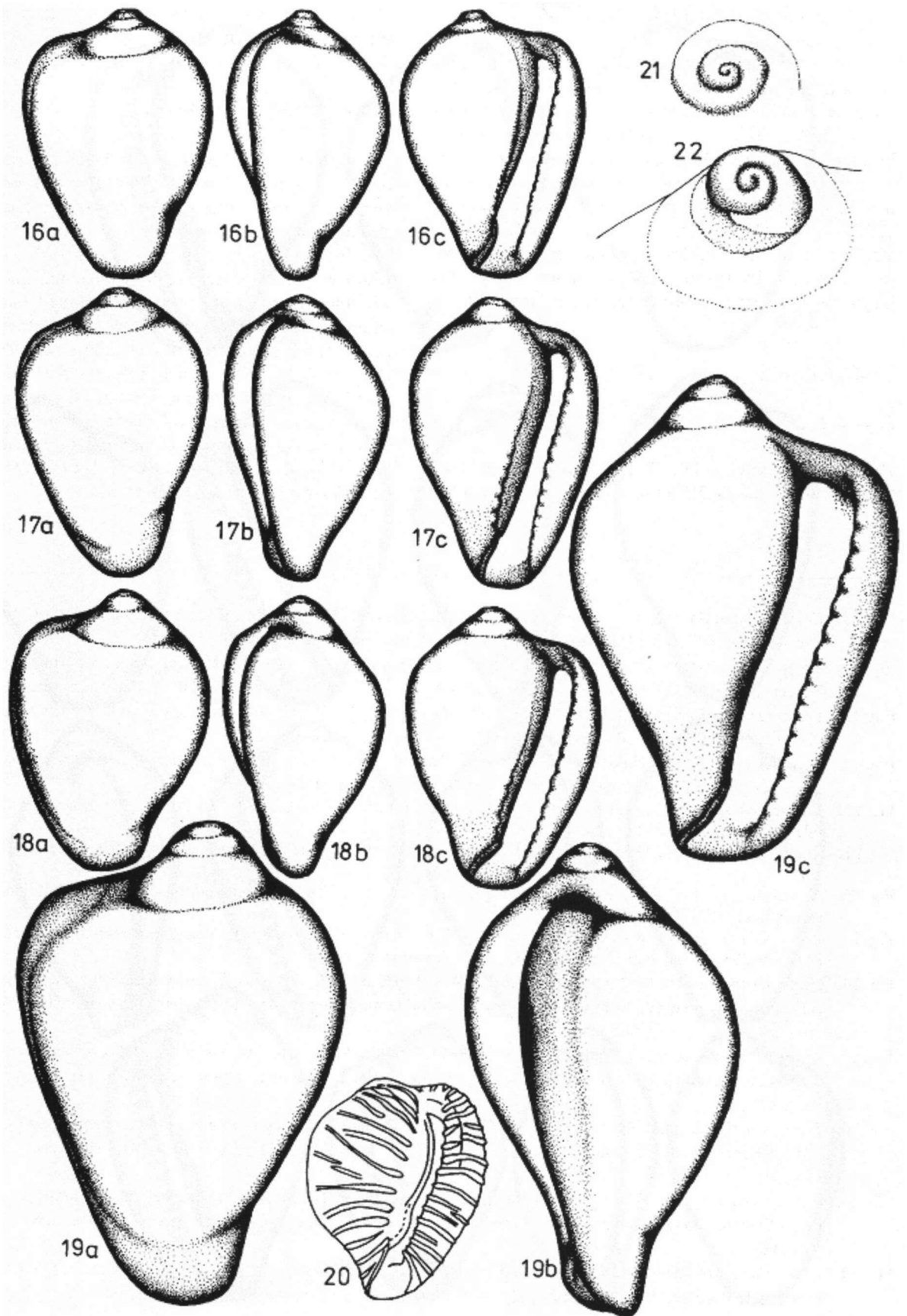
Derivatio nominis — Latin *globosus*, in reference to the spherical protoconch.

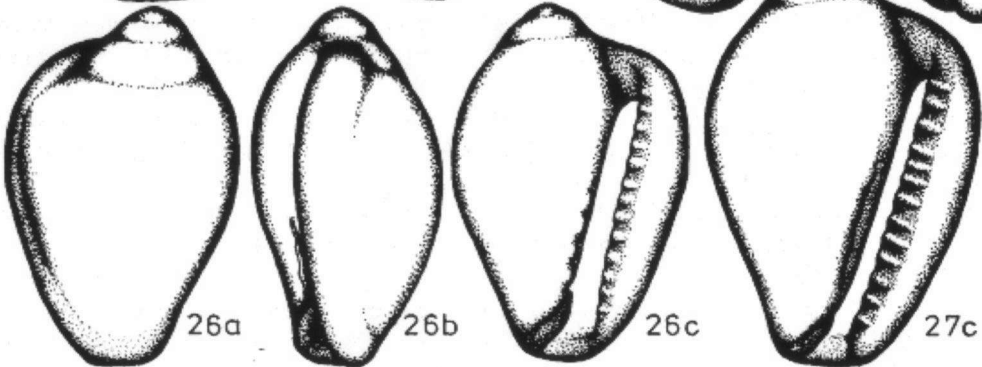
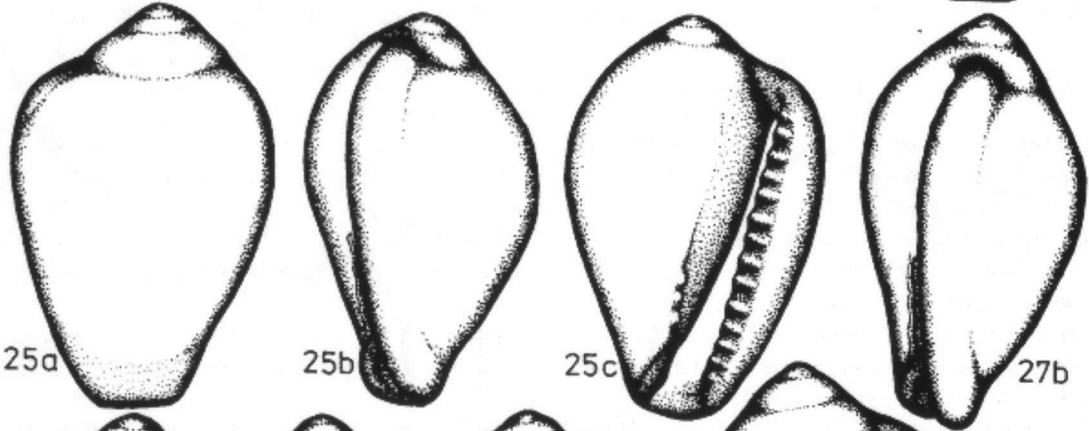
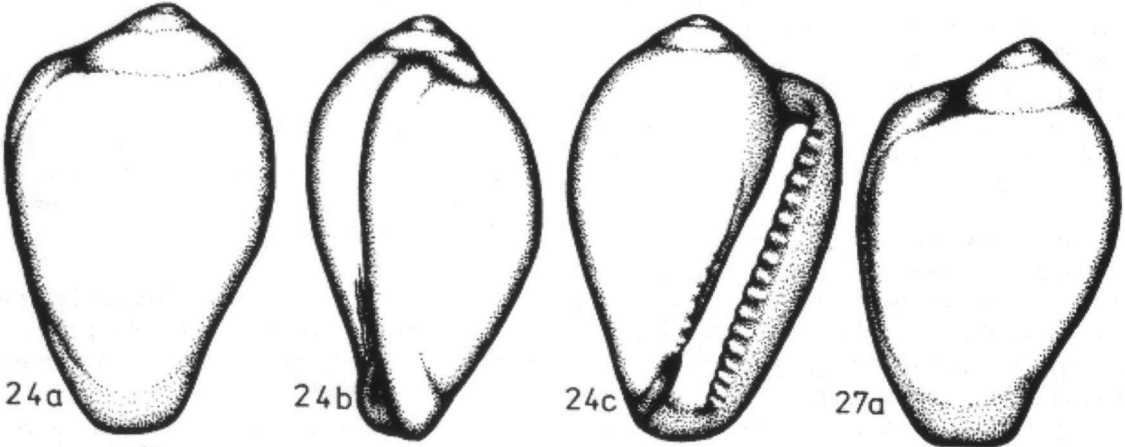
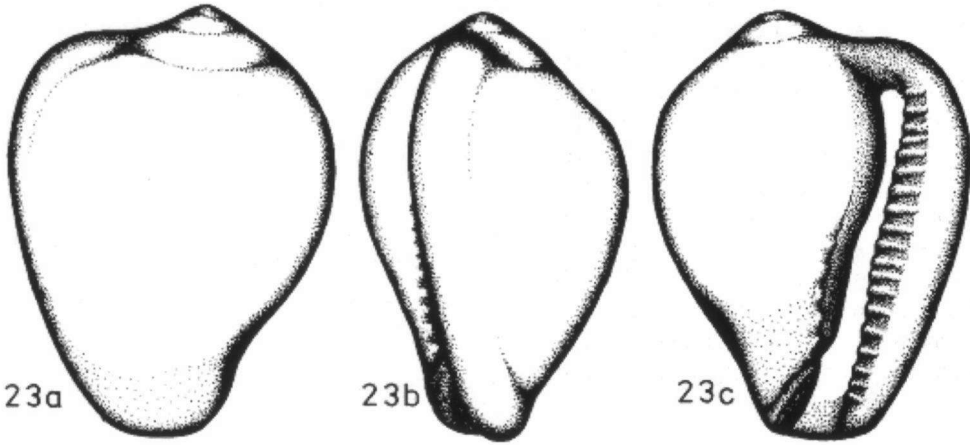
Distribution — Known only from the type locality.

Material studied — see above.

Description — Shell medium sized, solid, pyriform, globose and squat with a very low, rounded spire. Apex covered by thin callus, under which a broad, bubble-shaped protoconch, consisting of 2¼ whorls, is visible. The protoconch has a small nucleus with the second whorl very convex and rapidly expanding. The junction with the teleoconch is not clearly delimited, but the transitional area is much narrower than the preceding teleoconch whorl. Teleoconch of 2 straight-sided whorls, covered by thick callus, which obscures the suture. Body whorl 90% of total height, shouldered adapically, with the maximum diameter 1/4 distance from the adapical suture, rounded below and strongly constricted at the base. Dorsum smooth, rounded, without a dorsal sulcus, constricted at the anterior extremity.

- Fig. 16. *Erato pernana* Sacco, 1894, juvenile, coll. DFB No. 22I2A14211817[6470]A, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 16a - dorsal view, 16b - side view, 16c - ventral view, x9.
- Fig. 17. *Erato pernana* Sacco, 1894, juvenile, coll. DFB No. 22I2A14211817[6470]B, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 17a - dorsal view, 17b - side view, 17c - ventral view rotated to view fossular area, x9.
- Fig. 18. *Erato pernana* Sacco, 1894, juvenile, coll. DFB No. 22I2A14211817[6470]C, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 18a - dorsal view, 18b - side view, 18c - ventral view, x9.
- Fig. 19. *Hespererato cocconii* Schilder, 1933, DFB No. 22I2A14211811[6469], Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 19a - dorsal view, 19b - side view, 19c - ventral view, x9.
- Fig. 20. *Eratopsis barrandei* Hoernes & Auinger, 1880 (*hypotype*) coll. CS 3627, Niederleis, Austria, Badenian, middle Miocene (after Schilder, 1933, text fig. 61).
- Fig. 21. *Erato pernana* Sacco, 1894, coll. BLP, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; protoconch, x18.
- Fig. 22. *Hespererato cocconii* Schilder, 1933, coll. BLP, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; protoconch, x18.
- Fig. 23. *Erato pernana* Sacco, 1894, coll. DFB 22I2A14211613[6458], Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 23a - dorsal view, 23b - side view, 23c - ventral view, x9.
- Fig. 24. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211620[6461]A, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, elongated form with an edged, non-bifid terminal ridge; 24a - dorsal view, 24b - side view, 24c - ventral view, x9.
- Fig. 25. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211620[6461]B, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, elongated form with an edged, non-bifid terminal ridge; 25a - dorsal view, 25b - side view, 25c - ventral view, x9.
- Fig. 26. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211620[6461]C, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, elongated form with an edged, non-bifid terminal ridge; 26a - dorsal view, 26b - side view, 26c - ventral view, x9.
- Fig. 27. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211620[6461]D, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, elongated form with an edged, non-bifid terminal ridge; 27a - dorsal view, 27b - side view, 27c - ventral view, x9.
- Fig. 28. *Erato elongata* Seguenza, 1880, coll. DFB No. 22I2A14211724[6468], Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene; 28a - dorsal view, 28b - side view, 28c - ventral view, x9.





The shell surface is covered with a heavy, smooth, glossy callus. Aperture comprising almost 80% of total height, straight and narrow. Outer lip smooth and thickened, with the outer margin evenly rounded, bearing 15-18 strong, irregular denticles, which extend onto the lip. The denticulate area of the outer lip tapers into the aperture. Siphonal canal relatively short, rounded and abaxially recurved. Columella straight and smooth, bordered internally by a relatively strong carinal ridge. The outer border bears a row of 17-19 denticles, strongest in the anterior portion, weak to subobsolete in the median portion, weak in the posterior portion. The most anterior 2 denticles are developed into strong folds, which run obliquely across the base. Fossula deeply concave and well delimited from the columella. Terminal ridge simple and weakly developed.

Range of variation — The characteristics of this species are the broad bubble-shaped protoconch and the deeply concave fossula. The dentition on the outer lip is invariably strong, extending onto the lip, but is irregular and varies in number; the columellar denticles can be easily counted in some specimens, whilst they are obsolete in the median portion of others.

Discussion — The new species is easily distinguished by its very deep fossula and bubble-shaped, 'naticid' protoconch, which may indicate direct development. This species is most similar to *E. elongata*, which has an elongated shape and similarly arranged terminal teeth. Apart from having quite a different protoconch, the new species is distinguished by having a shorter fossula, more strongly developed labial teeth, an oblique labial lip and

a very fine terminal ridge. All other congeners differ essentially by the character of the terminal ridge which has several oblique folds.

Erato cerullii Schilder, 1933

Figures 9, 11, 37/5

*1933 *Erato (Erato) spiralis cerullii* Schilder, pp. 250, 254, 259, 262, text-figs 79, 80.

1971 *Erato (Erato) spiralis cerullii* Schilder, 1933E — Schilder & Schilder, p. 14.

Type — Holotype is CS 5138.

Stratum typicum — Lower Piacenzian (Middle Pliocene).

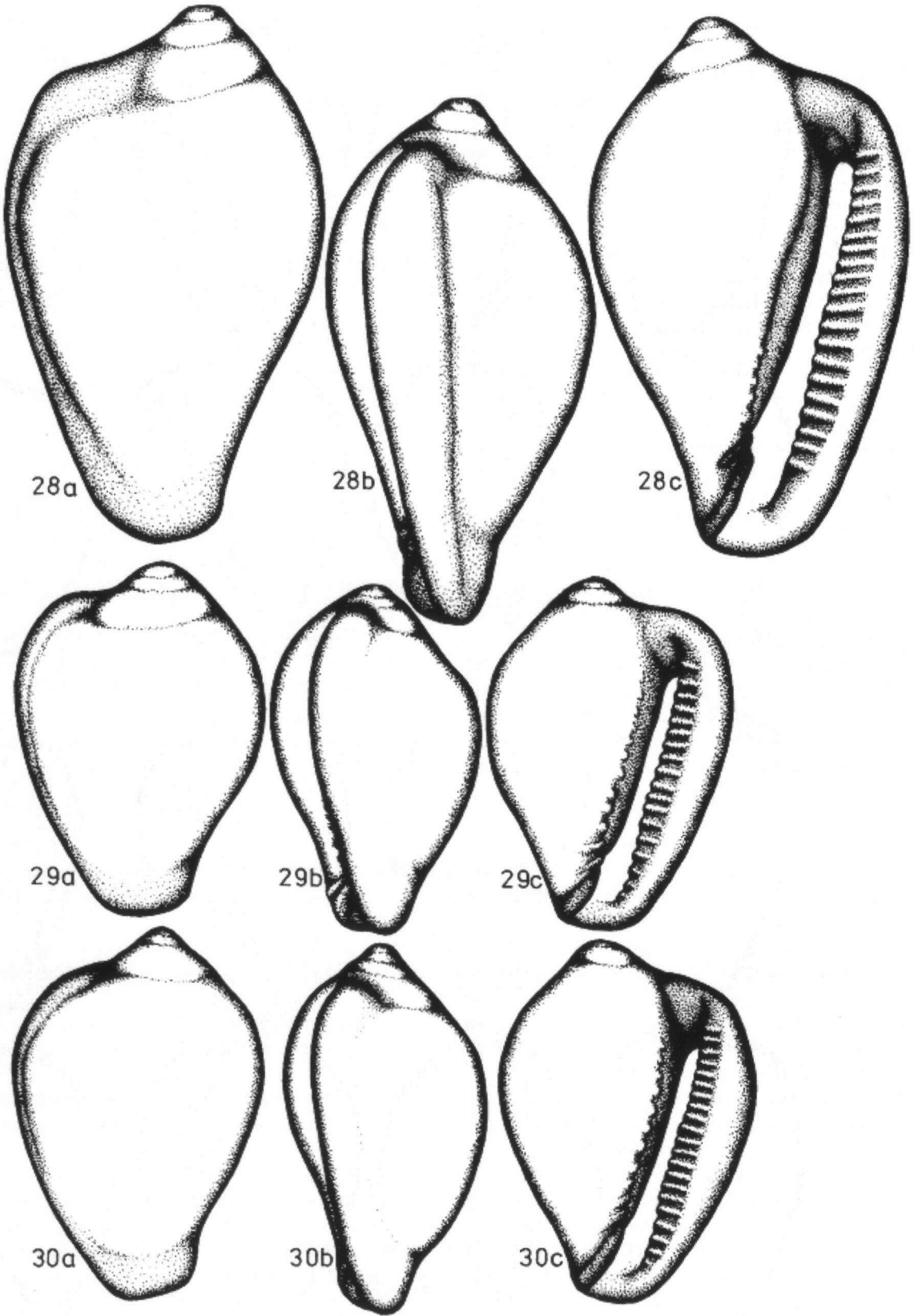
Locus typicus — Castell'Arquato (Tuscany, Italy).

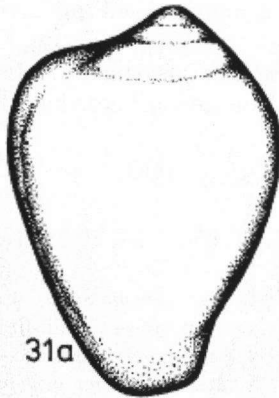
Distribution — Zanclean of Tangliata; Lower Piacenzian of Majatico, Campolasso, Rio Stramonte, Rio Torsero (Italy), and Zanclean (Velerín Conglomerates, Velerín Sands) of Estepona, Spain.

Material studied — from the Velerín Conglomerates, 3 specimens (BLP), 1 specimen (DFB); from the Velerín Sands, 6 specimens (BLP), 3 specimens (DFB).

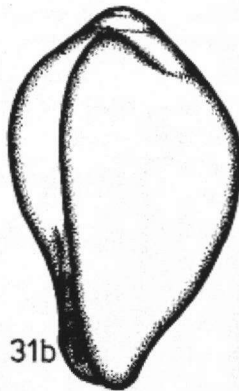
Description — Shell large, solid, elongated pyriform, inflated, with a broad, conical, pointed spire.

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- Fig. 29. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211619[6460]A, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, form with anterior columella and labial teeth extended and a non-bifid terminal ridge; 29a - dorsal view, 29b - side view, 29c - ventral view, x9.
- Fig. 30. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211619[6460]B, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, form with anterior columella and labial teeth extended and a non-bifid terminal ridge; 30a - dorsal view, 30b - side view, 30c - ventral view, x9.
- Fig. 31. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211619[6460]C, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, form with anterior columella and labial teeth extended and a non-bifid terminal ridge; 31a - dorsal view, 31b - side view, 31c - ventral view, x9.
- Fig. 32. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211618[6459]A, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, form with anterior columella and labial teeth extended and a non-bifid terminal ridge; 32a - dorsal view, 32b - side view, 32c - ventral view, x9.
- Fig. 33. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211618[6459]B, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, form with anterior columella and labial teeth extended and a non-bifid terminal ridge; 33a - dorsal view, 33b - side view, 33c - ventral view, x9.
- Fig. 34. *Erato pernana* Sacco, 1894, coll. DFB No. 22I2A14211618[6459]C, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, form with anterior columella and labial teeth extended and a non-bifid terminal ridge; 34a - dorsal view, 34b - side view, 34c - ventral view, x9.
- Fig. 35. *Erato pernana* Sacco, 1894, subadult, coll. BLP, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, x9.
- Fig. 36. *Erato pernana* Sacco, 1894, coll. BLP, Estepona, Spain, Velerín conglomerates, Zanclean, early Pliocene, form with less developed dentition; 36a - dorsal view, 36b - side view, 36c - ventral view, x9.

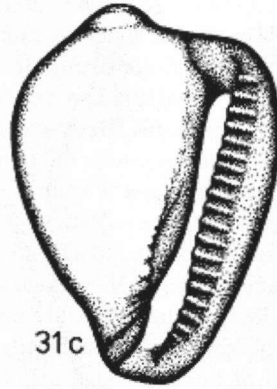




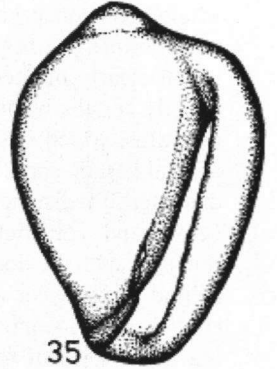
31a



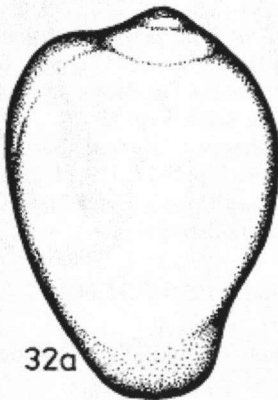
31b



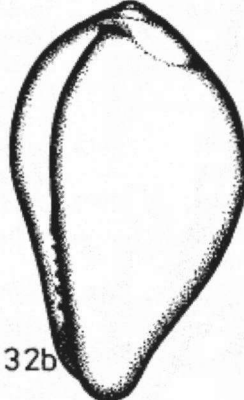
31c



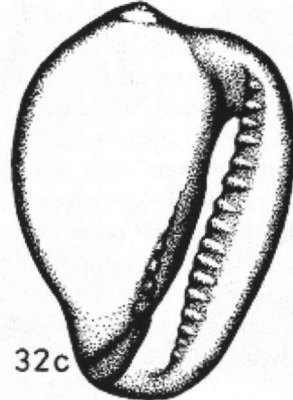
35



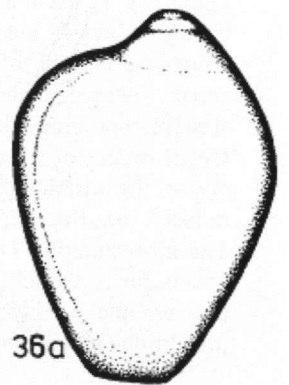
32a



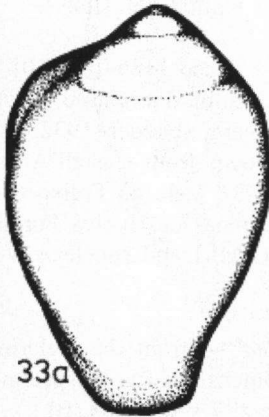
32b



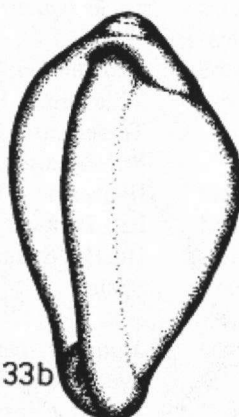
32c



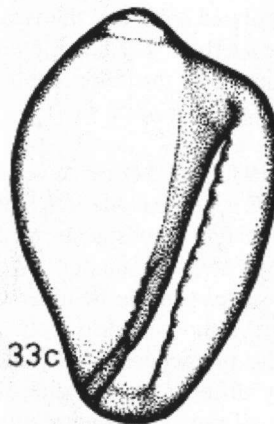
36a



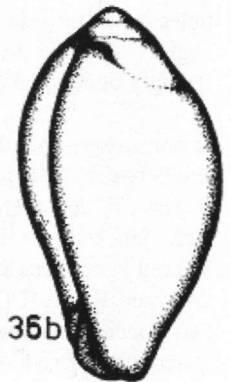
33a



33b



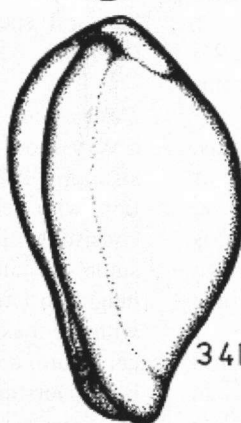
33c



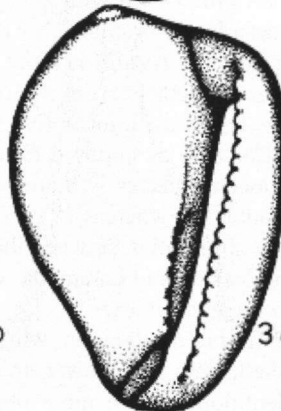
36b



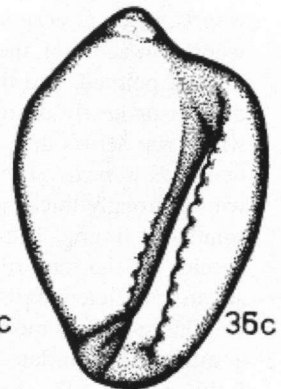
34a



34b



34c



36c

Protoconch eroded but visible in a single; consisting of $2\frac{1}{2}$ convex whorls, with a relatively large nucleus. The whole protoconch has a micro-ornament of minute pustules. Suture distinct but superficial. Junction with teleoconch clearly defined. Teleoconch consisting of $2\frac{1}{4}$ - $2\frac{1}{2}$ slightly convex whorls. Spire broad and conical, covered by callus, which obscures the sutures. Body whorl 80% of total height, shouldered adapically, with the maximum diameter $\frac{1}{4}$ distance from the adapical suture, convex below and constricted at the base. Dorsum smooth, rounded, with the dorsal sulcus reduced to a small dimple behind the anterior extremity. The shell surface is covered by thick, smooth, glossy callus. Aperture comprising about 75% of total height, straight and narrow, although wider in the area of the anal canal and fossula. Outer lip thickened, smooth, with the outer margin evenly rounded, bearing 20 irregular, weak denticles, which are limited to the inner edge of the lip. Siphonal canal rounded and not recurved. Columella almost straight, bordered internally by a strong carinal ridge. Upper border of columella delimited by a row of denticles in the anterior portion, becoming weaker adaxially, reduced to a ridge in the median and posterior portions. The most anterior 4 denticles are developed into folds, which run obliquely across the base. Fossula slightly concave and weakly delimited from the columella. Terminal ridge simple and weakly developed.

Range of variation — The characteristics of this species are the broadly conical, pointed spire and the weak denticles on either side of the aperture. The dentition may be slightly stronger to subobsolete; the folds on the base strongly developed and long to weak and short.

Discussion — Schilder (1933, p. 254) perceived a lineage between the Miocene *E. spiralis* Döderlein, 1862 and *E. cerullii*, considering the latter a subspecies of the former, but without offering any explanation. We have studied specimens of *E. spiralis* in the Schilder Collection (see Figure 14) and find no similarity between the two species. Although the protoconch of Schilder's *E. spiralis* was eroded, they differ in their shape, with *E. spiralis* having a very small protoconch with only 1- $1\frac{1}{2}$ whorls, while *E. cerullii* has a larger protoconch with $2\frac{1}{2}$ whorls. In addition, the spire of *E. cerullii* is more conical and pointed, and the labial teeth less developed, indistinct or nearly obsolete. There are four or five folds, which run across the anterior base as opposed to one or two in *E. spiralis*. The Miocene species is more robust, with a strongly thickened outer lip, whereas *E. cerullii* is somewhat fragile. The only similarities between the two species are the form of the fossula and columella, which are an insufficient basis to suggest a lineage.

This species is most similar to *E. elongata*, which has a smaller, less inflated shell, with a narrower spire. In fully-grown shells, the dentition is even more obsolete than in *E. cerullii*. The distinction is made more clearly

on examination of the protoconchs; *E. elongata* has a higher, more rounded, smooth protoconch, whereas that of *E. cerullii* is more pointed and covered in small pustules.

Erato cerullii is uncommon at Estepona, found in both the conglomerates and nearshore deposits.

Erato pernana Sacco, 1894

Figures 16-18, 21, 23-27, 29, 30-36, 37/7

- *1894 *Erato laevis* var. *pernana* Sacco, p. 60, pl. 3, fig. 64.
- 1911 *Erato laevis* Don. sp. — Cerulli-Irelli, pl. 26, fig. 25.
- 1932 *Erato (E.) pernana pernana* Sacco — Schilder, p. 87.
- 1933 *Erato (Eratopsis) pernana pernana* Sacco, 1894 — Schilder, pp. 249, 254, 258, 269, text-fig. 56.
- 1970 *Erato (Eratopsis) pernana pernana* Sacco, 1894 — Pavia & Demagistris, p. 131, pl. 1, fig. 3.
- 1971 *Erato (Eratopsis) pernana pernana* Sacco, 1894 — Schilder & Schilder, p. 13.
- 1984 *Erato laevis* var. *pernana* Sacco, 1894 — Ferrero Mortara *et al.*, pp. 157, 329; pl. 28, fig. 4.
- 1992 *Erato voluta* (Montagu, 1803) — Cavallo & Repetto, p. 66, fig. 120b (*partim*).

Type — Syntype is BS 043.15.004.

Stratum typicum — Middle/Upper Pliocene.

Locus typicus — Colli Astesi (Italy).

Distribution — Sacco (1894, p. 60) listed Astigiana, Villavernia, Fontanili, Piacentino, Savona, Zinola, Rio Torsero, Bordighera; Schilder (1932, p. 87) added Monte Rufoli; also known from Castell'Arquato, Guistrigona (Piacenzian, DFB); Vale do Freixo (Piacenzian), Pombal, Portugal; Arenas de Huelva Formation (Zanclean), Huelva, Spain (BML), and Zanclean (Velerin), Estepona, Spain.

Material studied — from the Velerin Conglomerates, over 100 specimens (BLP), 20 specimens (DFB); from Velerin Carretera, 7 specimens (BLP); from the Velerin Sands, 1 specimen (BLP); from Padrón, 30 specimens (BML).

Description — Shell small, solid, inflated, pyriform with a very short, rounded spire. Protoconch depressed, consisting of $2-2\frac{1}{2}$ whorls with a very small nucleus. Junction with teleoconch not clearly defined. Teleoconch consisting of 3 short whorls, mostly covered by callus, suture obscured by callus. Body whorl 90-95% of total height, inflated to greatly inflated, shouldered adapically, with the maximum diameter $\frac{1}{4}$ distance from the adapical suture, convex below and relatively constricted at the base. Dorsum smooth, rounded, without any dorsal sulcus, constricted abapically. Body whorl completely covered by a thin, glossy callus in well-preserved specimens,

which envelops the spire. Aperture comprising 85-90% of total height, narrow and straight. Outer lip thickened, smooth, with the outer margin evenly rounded, bearing 15-19 irregular denticles, which in most specimens extend onto the lip. Siphonal canal short, rounded and not recurved. Columella rounded in the abapical portion, straight below, smooth, bordered internally by a weak carinal ridge, which is not always present. The outer border usually bearing a row of 7-10 denticles, restricted to the anterior end, which become stronger abapically. Fossula not developed. Terminal ridge strongly developed, usually bifid but not bifurcate, in some specimens simple.

Range of variation — The characteristics of this species are the small size and squat appearance, together with the strongly developed terminal ridge, which is usually bifid. Some specimens are slightly more elongated, less inflated, and the strength and number of denticles on either side of the aperture are variable.

Discussion — Schilder (1932, p. 87) placed this species in the genus *Eratopsis* Hoernes & Auinger, 1880 (p. 63), which he relegated to the rank of subgenus of *Erato*. The distinguishing features of the genus *Eratopsis* were fully discussed by the original authors, differing from *Erato* in having teeth strongly developed into folds, which cover the ventral side of the shell, a strong dorsal sulcus and pustules on the surface. Unfortunately, in their illustrations, they united two distinct species, the genuine *Eratopsis barrandei* Hoernes & Auinger, 1880 (pl. 8, fig. 8) and *Erato transiens* Boettger, 1884 (pl. 8, figs 9, 10); in the latter, the teeth are poorly developed and folds are wanting.

At first, Schilder (1925, p. 59) considered a single species in the subgenus *Eratopsis* and noted, 'Nur fossil. - Schale winzig, kurz, R. stets gekörnt, oft mit RF., Sp. kürzer, ALVE. nicht decliv, Z. oft rippenartig über B. verlängert, nicht dicht, TZ. Rand- (und oft schräg-) faltig, Foss. und CF. deutlich, schmal, glatt. ... Nur eine Art im Mioc. von Österreich.' Later, he (Schilder, 1933, p. 246) changed the generic description to: 'Dorsum smooth or granular, fossula and columella smooth. Fossula distinctly concave (though often very narrow). Terminal ridges and anterior columellar teeth radial, mostly oblique to longitudinal, never in groups: Europe and Atlantic. Second terminal ridge oblique, stronger than the first which borders the outlet; fossula very broad.'

In his revised description, Schilder did not mention the strong teeth which extend right across the base and outer lip. In our opinion, this is the most important and only constant character distinguishing *Eratopsis* from *Erato*. The dorsal sulcus and pustules are not exclusive to the genus *Eratopsis* and seen in other Miocene eratoid species such as *E. subcypraeola* (d'Orbigny, 1852) and *E. praecedens* Schilder, 1933. Therefore, we prefer to maintain the full generic status of *Eratopsis* and ascribe to it the single species in which the teeth are developed

into strong folds, viz. *E. barrandei* (see Figure 20). *Eratopsis* is reminiscent of the Paleogene genus *Eratotrivia* Sacco, 1894, which also has basal ribs, but in the former these ribs are weaker, limited to the base and margins, while the dorsum is pustular. In contrast, the ribs are stronger and continue onto the dorsum in the genus *Eratotrivia*. *Erato pernana* is easily distinguished from all other species listed here, in its smaller size, squat appearance and usually bifid terminal ridge. The '*pernana*' lineage is restricted to the Mediterranean and Atlantic. *Erato praecedens* from the Middle Miocene, found in both the Mediterranean and in the northeast Atlantic, gave rise to *E. cooperi* Fehse & Landau, 2002, during the Late Miocene (northeast Atlantic), and to *E. pernana* during the Pliocene (Mediterranean and Atlantic coast of Iberia). The lineage survived into the Lower Pleistocene of Monte Mario, Italy (Cerulli-Irelli, 1911, pl. 26, fig. 25).

Erato cooperi has a lower density of labial teeth, its shells are generally larger, and the fossula is more developed, slightly narrow and very concave. In addition, it usually has no denticles above the terminal ridge. *Erato praecedens* again has a lower density of labial teeth, which are stronger. The terminal ridge is not always bifid and the dorsum occasionally pustulate.

Erato pernana had not previously been recorded from the Lower Pliocene; it is interesting that, although most of the specimens from Estepona have a bifid terminal ridge, in about 5% the ridge is well developed, but simple, as in *E. praecedens*. *Erato pernana* is the commonest species found at Estepona, occurring in all deposits.

Genus *Hespererato* Schilder, 1932

Type species — *Erato vitellina* Hinds, 1844, by original designation.

Discussion — Schilder (1932, p. 83) did not provide a full description of this genus, originally erected as a subgenus of *Erato*. Subsequently, Schilder (1933, p. 246) gave *Hespererato* full generic rank. Cate (1977, p. 360) followed Schilder's review of the status of the Eratoidae.

Hespererato cocconii Schilder, 1933

Figures 13, 19, 22, 37/8

- *1933 *Hespererato cocconii* Schilder, pp. 249, 254, 258, 262, text-fig. 43.
- 1933 *Erato (Erato) elongata etrusca* Schilder, pp. 250, 254, 259, 264, text-fig. 82.
- 1971 *Hespererato cocconii* Schilder, 1933E — Schilder & Schilder, p. 14.
- 1971 *Erato (Erato) elongata etrusca* Schilder, 1933E — Schilder & Schilder, p. 14.

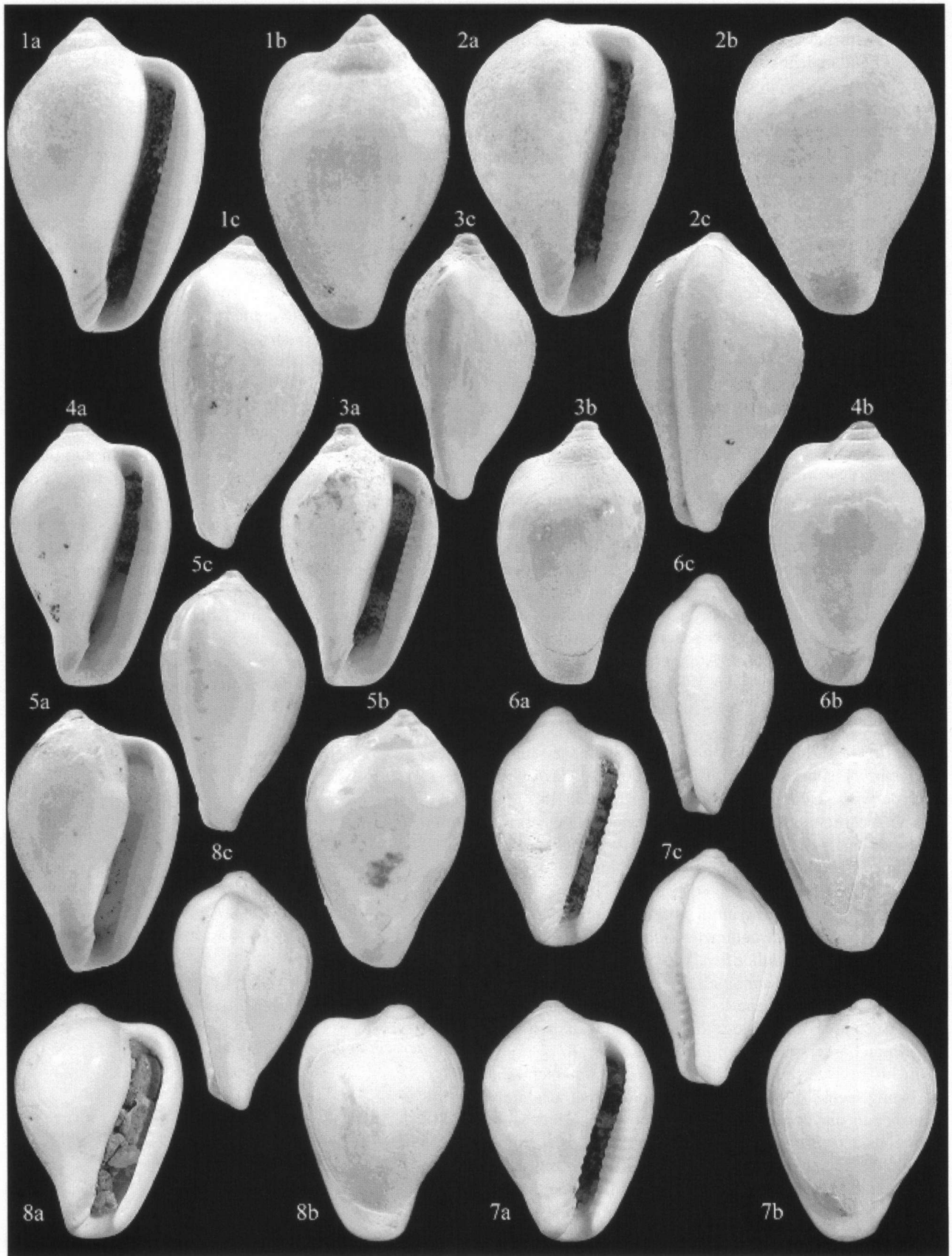


Figure 37

Figure 37. Species of *Erato* from Zanclean strata at Estepona (Spain; photos B. Landau):

1. *E. pieris* De Stefani & Pantanelli, 1879; BLP unregistered; Velerin Conglomerates, H = 13.0 mm;
2. *Erato subalata* Sacco, 1894; BLP unregistered; Velerin Conglomerates, H = 9.8 mm;
3. *Erato elongata* Seguenza, 1880; BLP unregistered; Velerin Carretera, H = 7.9 mm;
4. *Erato elongata* Seguenza, 1880; BLP unregistered; Velerin Conglomerates, H = 8.1 mm;
5. *Erato cerullii* Schilder, 1933; BLP unregistered; Velerin Conglomerates, H = 11.9 mm;
6. *Erato globosa* n. sp., HNC 57201 (**holotype**); Velerin Conglomerates, H = 6.3 mm;
7. *Erato pernana* Sacco, 1894; BLP unregistered; Velerin Carretera, H = 6.5 mm;
8. *Hespererato cocconii* Schilder, 1933; BLP unregistered; Velerin Carretera, H = 5.8 mm.

Type — Holotype is CS 5140.

Stratum typicum — Lower Piacenzian (Middle Pliocene).

Locus typicus — Castell'Arquato (Tuscany, Italy).

Distribution — Zanclean of Emilia; Lower Piacenzian of Emilia, Guistrigona; Upper Piacenzian of Altavilla, Italy; Zanclean (Arenas de Huelva Formation), Huelva (Spain); Zanclean (Velerin Conglomerates, Velerin Carretera), Estepona (Spain).

Material studied — from the Velerin Conglomerates, 10 specimens (BLP), 3 specimens (DFB); from the Velerin Sands, 3 specimens (BLP), 1 specimen (DFB); from Velerin Carretera, 1 specimen (BLP).

Description — Shell medium sized, relatively fragile, inflated, pyriform with a short, conical spire. Protoconch consisting of 2½ somewhat elevated, convex whorls with a small nucleus. Junction with teleoconch not clearly defined. Teleoconch comprising 2½-3 flat-sided whorls, covered by very thin callus, suture distinct. Body whorl about 80% of total height, inflated, shouldered adapically, with the maximum diameter just below the adapical suture, convex below and strongly constricted at the base. Dorsum smooth, rounded, without any dorsal sul-

cus and strongly constricted behind the anterior extremity. A thin callus covers the entire body whorl, which is usually eroded. Aperture wide and straight, almost 75% of total height. Outer lip weakly thickened, bearing 12-13 subobsolete denticles on the inner edge, which do not extend onto the lip. Siphonal canal short, rounded and not recurved. Columella smooth, evenly rounded and straight, usually with no carinal ridge or denticles. Fossula area marked by a very faint depression. Terminal ridge narrow, short and simple, running along the border of the siphonal canal.

Range of variation — This species is characterised by having a wide aperture, weak dentition on the outer lip and a poorly developed columella, fossula and terminal ridge. Schilder (1933, p. 254) tabulated that 60% of specimens of *H. cocconii* had all the columellar teeth well developed and folds on the anterior part of the base. In our specimens from Estepona, the columella denticles are less well developed, in some specimens subobsolete and, in most specimens, the folds are not developed.

Discussion — The genus *Hespererato* comprises inflated species which have a very simple dentition, terminal ridge and fossula; *H. cocconii* typifies the characteristics of this group.

<i>H. cocconii</i>	56-66	106	76	-	-	15	15	AC	60	v
<i>H. marqueti</i> nov. sp. <i>in press</i>	43-50	114	79	-	-	13	+	A	0	v
<i>E. cerullii</i>	65-81	108	67	-	-	16	19	FC	77	s
<i>E. spiralis</i>	62-74	115	67	-	-(v?)	16	15	FC	22	sn
<i>E. elongata</i>	60-65	108	68	-	-	18	20	FC	100	s
<i>E. globosa</i> nov. sp.	52-57	108	72	-	-	17	18	FE	100	n
<i>E. pieris</i>	74-84	101	75	-	v	16	18	F	100	n
<i>E. subalata</i>	84-119	99	72	-	v	15	-	D	0	p
<i>E. pernana</i>	34-41	106	76	-	-	17	15	EB	19	np
<i>E. praecedens</i>	46-53	107	73	G	-	14	(13?)	EB	17	n?
<i>E. cooperi</i> nov. sp. <i>in press</i>	38-43	107	79	-	-	14	+	B	0	s

Table 1. Differences in shell morphology of the Eratoid species discussed in this paper (after Schilder (1933, p. 254); changes in order of better knowledge are in italics and extra bold).

The species occurs throughout the Pliocene of the north-western Mediterranean. Another species from the Upper

Miocene of the Atlantic (Lower Redonian) at Sceaux (NW France), *Hespererato marqueti* Fehse & Landau,

2002, differs in being invariably smaller, with a relatively broader, squatter shell and higher spire. The density of the labial teeth is lower, while the folds on the anterior part of the base are always absent, and the columella teeth always sub-obsolete.

We have examined the type of *Erato (E.) elongata etrusca*, illustrated here in Fig. 13. Schilder's illustration (1933, text-fig. 82) does not match the shell found in his

collection marked as type, bearing number 5118. Although the dorsal border of the siphonal canal looks strange, probably due to damage during life, the shell fits well within the range of variation of *H. cocconii*, showing elongated anterior columellar folds and fully developed columellar denticles. In addition, the protoconch of Schilder's specimen also matches that of *H. cocconii*.

Identification key for eratoid species from Estepona, Spain

- | | |
|---|-----------------------------|
| 1. Adult shell larger than 6mm | 2 |
| Adult shell smaller than 6mm | <i>Erato pernana</i> |
| 2. Adult shell with narrow aperture, dentition, columella and fossula defined | 3 |
| Adult shell with wide aperture, weak dentition and almost smooth columella | <i>Hespererato cocconii</i> |
| 3. Shell with relatively weak dentition | 4 |
| Shell with relatively strong dentition | 5 |
| 4. Spire narrowly conical, folds on the base reduced to two | <i>Erato elongata</i> |
| Spire broadly conical, usually larger, with more than two folds on the base | <i>Erato cerullii</i> |
| 5. Adult shell with narrow aperture, dentition, columella and fossula defined | 6 |
| 6. Outer lip greatly thickened, usually larger than 7mm | 7 |
| Outer lip thickened, rounded apex | <i>Erato globosa</i> |
| 7. Large, with wing-shaped outer lip, deep fossula with a groove on the posterior part of the columella | <i>Erato subalata</i> |
| 8. Largest species, outer lip not winged, fossula broad and poorly delimited | <i>Erato pieris</i> |

Key to protoconch characteristics of eratoid species from Estepona, Spain

- | | |
|--|---|
| 1. 2½ rapidly expanding, more or less elevated whorls, with a small nucleus.
An axial ornament of fine, close-set, wavy lines | <i>Erato pieris, E. subalata</i> |
| 2. First protoconch whorl tightly coiled and depressed, second one convex, elevated and expanding rapidly | <i>Erato elongata,</i>
<i>Hespererato cocconii</i> |
| 3. Bubble-shaped, consisting of 2½ whorls, with a small nucleus and second whorl very convex and rapidly expanding | <i>Erato globosa</i> |
| 4. 2½ convex whorls, with relatively large nucleus, micro-ornament of minute pustules | <i>Erato cerullii</i> |
| 5. Depressed, consisting of 2-2½ whorls with very small nucleus | <i>Erato pernana</i> |

Conclusions

As may be seen from the descriptions above, the eratoid faunas of the Mediterranean Pliocene cannot be considered to comprise but a single species. Differences in shell characters are constant and, together with protoconch features, clearly show that several species co-occurred during the Pliocene.

The protoconchs of all eratoid species from Estepona have more than 2 and fewer than 3 whorls. In other groups of gastropods, this would suggest a planktotrophic or lecithotrophic development (Jackson *et al.*, 1996, fig. 9.6). Fretter & Graham (1981, p. 327) described the breeding pattern of the extant European *Erato voluta* (Montagu, 1803) as having a planktotrophic larval stage of the echinospira type. Planktotrophic development tends to favour longevity and a wide geographical distribution. The species found at Estepona are all known from the Italian Pliocene as well, and extend downwards the stratigraphical ranges of *E. pieris*, *E. subalata*, *E.*

elongata and *E. pernana* from the Middle into the Lower Pliocene.

Eratoids are not only abundant in number of species, but also in quantity, especially so in the Velerín Conglomerates. In recent settings, they are invariably sublittoral and found on hard bottoms in association with ascidians, at depths between 20 and 150 m (Fretter & Graham, 1981, p. 327). There are numerous other gastropod genera favouring rocky shores and hard bottoms, in the same deposits at Estepona, such as *Fissurella*, *Gibbula*, *Trivia* and *Cypraea*. The number of eratoids found at Estepona contrasts sharply with the coeval Lower Pliocene (Zanclean) Arenas de Huelva Formation, which represents a sandy bottom deposit, where they are extremely rare. The habitat at Estepona was obviously favourable, as may be determined not only from their number and diversity, but also by the large size attained by the individuals, which clearly exceed those recorded from Italy.

References

- Boettger, O. 1884. Übergänge von *Eratopsis* zu *Erato*. Hörnes' und Auinger's neuestes Werk. Realia fossil. Lebende Vertreter zweier Hochheimer untermiocäner Landschnecken. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 2, 136-138.
- Brocchi, G. 1814. *Conchologia fossile subappennina, con osservazioni geologiche sugli Appennini e sul suolo adiacente*, 712 pp., 16 pls Milano (Stamperia Reale).
- Caprotti, E. 1976. Malacofauna dello Stratotipo Piacenziano (Pliocene di Castell'Arquato). *La Conchiglie* 12, 1-56, 20 pls.
- Cate, C.N. 1979. A review of the Triviidae (Mollusca: Gastropoda). *Memoir of the Dan Diego Society of Natural History* 10, 1-126.
- Cavallo, O. & Repetto, G. 1992. Conchiglie fossili del Roero. Atlante Iconografico. *Associazione Naturalistica Piemontese Memorie* 2, 1-251.
- Cerulli-Irelli, S. 1911. Fauna malacologica mariana, 5. Cancellariidae, Marginellidae, Mitridae, Fusidae, Chrysodomiidae, Buccinidae, Nassidae, Columellidae, Muricidae, Tritonidae, Cassididae, Cypraeidae, Chenopodidae. *Palaeontographia Italica* 17, 229-276, pls 21-26.
- De Stefani, C. & Pantanelli, D. 1879. Molluschi pliocenici di dintorni di Siena. *Bollettino della Società malacologica italiana* 4, 113-160.
- Döderlein, L. 1862. Cenni geologici intorno la giacitura dei terreni miocenici superiori dell'Italia Centrale. *Atti X^o Congresso Scienziati Italia, Siena*.
- Fehse, D. & Landau, B. 2002. Contributions to eratoid systematics (Mollusca, Gastropoda), 2. Late Miocene Eratoidae from Sceaux d'Anjou (Loire Basin, France), with descriptions of new taxa. *Cainozoic Research* 1(2001), 13-33 (this issue).
- Fehse, D. 2002. Beiträge zur Kenntnis der Triviidae (Mollusca, Gastropoda). V. Kritische Beurteilung der Genera und Beschreibung einer neuen Art der Gattung Gemitrivia Cossman, 1903. ? *Acta Conchyliorum* 6, 1-48, pls. 1-7, tabs. 1-3.
- Ferrero Mortara, E.L., Montefameglio, L., Novelli, M., Opesso, G., Pavia, G. & Tampieri, R. 1984. *Cataloghi. 7 - Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco* 2, 484 pp., 56 pls. Torino (Museo regionale di Scienze Naturali).
- Fretter, V. & Graham, A. 1981. The prosobranch molluscs of Britain and Denmark, 6. Cerithiacea, Strombacea, Hipponicacea, Calyptraeacea, Lamellariacea, Cypraeacea, Naticacea, Tonnacea, Heteropoda. *Journal of Molluscan Studies*, Supplement 9, 285-363.
- Hinds, R.B. 1844. Descriptions of Marginellae collected during the voyage of H.M.S. Sulphur, and from the collection of Mr. Cuming. *Proceedings of the Zoological Society of London*, 14, 72-77.
- Hoernes, R. & Auinger, M. 1880. Die Gastropoden der Meeresablagerungen der ersten und zweiten miocänen Mediteranstufe in der österreich-ungarischen Monarchie. *Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt* 12, 53-113, pls 7-12.
- Inzani, A. 1985. Le famiglie Eratoidae ed Ovulidae nel Pliocene italiano. *Hobby Fauna International News* 1, 3-7, 5 pls.
- Jackson, J.B.C., Jung, P. & Fortunato, H. 1996. *Paciphilia* revisited: Transisthmian evolution of the *Strombina* group (Gastropoda: Columbellidae). *Evolution and Environment in Tropical America*, 234-270.
- Landau, B.M. & Marquet, R. 1999. A new species of *Cyllena* (*Cyllenina*) (Mollusca, Mesogastropoda) from the Arenas de Huelva Formation (Pliocene, southern Spain). *Contributions to Tertiary and Quaternary Geology* 36, 41-44.
- Landau, B.M. & Marquet, R. 2000. The genus *Cymbium* in the Iberian Neogene. *Contributions to Tertiary and Quaternary Geology* 37, 23-34, 4 pls.
- Malatesta, A. 1974. Malacofauna pliocenica Umbra. *Memorie della Carta geologica d'Italia* 13, 498 pp., 32 pls.
- Montagu, G. 1803. *Testacea Britannica, or Natural History of British shells*, 606 pp. London (J.S. Hollis).
- Muñiz-Solis, R. 1995. *Gibberula pliarae* nueva especie de la familia Marginellidae Fleming, 1828 (Gastropoda, Prosobranchia) del Plioceno de Estepona (Málaga, España). *Bollettino de Malacologia* 32, 89-93, 1 pl.
- Orbigny, A.D. d' 1852. *Prodrome de paléontologie* 3, 196 pp. Paris (Masson).
- Pavia, G. & Demagistris, L. 1970. Cypraeacea del Pliocene medio-superiore di Valleandona (Asti). *La Conchiglie* 6, 128-144, 3 pls.
- Risso, A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes* 4, vii + 439 pp., 12 pls. Paris/Strasbourg (F.G. Levrault).
- Sacco, F. 1894. I Molluschi dei terreni terziari del Piemonte e della Liguria 15, 71 pp., 3 pls. Torino (Carlo Clausen).
- Sanz de Galdeano, C. & Lopez Garrido, A.C. 1991. Tectonic evolution of the Malaga Basin (Betic Cordillera). Regional implications. *Geodinamica Acta* 5, 173-186.
- Schilder, F.A. 1925. Revision der Cypraeacea (Moll., Gastr.). *Archiv für Naturgeschichte* 91, 1-171.
- Schilder, F.A. 1932. Cypraeacea. In: Quenstedt, W. (ed.). *Fossilium Catalogus*, 1. Animalia, A55, 276 pp. Berlin (W. Junk).
- Schilder, F.A. 1933. Monograph of the subfamily Eratoinae. *Proceedings of the Malacological Society of London* 20, 244-283.
- Schilder, M. & Schilder, F.A. 1971. A catalogue of living and fossil cowries. Taxonomy and bibliography of Triviacea and Cypraeacea (Gastropoda Prosobranchia). *Mémoires de l'Institut royal des Sciences naturelles de Belgique* (2)85, 1-246.
- Seguenza, G. 1880. Le formazioni terziarie nella provincia di Reggio (Calabria). *Atti della reale Accademia dei Lincei, Memorie della Classe di Scienze fisiche, matematiche e naturali*, 6, 1-446, 17 pls.
- Troschel, F.H. 1863. *Das Gebiss der Schnecken*, 1, 214 pp. Berlin.
- Véra-Peláez, J.L., Lozano-Francisco, M.C., Muñiz-Solis, R., Gili, G., Martinell, J., Domenèch, R., Palmqvist, P. & Guerra-Merchán, A. 1995. Estudio preliminar de la malacofauna del Plioceno de Estepona (Málaga, España). *Iberus* 13, 93-117.