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Contributions to eratoid systematics (Mollusca, Gastropoda), 2. Late Miocene Eratoidae from Sceaux d'Anjou (Loire Basin, France), with descriptions of new taxa

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Species-rich, Late Miocene eratoid faunas collected at Sceaux d'Anjou (Loire Basin, France) are revised, and two new species, *Hespererato marqueti* n. sp. and *Erato cooperi* n. sp., are described. These faunas are compared with those recorded from other Neogene deposits elsewhere in the Mediterranean. Added are notes on possible evolutionary trends and migrations during the Neogene, as based on shell morphology.

KEY WORDS: Mollusca, Gastropoda, Eratoidae, Late Miocene, France, systematics, new taxa.

Introduction

In another paper (Fehse & Landau, 2002) on representatives of the genus *Erato* Risso, 1826 from the Lower Pliocene (Zanclean) of Estepona (southern Spain), we have drawn attention to difficulties of taxonomy and to the controversy that surround the family Eratoidae. In the present paper, the Late Miocene (Early Redonian) faunas of the French Atlantic are reviewed.

The locality of Ferme la Presselière (Sceaux d'Anjou), near Angers (département Main-et-Loire, France), is the richest Redonian deposit (latest Miocene-earliest Pliocene) to date, with almost 250 species recorded by Brébion (1964, p. 213). Almost all of the species represented are small; this is due to a mechanical sieving effect by water currents (Brébion, 1964, p. 680). The deposit represents a nearshore fauna under slightly warmer conditions than currently at the same latitude, which is indicated by the occurrence of numerous thermophilic gastropod genera, including *Oliva*, *Conus*, *Ficus*, *Terebra*, *Pterynotus* and others. Yet, other 'warm-water' families, such as the Cypraeidae and Ovulidae, are poorly represented.

The presence of the genus *Erato* in these deposits was first noted by Millet in 1864 (see Brébion 1964, p. 320). The genus has featured consistently in subsequent reports on the Redonian, albeit under different names. Schilder (1933a, b) distinguished various species occurring in the Pliocene deposits; his classification was accepted by some authors (Glibert, 1963, pp. 45, 46), but rejected by others such as Brébion (1964, p. 321), who considered them all to represent but a single variable species, *Erato laevis* (Donovan, 1804) [= *E. voluta* (Montagu, 1803)].

The stratigraphical position (Late Miocene or Early Pliocene) of the 'étage Rédonien' has always remained controversial. Brébion (1964, 1988) suggested that these deposits represented a series of transgressions, ranging in age from Late Miocene to Middle Pliocene. During the first of these marine Redonian incursions, of Late Miocene age, the deposits around Sceaux d'Anjou, the type locality of the Lower Redonian, were laid down. On the other hand, Lauriat-Rage (1981) ascribed a Pliocene age to the entire Redonian, on the basis of a study of the bivalve faunas. Although many of the Redonian strata undoubtedly are of Pliocene age, on account of the high percentage of more tropical genera present at Sceaux we follow Brébion (1964) in accepting a Late Miocene (possibly Messinian) age for these Lower Redonian deposits.

Systematic palaeontology

Abbreviations — To denote the repositories of material referred to in the text, the following abbreviations are used:

BLP	B. Landau Colln, Albufeira;
DFB	D. Fehse Colln, Berlin;
HNC	Haus der Natur, Cismar;
IRScNB	Institut royal des Sciences naturelles de Belgique, Bruxelles;
NHM	The Natural History Museum, London;
SMF	Senckenberg Museum, Frankfurt am Main.

To describe shell morphology the following abbreviations are used (after Schilder, 1933a, pp. 2-4; 1933b, pp. 250-253):

TZ terminal teeth;
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. The anterior columellar ridges have been included. Of species in which the columellar teeth always 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 columellar ridge:
A coarse, simply bordering the outlet, following columellar teeth are small
B coarse, double (split longitudinally), columellar teeth small
C several oblique ridges gradually passing into columellar teeth
D like C, but ridges nearly transverse;
F fossula:
- completely absent
v obsolete or nearly so
s narrow, gradually sloping from 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 posterior columellar teeth are well developed so that they can be counted along the whole length of the lip.

Superfamily Trivioidea Troschel, 1863
Family Eratoidae Schilder, 1927

Subfamily Eratoinae Schilder, 1927
Genus *Erato* Risso, 1826

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

Erato britannica Schilder, 1933a
Figures A, 20, 25, 27, 29, 33/1

1848 *Erato laevis* Don. — Wood, p. 18, pl. 2, fig. 10.
1920 *Erato laevis* (Donovan) — Harmer, p. 511, pl. 45, fig. 1.
*1933a *Erato (Erato) cypraeola britannica* Schilder, p. 7.
1933b *Erato (Erato) spiralis britannica* Schilder — Schilder, pp. 250, 254, 259, 261.
1958 *Erato (Erato) cypraeola britannica* Schilder, 1933 — Glibert, p. 26, pl. 2, fig. 25.
1971 *Erato (Erato) voluta britannica* Schilder, 1933b — Schilder & Schilder, p. 14.

Type — Lectotype, here designated, is NHM G1845/1; paralectotype is NHM G1845/2.

Stratum typicum — Coralline Crag Formation (Zanclean, Lower Pliocene).

Locus typicus — Sutton (East Anglia, England).

Distribution — Lower Redonian (Upper Miocene), Sceaux d'Anjou, France; Coralline Crag Formation (Lower Pliocene) and Red Crag Formation (Upper Pliocene), Sutton (Harmer, 1920, p. 511); Waltonian, Walton-on-the-Naze and Little Oakley; Newbournian, Bentley, Waldringfield, Newbourn, Sutton; Butleyan, Butley; Icenian, Bramerton (East Anglia, England; Schilder, 1933a); Kattendijk Formation (Zanclean), Luchtbal Member (Lillo Formation), Oorderen, Belgium (Glibert, 1958).

Material studied — from Sceaux d'Anjou, 50 specimens (BLP), 8 specimens (DFB); from Sutton, 17 specimens (Wood Colln, NHM).

Description — Shell medium sized, relatively fragile, elongated pyriform, with an elevated, somewhat pointed spire. Protoconch mostly covered by callus, but visible in several specimens; consisting of 2¼ convex whorls, with a small nucleus. The first protoconch whorl is elevated, the second becoming depressed. Suture clearly marked and incised. Junction with teleoconch obscured by callus. Teleoconch consisting of about 3 whorls. Spire covered by very thick callus, which covers the suture. Body whorl 80% of total height, shouldered adapically, with the maximum diameter ¼ distance from the adapical suture, evenly tapered below and only slightly constricted at the base. Dorsum smooth, rounded, with the dorsal sulcus reduced to a small dimple behind the anterior extremity. The whole shell surface covered by thick, smooth, glossy callus. Aperture comprising about 75% of total height,

straight and narrow. Outer lip thickened, smooth, basally flattened with an angular outer margin, bearing 19-23 strong, regular, knob-like denticles, which extend onto the lip to a variable distance. Siphonal canal short, rounded and straight. Columella almost straight, with a well-developed rounded carinal ridge. Outer edge of columella delimited by a row of 17-22 denticles, becoming weaker adaxially. The most anterior 5 denticles are developed into folds, which run obliquely across the base. Fossula deeply concave, but not delimited from the columella. Terminal ridge simple, short and strongly developed.

Range of variation — The characteristic features of this species are the high spire, elongated shape, the knob-like denticles on the basally flattened outer lip, deeply concave fossula and large number of strongly developed folds on the anterior portion of the base. The species is constant in shape, varying only slightly in number of denticles.

Remarks — Schilder (1933a, pp. 7, 8) changed Wood's original assignment, describing the Crag specimens as a new subspecies, and adding to Wood's original description, '... die Form des Crag ist meist etwas grösser als der gleich alte Typus aus Italien und hat gröbere und weniger zahlreiche IZ, die bei allen Exemplaren bis hinten deutlich ausgebildet sind. 1 Stück aus dem Diestien von Anvers (Bassin Africa) L = 7.7 mm, Sp = 110, BL = 61, mit 22 AZ (= pd) und 19 IZ (= ps), von denen die beiden vordersten durch ihre Länge und Richtung als TZ zu erkennen sind; R glatt, Fossula schmal.'

Species and subspecies	Stratum	True deposits	L.	Sp.	BL.	Average of AZ.	IZ.	az.	iz.	IZ. %
cyp. britannica nov.	Diest.	Anvers	(7.7)	110	61	22	19	20	17	100
>> >> >>	Corall. Crag		7.8	107	70	17	18	15	16	100
>> >> >>	Red Crag		8.0	106	67	18	19	16	17	100

Table 1. Comparison between a Belgian and an English specimen (Wood Colln, NHM) of *E. britannica* (after Schilder, 1933a, p. 8).

Discussion — Schilder (1933a, p. 7) wrote, 'Der Name *britannica* sei hier für *cypraeola* Wood (1848) nec Brocchi (1814) vorgeschlagen ...' Wood, however, only used the name *Erato cypraeola* in his synonymy of *E. laevis*, and referred (1848, pp. 18, 19) to specimens from the Coralline and Red crags of Sutton as '*Erato laevis* Don. Tab. II, fig. 10, a-b', and '*Erato maugeriae* Gray, Tab. II, fig. 11, a-b', respectively. Therefore, it was not clear which of the two species Schilder had renamed.

Two months later, Schilder (1933b, p. 282) clarified this when he noted, '*britannica*, see S.V. Wood, Monogr. Crag. Moll., vol. 1, pl. 2, fig. 10 (1848), ...', but he did not adapt the identification labels with Wood's specimens (NHM), where only three boxes contain Wood's specimens from Sutton:

NHM G.1829, containing three shells, Red Crag;
NHM G.1845, containing seventeen shells, Coralline Crag;
NHM H.1883, containing one shell, Coralline Crag.

None of the shells is marked as having been renamed by Schilder (1933a) or by Schilder & Schilder (1971) (J. Cooper, pers. comm.).

While working on the IRScNB collections (Table 1), Schilder noted that he had examined Wood's material (NHM). Confusion in his notes or a lapse of concentration may have led him to believe that Wood described an eratoid species as *E. cypraeola*. The result of this is that there is no clear illustration of *E. britannica* and no type specimen; we here designate NHM G.1845/1 lectotype.

Schilder added to the confusion by ranking *britannica* as a subspecies of *E. cypraeola* (Brocchi, 1814), some months later of *E. spiralis* (Döderlein, 1862), and finally of *E. voluta* (Montagu, 1803), in each case without justifying his decision. We here consider *E. britannica* to be a distinct species.

Erato britannica might be ancestral to *E. cypraeola* (Pliocene, Mediterranean; see Figure 15) and the extant *E. voluta* (see Figure 21), in showing a combination of features characteristic of each of these, which probably explains Schilder's indecision which species *britannica* should be attributed to as a subspecies. In shape, size and aperture, *E. britannica* resembles *E. voluta*, whereas dentition, columella, fossula, and terminal ridge are similar to *E. cypraeola*.

We assume *E. spiralis* to be ancestral to *E. britannica*, on account of their having similar shell features (Table 2). *Erato spiralis* occurs in the Middle Miocene (Serravalian) of the Mediterranean (Italy) and the North Sea Basin (Germany). In view of the fact that the North Sea Basin became isolated from the Atlantic during the Middle Miocene, by a landmass between northern France and southern England, as well as from the Mediterranean by Alpine orogeny, the population of *E. spiralis* there adapted to the colder waters and evolved into *E. britannica*. A migration event from the North Sea Basin to the northeast Atlantic, north of the British Isles during the late Middle Miocene is considered possible, which

would account for the presence of this species at Sceaux d'Anjou, and its absence in the earlier Middle Miocene (Pontilevien) Atlantic faunas of France. *Erato britannica* may have repopulated the Mediterranean, and developed into *E. cypraeola*, although it is also possible that a Mediterranean population of *E. spiralis* gave rise to *E. cypraeola*. To be more certain of these relationships on the basis of shell morphology alone is impossible.

	E. spiralis	***E. cypraeola*** pl. 3, fig. 15	***E. britannica*** pl. 4, fig. 20; pl. 6, fig. 1	***E. voluta*** pl. 4, fig. 21
Fossula	slightly narrow, gradually sloping from the terminal ridge to behind, anteriorly angularly projecting	slightly broad to broad concave	narrow, slightly narrowed	narrow to nearly obsolete, gradually sloping
Labial teeth	coarse, dense, pd = 16	fine, very dense, pd = 18	fine, dense, pd = 16	coarse, sometimes somewhat obsolete, lesser dense, pd = 14
Columellar teeth	coarse, lesser dense, ps = 14	fine, sometimes obsolete, very dense, ps = 17	fine, dense, ps = 16	coarse, sometimes obsolete, lesser dense, pd = 14
Aperture lip	thickened, calloused	very slightly thickened, slightly calloused	slightly thickened, calloused	thickened, calloused
Spire	very projected, Sp = 115	somewhat projected, Sp = 106	slightly projected, Sp = 108	projected, Sp = 111
Stratum	Serravalian, M. Miocene	L. to U. Piacenzian, M. to U. Pliocene	Messinian, U. Miocene to U. Piacenzian, U. Pliocene	Pleistocene? to recent
Distribution	Italy (Mediterranean)	Italy (Mediterranean)	North Sea Basin	North Eastern Atlantic to Western Mediterranean Sea

Table 2. Comparison of species in the *spiralis* lineage.

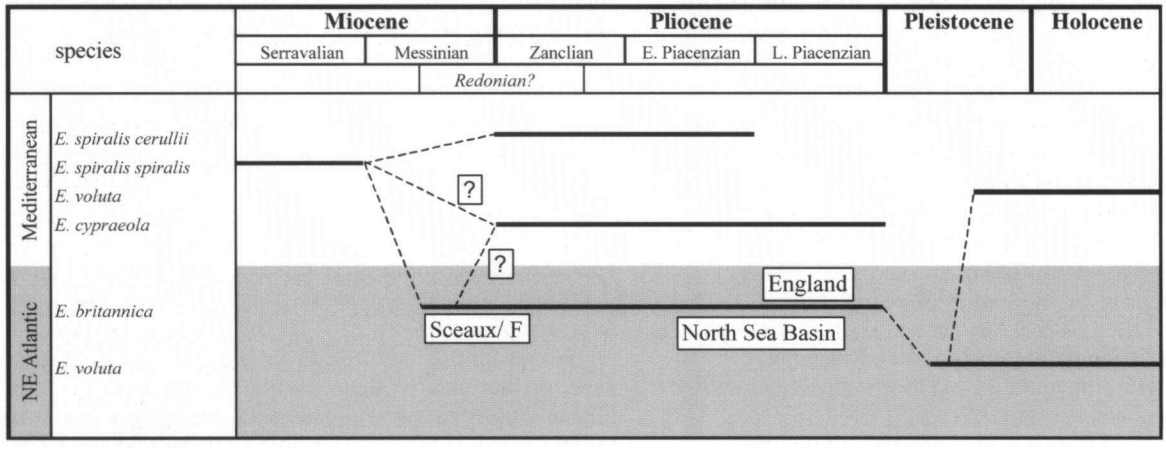


Figure A. Possible phylogeny of *E. britannica*, as based on shell morphology.

The rich eratoid faunas of the Mediterranean, the northeast Atlantic and the North Sea Basin became extinct during the Late Pliocene and Early Pleistocene. Only *E. voluta* survived, and this species possibly repopulated the Mediterranean coming from the W European Atlantic coasts during the Early Pleistocene.

Erato andecavica Schilder, 1933b
Figures B, 10, 11, 14, 30, 33/2

*1933b *Erato (Erato) incrassata andecavica* Schilder, pp. 250, 254, 259, 260, 282, 283, text-fig. 68.

1971 *Erato (Erato) gallica andecavica* Schilder, 1933e — Schilder & Schilder, p. 14.

Type — Holotype is SMF 2097a.

Stratum typicum — 'Tortonian, Upper Miocene' (Schilder, 1933b, p. 250); this is an error, as Schilder was not aware of the stratum typicum. In fact, the specimen came from the Lower Redonian (Upper Miocene).

Locus typicus — Sceaux d'Anjou (France).

Distribution — Known exclusively from the type locality.

Material studied — from Sceaux d'Anjou, 50 specimens (BLP), 8 specimens (DFB).

Description — Shell large, solid, highly inflated, pyriform, with a broad, conical spire. Protoconch mostly covered by callus, but visible in two specimens; consisting of 1½-1¾ somewhat depressed, convex whorls, with a large nucleus. Suture clearly marked and incised. Junction with teleoconch sharply delimited. Teleoconch consisting of about 3 whorls. Spire covered by very thick callus, which covers the suture. Body whorl 80% of total height, shouldered adapically, with the maximum diameter ¼ distance from the adapical suture, convex below and strongly constricted at the base. Dorsum smooth, rounded, with a weak dorsal sulcus and a strong dimple behind the anterior extremity, where the dorsum is also constricted. The whole shell surface covered by thick, smooth, glossy callus. Aperture comprising about 75% of total height, straight and relatively wide. Outer lip very thickened, smooth, basally flattened with an angular outer margin, bearing 15-18 strong, regular, denticles, which extend onto the lip. Siphonal canal long, rounded and straight. Columella almost straight, with a well-developed rounded carinal ridge, which is slightly produced in the fossula area. Outer edge of columella delimited by a row of 7-17 denticles, strong and knob-like in the anterior portion, weak to obsolete in the posterior part. The most anterior 3 denticles are developed into strong folds, which run obliquely across the base. Fossula concave, but not delimited from the columella. The concavity is emphasised by the rounded carinal ridge. Terminal ridge simple, very weakly developed.

Range of variation — The characteristic features of this species are the highly inflated shape, strong dimple on the anterior end of the dorsum and greatly thickened, basally flattened outer lip, with an angular margin and strong denticles. The species is constant in shape, but varies greatly in the character of the denticles on the columella.

Discussion — Schilder (1933b, p. 250) assigned *E. andecavica* as subspecies to the Mediterranean Miocene *E. incrassata* (Döderlein, 1862) (see Figure 16). Schilder & Schilder (1971, p. 14) reassigned it to *E. gallica*, a taxon from the Middle Miocene (Serravallian) of Touraine (France) (see Figure 22). In both these instances, taxonomic choices lack explanation. Teeth density, terminal ridge, aperture, apertural lip, and sometimes shell shape are reminiscent of *E. gallica*. However, *E. andecavica* displays several specialised features, *viz.* a large, generally highly inflated shell, with more denticles on the outer lip, which is also much thicker. It seems more likely that the Redonian *E. andecavica* represents a distinct endemic species, which possibly developed from *E. gallica*.

Erato subalata Sacco, 1894, from the Pliocene (Mediterranean), has an inflated shell, and the disposition of the denticles and folds on the base are also similar. It differs in having a lower spire, and the adapical part of the outer lip is elevated and shouldered. *Erato subalata* may have evolved from *E. andecavica*.

Erato cooperi n. sp.
Figures 18, 23, 24, 31, 33/3

Types — Holotype is HNC 53514; paratypes are HNC 53515 and 53516.
Stratum typicum — Lower Redonian (Upper Miocene).

Locus typicus — Ferme la Presselière, Sceaux d'Anjou (France).

Derivatio nominis: Named after John Cooper (NHM), who kindly assisted us during our studies.

Distribution — Known only from the type locality.

Material studied — 100 specimens (BLP), 11 specimens (DFB)

Description — Shell small, solid, inflated, pyriform with a very short, rounded spire. Protoconch consisting of 2-2½ depressed whorls with a very small nucleus. Junction with teleoconch clearly defined. The first teleoconch whorl is narrowed at the junction with the protoconch. 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 ¼ distance from the adapical suture, convex below and relatively constricted at the base. Dorsum smooth, rounded, without any dorsal sulcus, not 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 11-15 denticles, which in most specimens extend onto the lip. Siphonal canal short, rounded and straight. Columella rounded in the abapical portion, straight below, smooth, bordered internally by a weak carinal ridge.

	E. incrassata pl. 3, fig. 16	*E. gallica* pl. 4, fig. 22	*E. andecavica* pl. 2, figs. 10, 11, 14; pl. 6, fig. 2
Fossula	broad, angularly projecting anteriorly	narrow, sloping gradually from the terminal ridge posteriorly	broad, angularly projecting anteriorly
Labial teeth	coarse, less dense, pd = 13	coarse, extending onto the apertural lip, very dense, pd = 17	Irregularly shaped and positioned, sometimes somewhat obsolete, dense, pd = 15
Columellar teeth	somewhat coarse, almost obsolete, less dense, ps = 13	fine, sometimes nearly obsolete, dense, ps = 15	Almost obsolete, forming a callosity along the parietal lip
Apertural lip	very thickened and callused	very thickened and callused	very thickened and callused
Spire	somewhat elevated, Sp = 107	somewhat elevated, Sp = 107	Somewhat elevated, Sp = 107
Dorsal sulcus	small impression at the anterior extremity	small impression at the anterior extremity	Absent
Stratum	Serravalian, M. Miocene	Langhian, M. Miocene	Messinian, U. Miocene to Zanclian, L. Pliocene (?U. Piacenzian, U. Pliocene of England)
Distribution	Italy (Mediterranean)	North Sea Basin	North Sea Basin

Table 3. *Erato incrassata*, *E. gallica* and *E. andecavica* compared.

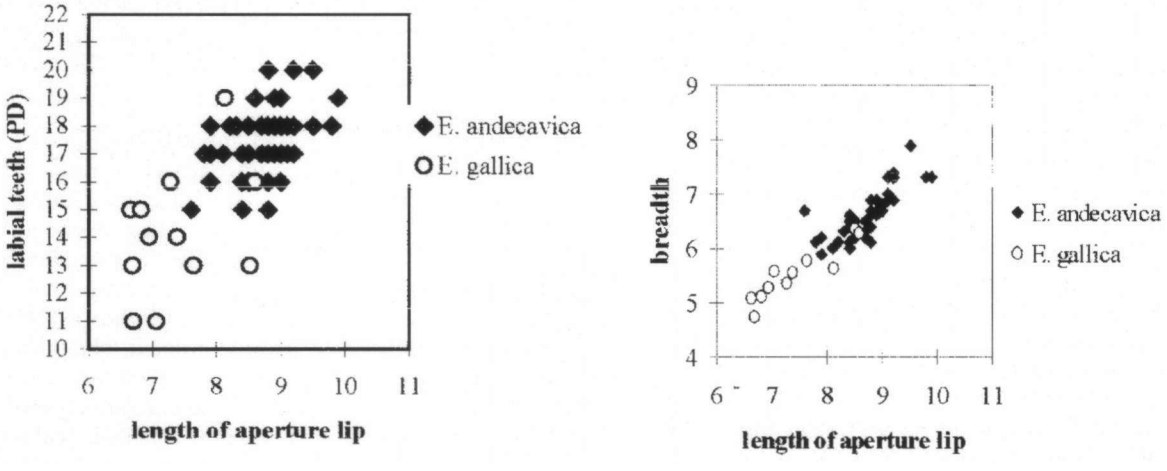


Figure B. The morphology of randomly chosen specimens of *E. andecavica* and *E. gallica* from the Middle Miocene of Manthelan, Thenay, Paulmy, and Villandraut (NW France) compared.

The outer border usually bearing a row of 2-5 denticles, restricted to the anterior end, which become stronger abapically. Fossula marked by a weak concavity. Terminal ridge strongly developed, bifid but not bifurcate.

Range of variation — The characteristics of this species are the small size and squat appearance, together with the strongly developed terminal ridge, which is bifid. The shape in some specimens is slightly more elongated, less

Measurements:

Specimen	Catalogue Number	total length mm	length of lip mm	Breadth mm	Diameter mm	PS	PD	remarks
Holotype	HNC 52533	4.92	4.28	3.41	2.78	4	13	
Paratype 1	HNC 52534	4.71	4.25	3.27	2.67	6	15	
Paratype 2	HNC 52772	4.54	3.70	2.95	2.40	-	-	subadult
Paratype 3	HNC 52773	5.57	4.81	3.84	3.40	4	15	
Paratype 4	HNC 52774	5.30	4.73	3.84	3.15	6	11	
Paratype 5	HNC 52775	5.00	4.52	3.81	2.98	4	12	
Paratype 6	HNC 52776	5.13	4.69	3.69	3.03	5	12	
Paratype 7	HNC 52777	5.16	4.57	3.59	2.87	6	12	

inflated, and strength and number of denticles on either side of the aperture are variable.

Discussion — *Erato pernana* (Figure 17), *E. praecedens* (Figure 19) and *E. cooperi* belong to a group of small, squat eratoids which Schilder (1933b, p. 246) placed in the genus *Eratopsis* Hoernes & Auinger, 1880, which he relegated to the rank of subgenus. Typical of *Eratopsis* are the strongly extended teeth, which cover the ventral side. Schilder redescribed this taxon, but omitted this feature, using the name to group small, squat species with or without a dorsal sulcus and pustules on the dorsum. In our opinion, none of these characters are specific to the genus *Eratopsis*, which should be restricted to eratoid species with strong teeth which cover the base.

Marquet (1997, p. 75), who considered both *E. scaldisia* Schilder, 1933a (see Figure 13) and *E. exmaugeriae* Sacco, 1894 (see Figures 26, 28) to be synonymous with *E. pernana*, noted, 'Glibert (1958a) pointed out that it seems inappropriate to distinguish the subspecies *E. p. exmaugeriae* and *E. p. scaldisia*, with both occurring in the same layer and differences too slight to justify separation at the species level'. We consider there to be two separate lineages in this group of small species. *Erato hemmorensis* Schilder, 1929 from Middle to Upper Miocene of the North Sea Basin (NW France and northern Germany), possibly gave rise *E. exmaugeriae* in the Lower Pliocene (Coralline Crag) of East Anglia (England), and to *E. scaldisia* from the Middle Pliocene (Lillo Formation) of Belgium. The second lineage is restricted to the Mediterranean and Atlantic: *E. praecedens* from the Middle Miocene (Mediterranean and NE Atlantic) possibly gave rise to *E. cooperi* (Upper Miocene, NE Atlantic) and *E. pernana* (Pliocene, Mediterranean and Atlantic coast of Iberian peninsula).

The specimen illustrated by Marquet (1997, pl. 2, fig. 9) is only the second known individual of *E. scaldisia*, the holotype being IRScNB IST 4965. *Erato scaldisia* is distinguished from *E. exmaugeriae* in having a broadened fossula, a blunter spire, a lesser width and by the fineness of the columellar and labial teeth. We do not consider the differences between *E. pernana* and *E. exmaugeriae* to be insignificant. This is illustrated in the tabulation of differences in shell morphology supplied by Schilder (1933b, p. 254), parts of which are here reproduced (Table 6), with our own additions and corrections. Schilder & Schilder (1971, p. 13) also ranked *E. exmaugeriae* and *E. pernana* as distinct species. *Erato exmaugeriae* is of similar size to *E. pernana* and *E. cooperi*, but is easily distinguished from these in having a more elevated spire, a less well-developed fossula, a curved aperture and a distinctly lower density of labial teeth. Differences between *E. cooperi* and *E. pernana* are smaller, but constant, justifying separation at the species level on the basis of shell morphology, as well as stratigraphical and geographical distribution. The density of labial teeth is lower, shells generally are larger, and the fossula is slightly narrower and very concave in *E. cooperi*, whereas that in *E. pernana* is nearly absent.

Differences between *E. cooperi* and the Middle Miocene *E. praecedens* are shown in Tables 4 and 6, which also include data for other species discussed here.

Erato (Eratopsis) exmaugeriae was redescribed by Sacco (1894), on the basis of Wood's specimens which were identified as *E. maugeriae* Sowerby, 1832 (Wood, 1848, p. 19, pl. 2, fig. 11), but Sacco failed to designate a type specimen, and did not examine specimens from the NHM collections. We here designate one of Wood's specimens (NHM G.1840/1) lectotype (see Figure 26).

Genus *Hespererato* Schilder, 1932

Hespererato marqueti n. sp.
Figures 1, 3, 9a, b, 32, 33/4

Types — Holotype is HNC 52531; paratypes are HNC 52532 and 52772.

Stratum typicum — Lower Redonian (Upper Miocene).

Locus typicus — Ferme la Presselière, Sceaux d'Anjou (France).

Derivatio nominis — Named for Dr Robert Marquet, a keen and dedicated molluscan palaeontologist, who first drew our attention to the locality.

	E. pernana pl. 3, fig. 17	*E. cooperi* pl. 3, fig. 18; pl. 5, figs 23, 24; pl. 6, fig. 3	*E. praecedens* Pl. 3, fig. 19	*E. exmaugeriae* pl. 5, fig. 26, 28
Fossula	broad to very broad and concave	broad, angularly projecting anteriorly	broad, angularly projecting anteriorly	broad to very broad and concave
Labial teeth	fine, continued on the aperture lip, very dense, pd = 17	fine, sometimes obsolete, dense, pd = 14	Coarse to very coarse, dense, pd = 14	coarse, lesser dense, pd = 12
Columellar teeth	fine, sometimes obsolete, dense, ps = 15	obsolete	almost obsolete, coarse, lesser dense, ps = 13	fine, sometimes obsolete, very less dense, ps = 9
Aperture lip	very thickened, somewhat calloused	lesser thickened and calloused	thickened and calloused	thickened and calloused
Spire	somewhat projected, Sp = 106	somewhat projected, Sp = 107	somewhat projected, Sp = 107	somewhat projected, Sp = 109
Stratum	Zanclian to U. Piacenzian, L. to U. Pliocene	Messinian, U. Miocene to U. Piacenzian, U. Pliocene	Serravalian, M. Miocene	U. Piacenzian, U. Pliocene
Distribution	Italy (Mediterranean)	North Sea Basin	Italy (Mediterranean)	North Sea Basin

Table 4. *Erato pernana*, *E. cooperi*, *E. praecedens* and *E. exmaugeriae* compared.

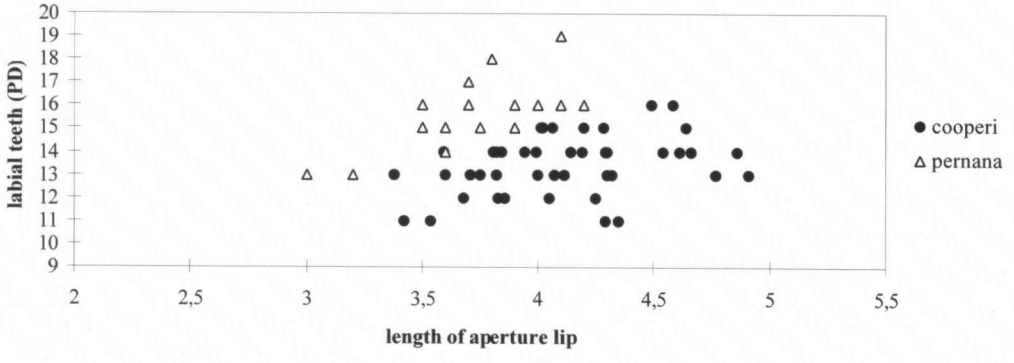


Figure C. The morphology of *E. pernana* (Lower Piacenzian, Guistrigona, Italy) and of *E. cooperi*, both chosen at random, compared.

Distribution — Known exclusively from the type locality.

Material studied — 50 specimens (BLP), 12 specimens (DFB).

Description — Shell medium sized, relatively fragile, inflated, pyriform with a short, conical spire. Protoconch consisting of 1½-1¾ somewhat elevated, convex whorls with a small nucleus. Junction with teleoconch clearly defined, with a constriction in the junction area.
Teleoconch comprising 4 flat-sided whorls, covered by very thin callus, suture distinct but superficial. Body whorl about 80-90% 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 sulcus and strongly constricted behind the anterior extremity. A thin callus covers the entire body whorl, which is usually eroded. Aperture wide and straight, 70-80% of total height. Outer lip weakly thickened, bearing 11-15 subequal denticles on the inner border, which do not usually extend onto the lip. Siphonal canal short, rounded and straight. Columella smooth, straight, bordered internally by a weak carinal ridge. The outer border delimited by a ridge in the anterior portion, which may bear 1-5 weak denticles. Fossula marked by a weak concavity. Terminal ridge simple and strong, running along the border of the siphonal canal.

Range of variation — This species is characterised by having a wide aperture, short, conical spire and a more

clearly developed fossula and terminal ridge than is usual for the genus. The labial teeth vary from pointed, fully developed denticles, sometimes continuous as folds on the apertural lip to very obscure, almost obsolete knobs. Both labial and columellar teeth are absent in juvenile specimens. The spire varies considerably in height.

Measurements —

Specimen	Catalogue Number	total length mm	length of lip mm	Breadth mm	Diameter mm	PS	PD	remarks
Holotype	HNC 52533	4.92	4.28	3.41	2.78	4	13	
Paratype 1	HNC 52534	4.71	4.25	3.27	2.67	6	15	
Paratype 2	HNC 52772	4.54	3.70	2.95	2.40	-	-	subadult
Paratype 3	HNC 52773	5.57	4.81	3.84	3.40	4	15	
Paratype 4	HNC 52774	5.30	4.73	3.84	3.15	6	11	
Paratype 5	HNC 52775	5.00	4.52	3.81	2.98	4	12	
Paratype 6	HNC 52776	5.13	4.69	3.69	3.03	5	12	
Paratype 7	HNC 52777	5.16	4.57	3.59	2.87	6	12	

Discussion — In having a wide aperture, weak dentition and a poorly developed fossula, *H. marqueti* shows features typical of the genus *Hespererato*. However, the terminal ridge is much stronger than normal for the genus, being intermediate between *Hespererato* and *Erato*.

	H. emmonsi pl. 1, fig. 6	*H. trochala* pl. 1, fig. 7	*H. cocconii* pl. 1, fig. 4; pl. 2, fig. 12	*H. marqueti* pl. 1, figs 1, 3, 9; pl. 2, fig. 9; pl. 6, fig. 4	*H. maugeriae* pl. 1, fig. 2	*H. martinicensis* pl. 1, fig. 5
Fossula	obsolete or nearly so	narrow, sloping gradually from the terminal ridge to behind	obsolete or nearly so	slightly concave, nearly obsolete	obsolete or nearly so	narrow, sloping gradually from the terminal ridge to behind
Labial teeth	very fine, lesser dense, pd = 11	fine to somewhat coarse, very dense, pd = 17	fine, sometimes nearly obsolete, dense, pd = 15	coarse, sometimes somewhat obsolete, lesser dense, pd = 13	coarse, lesser dense, pd = 13	coarse, dense, pd = 15
Columellar teeth	obsolete	obsolete	fine, sometimes nearly obsolete, dense, ps = 15	obsolete	fine, sometimes somewhat obsolete, dense, ps = 14	coarse, dense, ps = 15
Aperture lip	thickened, calloused	thickened, calloused	slightly thickened, somewhat calloused	thickened, somewhat calloused	thickened, very calloused	thickened, very calloused
Spire	projected, Sp = 110	projected, Sp = 112	somewhat projected, Sp = 106	very projected, Sp = 114	somewhat projected, Sp = 106	somewhat projected, Sp = 107
Stratum	Burdigalian, early Miocene to early Piacenzian, middle Pliocene	Early to late Pliocene	Zanclian to late Piacenzian, Pliocene	Messinian, late Miocene to Zanclian, early Pliocene	Pleistocene? to recent	recent
Distribution	New Jersey, Maryland, N. Carolina, Florida/U.S.A.	Jamaica to Florida/U.S.A.	Italy (Mediterranean)	North Sea Basin	West Indies to Carolina/U.S.A.	Martinique to S. Brazil

Table 5. Species of the genus *Hespererato* compared.

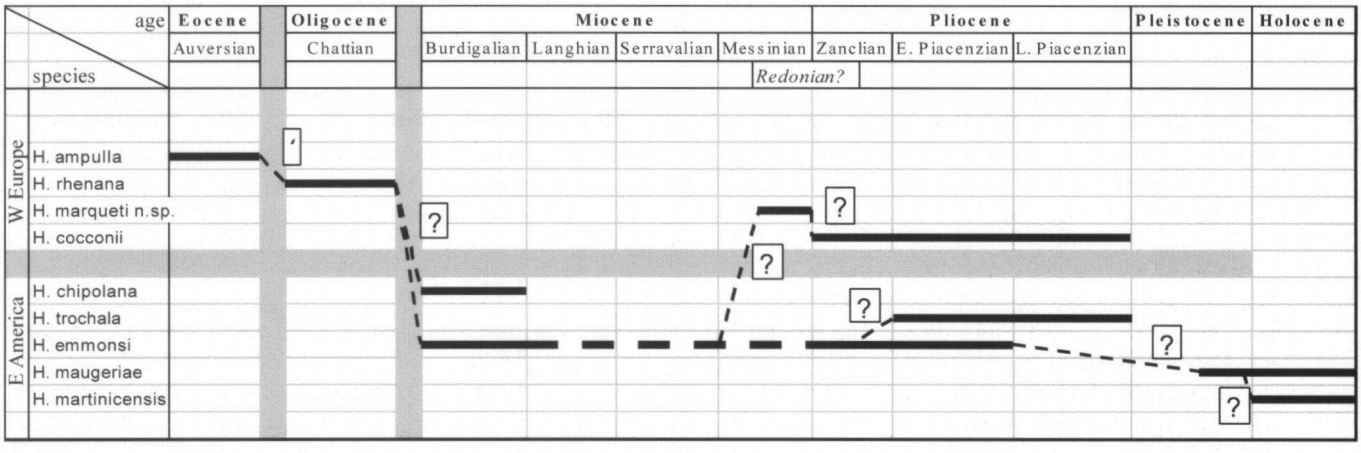


Figure D. Possible phylogeny of the genus *Hespererato*, as based on the shell morphology.

species	L	Sp	BL	D	SD	pd	ps	PT	psp	F
H. cocconii	56-66	106	76	-	-	15	15	AC	60	v
H. trochala	35	112	82	-	-	17	+	AC?	0	s?
H. emmonsi	62-80	110	76	-	-	11	10?	BC	(50)?	***V***
H. martinicensis	39-45	107	77	-	-	15	14	B	72	v
H. maugeriae	47-54	106	77	-	-	13	14	B	70	v
H. marqueti nov. sp.	43-50	114	79	-	-	13	+	A	0	v
H. rhenana	33-40	117	68	-	-	14	18	A	100	s
E. pernana	34-41	106	76	-	-	17	15	EB	19	np
E. praecedens	46-53	107	73	***G***	-	14	(13?)	EB	17	n?
E. cooperi nov. sp.	38-43	107	79	-	-	14	+	B	0	s
E. exmaugeriae	46-51	109	82	-	***v***	12	(9)	EB	13	np
E. scaldisia	48	104	77	-	-	18	15	BE	(100)	n
E. hemmoorensis	38-46	108	77	-	-	12	+	E	0	n
E. incrassata	78-90	107	76	-	v	13	(13)	FD	9	n
E. gallica	64-89	107	72	g-	v	17	16	F	86	s
E. andecavica	84-105	107	74	-	v-	15	12	F	35	n
E. voluta	80-91	111	71	-	-	14	14	CF	80	v
E. britannica	70-85	108	69	-	-	16	16	FC	90	s
E. spiralis	62-74	115	67	-	-(v?)	16	15	FC	22	sn

Table 6. Differences in shell morphology of eratoid species discussed in the present paper (compare Schilder, 1933b, p. 254); our own changes are in italics and extra bold.

To date, *Hespererato marqueti* is only the second species in the genus on record from the European Neogene. *Hespererato cocconii* Schilder, 1933b occurs in the Pliocene of the Mediterranean (see Figures 4, 12). All the morphological shell characteristics used by Schilder to distinguish eratoid taxa separate *H. marqueti* from *H. cocconii*. The former is invariably smaller with a relatively broader shell and higher spire; the density of the labial teeth is lower. Schilder (1933b, p. 254) tabulated that 60% of specimens of *H. cocconii* have all the columellar teeth well developed, whereas the posterior columellar teeth of *H. marqueti* are always absent. In Italian specimens, however, this figure is much higher than that seen in specimens from the Lower Pliocene (Zanclean) of Estepona (southern Spain; see Fehse & Landau, 2002). The terminal ridge of the new species is simple, as in *H. cocconii*, but is much stronger.

A greater resemblance exists between *H. marqueti* and *H. maugeriae* (Sowerby, 1832) (see Figure 2), but these differ not only in geographical distribution and an extensive time gap, but also in the fact that the former has a higher spire and broader shell. The terminal ridge

occasionally is bifid in *H. maugeriae* and over 70% of the posterior columellar teeth are fully developed as opposed to being absent in *H. marqueti*.

Hespererato marqueti is distinguished from the Late Oligocene (Chattian) *H. rhenana* Schilder, 1933b (North Sea Basin) in having a larger, wider shell. The posterior columellar teeth are absent, there is a somewhat lesser density and strength of labial teeth, the fossula is almost obsolete, the columellar edge is almost straight and the spire is more depressed. Differences with this and other related species are tabulated in Table 6.

The phylogenetic relationships of the genus *Hespererato* are still unclear. The first member, *H. ampulla* (Deshayes, 1835), occurs in the Middle Eocene (Auversian, Bartonian) of the Paris Basin. The second known species is *H. rhenana*, from the Upper Oligocene. During this time gap, *Hespererato* possibly spread to the east coast of North America, where *H. chipolana* (Maury, 1910) is known from the Lower Miocene (Burdigalian, Alum Bluff Formation) of Florida, as well as *H. emmonsi* (Whitfield, 1894) from the Burdigalian Kirkwood Formation of New Jersey and the Middle Pliocene (Pinecrest Beds) of Florida (see Figure 6). Then there is another time gap in the European record, until *H. marqueti* appears in the Upper Miocene of the northeast Atlantic, followed by the Pliocene *H. cocconii* (Mediterranean).

Hespererato cocconii may continue the phylogenetic lineage of the new species, which emigrated to the warmer Mediterranean waters following the cooling event in the North Atlantic. Holocene-Recent members of this thermophilic genus, which are restricted to (sub)tropical waters. This suggests that the deposit at Sceaux d'Anjou retained a somewhat subtropical character and may thus be of Late Miocene age. There are fewer similarities between *H. marqueti* and *H. trochala* (Woodring, 1928) from the Bowden Formation (Lower-Upper Pliocene) of Jamaica (see Figures 7, 8). This might indicate a remigration of the genus into western European waters, which was already suggested on the basis of studies of other molluscan genera (Dolin, 1991; Fehse, 1999; Fehse, in press).

Identification key for eratoid species from Sceaux d'Anjou

1.	Adult shell larger than 6mm	2
	Adult shell smaller than 6mm	3
2.	Adult shell large, inflated, with a very thickened outer lip	*Erato andecavica*
	Adult shell elongated, with numerous folds on anterior part of base	*Erato britannica*
3.	Shell with broad aperture, simple terminal ridge	*Hespererato marqueti* n. sp.
	Shell with narrow aperture, bifid terminal ridge	*Erato cooperi* n. sp.

(Figures x9; drawings by D. Fehse)

Fig. 1. *Hespererato marqueti* n. sp., (**holotype**), HNC 52533, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 1a - dorsal view, 1b - side view, 1c - ventral view.

Fig. 2. *Hespererato maugeriae* (Sowerby, 1832), coll. DFB 5141, Sarasota, Florida, U.S.A., recent; 2a - dorsal view, 2b - side view, 2c - ventral view.

Fig. 3. *Hespererato marqueti* n. sp. (**paratype 1**), HNC 52534, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 3a - dorsal view, 3b - side view, 3c - ventral view.

Fig. 4. *Hespererato cocconii* Schilder, 1933, coll. DFB 423, Guistrigona, Italy, early Piacenzian, middle Pliocene; 4a - dorsal view, 4b - side view, 4c - ventral view.

Fig. 5. *Hespererato martinicensis* Schilder, 1933, coll. DFB 6125, off Guarapari, Espirito Santo, Brazil, recent; 5a - dorsal view, 5b - side view, 5c - ventral view.

Fig. 6. *Hespererato emmonsi* (Whitfield, 1894), coll. DFB 5439, Sarasota, Florida, U.S.A., Pinecrest Beds, middle Pliocene; 6a - dorsal view, 6b - side view, 6c - ventral view.

Fig. 7. *Hespererato trochala* (Woodring, 1928), coll. DFB 5413, Arcadio, Florida, U.S.A., Caloosahatchee Beds, late Pliocene; 7a - dorsal view, 7b - side view, 7c - ventral view.

Fig. 8. *Hespererato trochala* (Woodring, 1928), coll. DFB 5122, Sarasota, Florida, U.S.A., Pinecrest Beds, middle Pliocene; 8a - dorsal view, 8b - side view, 8c - ventral view.

Fig. 9. *Hespererato marqueti* n sp. (**paratype 2**), subadult, HNC 52772, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 9a - dorsal view, 9b - ventral view.

Fig. 9. *Hespererato marqueti* n. sp. (**paratype 2**), subadult, HNC 52772, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 9c - side view.

Fig. 10. *Erato andecavica* Schilder, 1933, coll. DFB No. 6110A, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 10a - dorsal view, 10b - side view, 10c - ventral view.

Fig. 11. *Erato andecavica* Schilder, 1933, coll. DFB No. 6110B, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 10a - dorsal view, 10b - side view, 10c - ventral view.

Fig. 12. *Hespererato cocconii* Schilder, 1933 (**holotype**), CS 5140, Castell'Arquato, Italy, early Piacenzian, middle Pliocene; after Schilder, 1933, text fig. 43.
Fig. 13. *Erato scaldisia* Schilder, 1933 (**holotype**), IRScNB IST 4965, Kruisschans, Antwerp, Belgium, Lillo Formation, middle Pliocene; after Schilder, 1933, text fig. 57.
Fig. 14. *Erato andecavica* Schilder, 1933 (**holotype**), SMF 2097a, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; after Schilder, 1933, text fig. 68.

Fig. 15. *Erato cypraeola* (Brocchi, 1814), coll. DFB No. 4678, Rio Torsero, Italy, early Piacenzian, middle Pliocene; 15a - dorsal view, 15b - side view, 15c - ventral view.
Fig. 16. *Erato incrassata* (Döderlein, 1862 *in* Coppi, 1876), coll. DFB No. 5411, Montegibbio, Italy, Langhian, middle Miocene; 16a - dorsal view, 16b - side view, 16c - ventral view.
Fig. 17. *Erato pernana* Sacco, 1894, coll. DFB No. 5738, Guistrigona, Italy, early Piacenzian, middle Pliocene; 17a - dorsal view, 17b - side view, 17c - ventral view.
Fig. 18. *Erato cooperi* n. sp., coll. DFB No. 413, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 18a - dorsal view, 18b - side view, 18c - ventral view.
Fig. 19. *Erato praecedens* Schilder, 1933, coll. DFB No. 5410, Montegibbio, Italy, Langhian, middle Miocene; 19a - dorsal view, 19b - side view, 19c - ventral view.

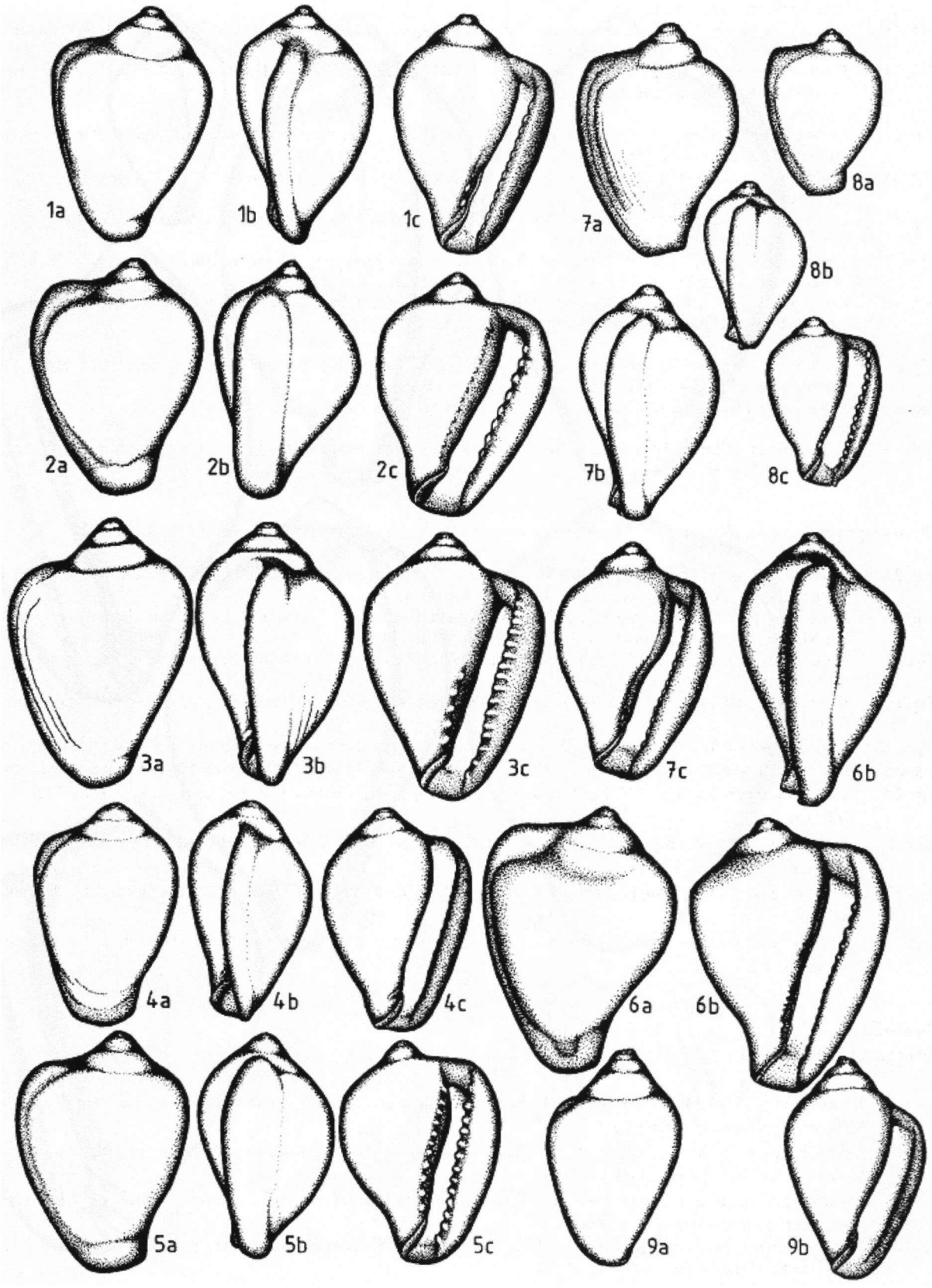
Fig. 20 *Erato britannica* Schilder, 1933, coll. DFB 6111, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 20a - dorsal view, 20b - side view, 20c - ventral view.
Fig. 21 *Erato voluta* (Montagu, 1803), coll. DFB 973, off Malaga, Spain, recent; 21a - dorsal view, 21b - side view, 21c - ventral view.
Fig. 22 *Erato gallica* Schilder, 1932, coll. DFB 5808, Paulmy, France, Serravalian, middle Miocene; 22a - dorsal view, 22b - side view, 22c - ventral view.

(Photographs by P. Hurst; photographs of the protoconchs x14.2, by B. Landau; other illustrations x9, by D. Fehse)

Fig. 23. *Erato cooperi* n. sp. (**holotype**), HNC 53514, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 27a - dorsal view, 27b - side view, 27c - ventral view.
Fig. 24. *Erato cooperi* n. sp. (**paratype 1**), HNC 53515, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; 28a - dorsal view, 28b - side view, 28c - ventral view.
Fig. 25. *Erato britannica* Schilder, 1933 (**lectotype**), BMNH G1845/1, Sutton, England, Coralline Crag Formation, early Pliocene.
Fig. 26. *Erato exmaugeriae* Sacco, 1894 (**lectotype**), BMNH G1840/1, Sutton, England, Coralline Crag Formation, early Pliocene.
Fig. 27. *Erato britannica* Schilder, 1933, coll. S.V. Wood, BMNH, No. G1845. ? The designated lectotype is marked with "**X**".
Fig. 28. *Erato exmaugeriae* Sacco, 1894, coll. S.V. Wood, BMNH, No. G1840. ? The designated lectotype is marked with "**X**".
Fig. 29. *Erato britannica* Schilder, 1933, coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene.
Fig. 30. *Erato andecavica* Schilder, 1933, coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene.
Fig. 31. *Erato cooperi* n. sp. (**paratype**), coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene.
Fig. 32. *Hespererato marqueti* n. sp. (**paratype**), coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene.

Figure 33
(photographs by B. Landau)

1. *Erato britannica* Schilder, 1933, coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; Figs. 1a-d. Original size, 8.5mm.
2. *Erato andecavica* Schilder, 1933, coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; Figs. 2a-d. Original size, 10.2mm.
3. *Erato cooperi* n. sp. (**paratype**), coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; Figs 3a-d. Original size, 5.4mm.
4. *Hespererato marqueti* n. sp. (**paratype**), coll. BLP, Sceaux d'Anjou, département Maine et Loire, France, early Redonian, late Miocene; Figs. 4a-d. Original size, 5.9mm.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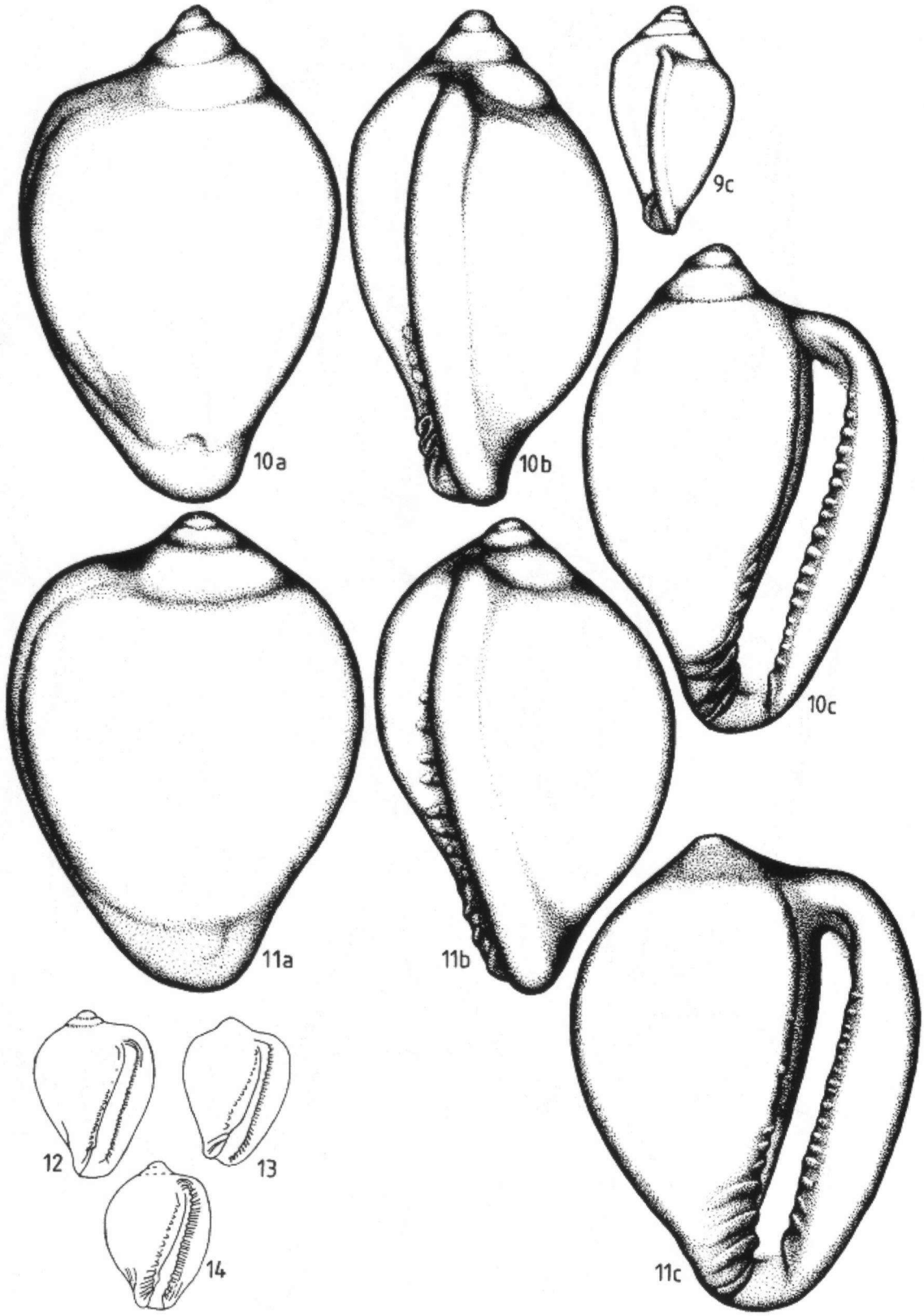
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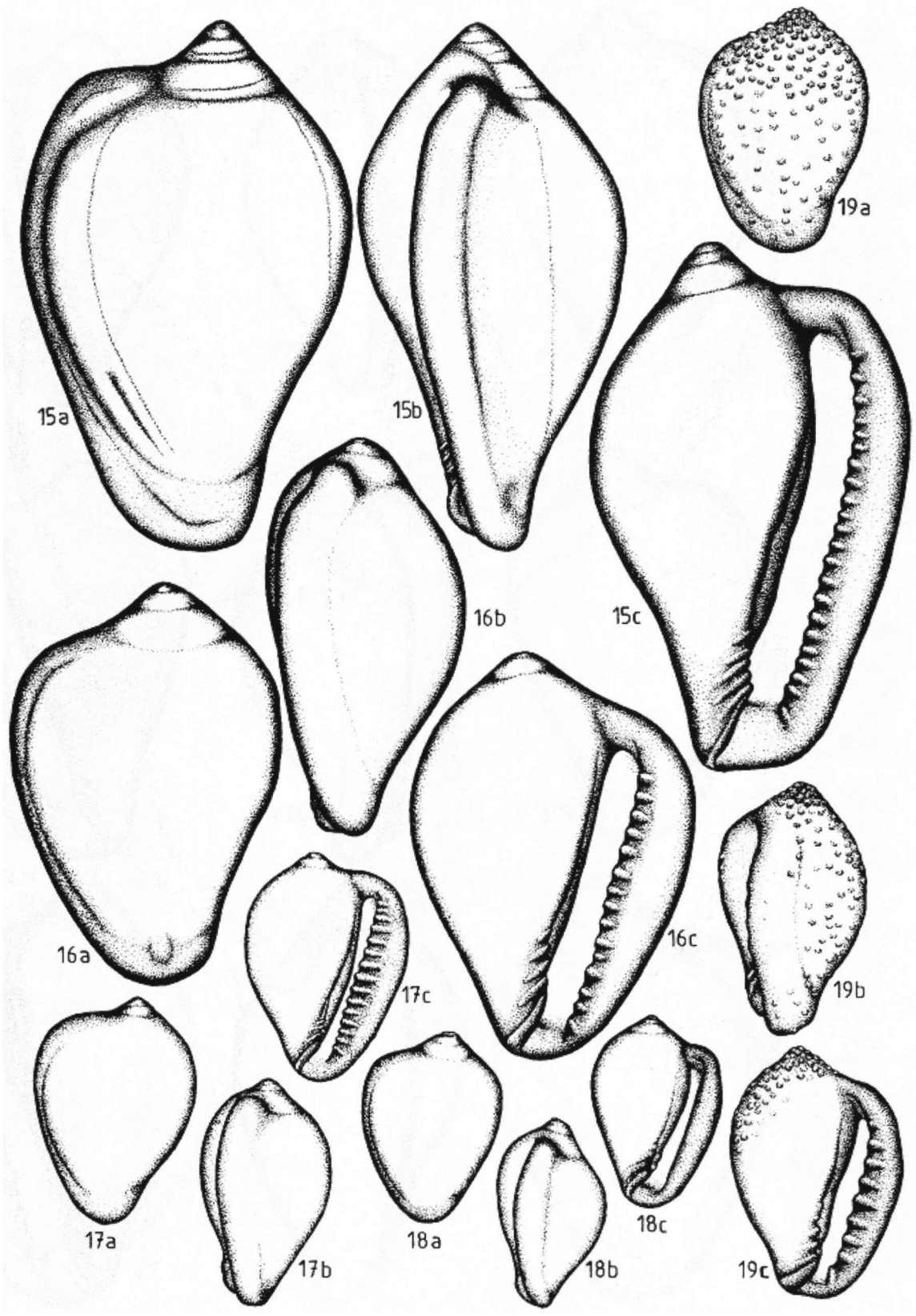
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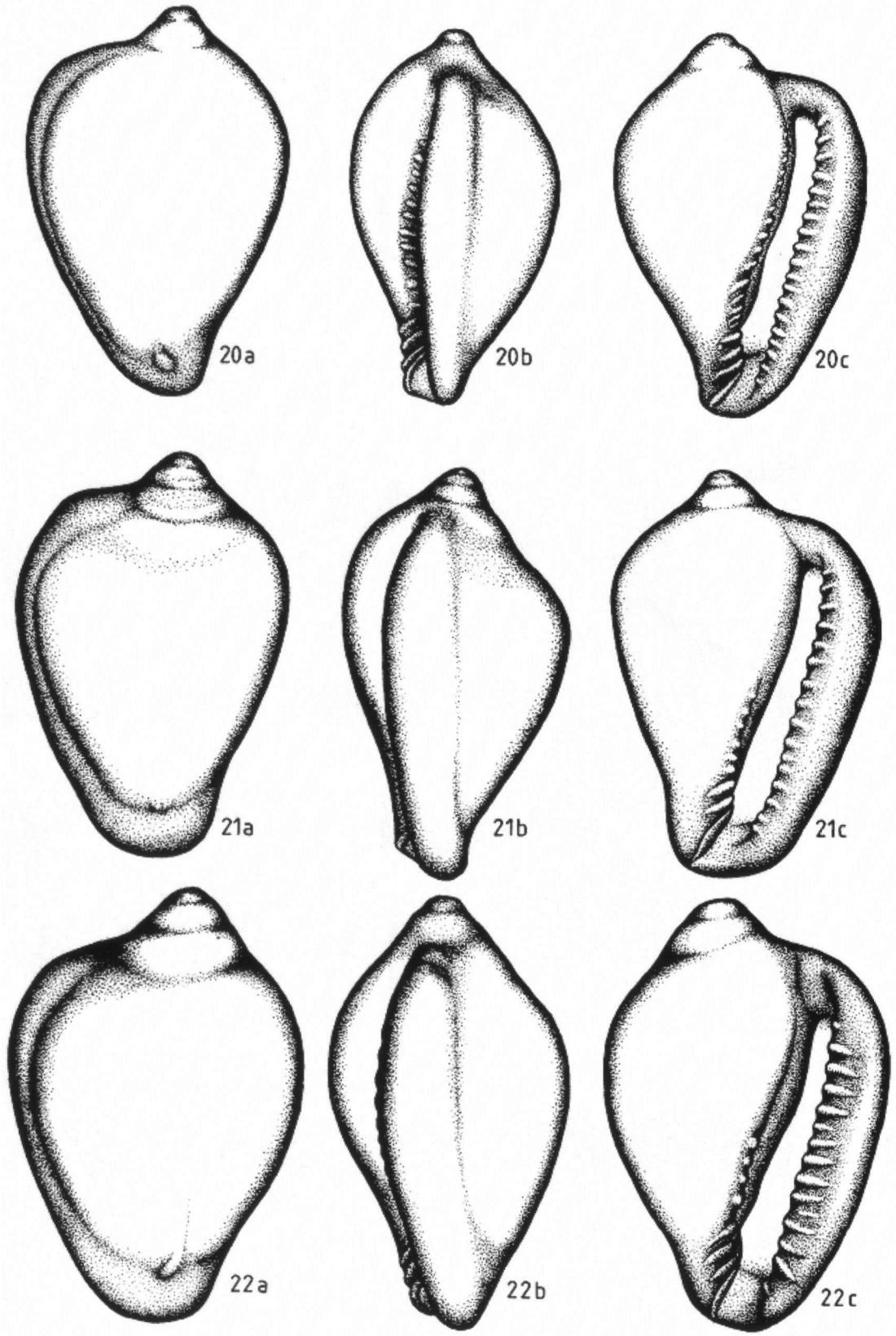
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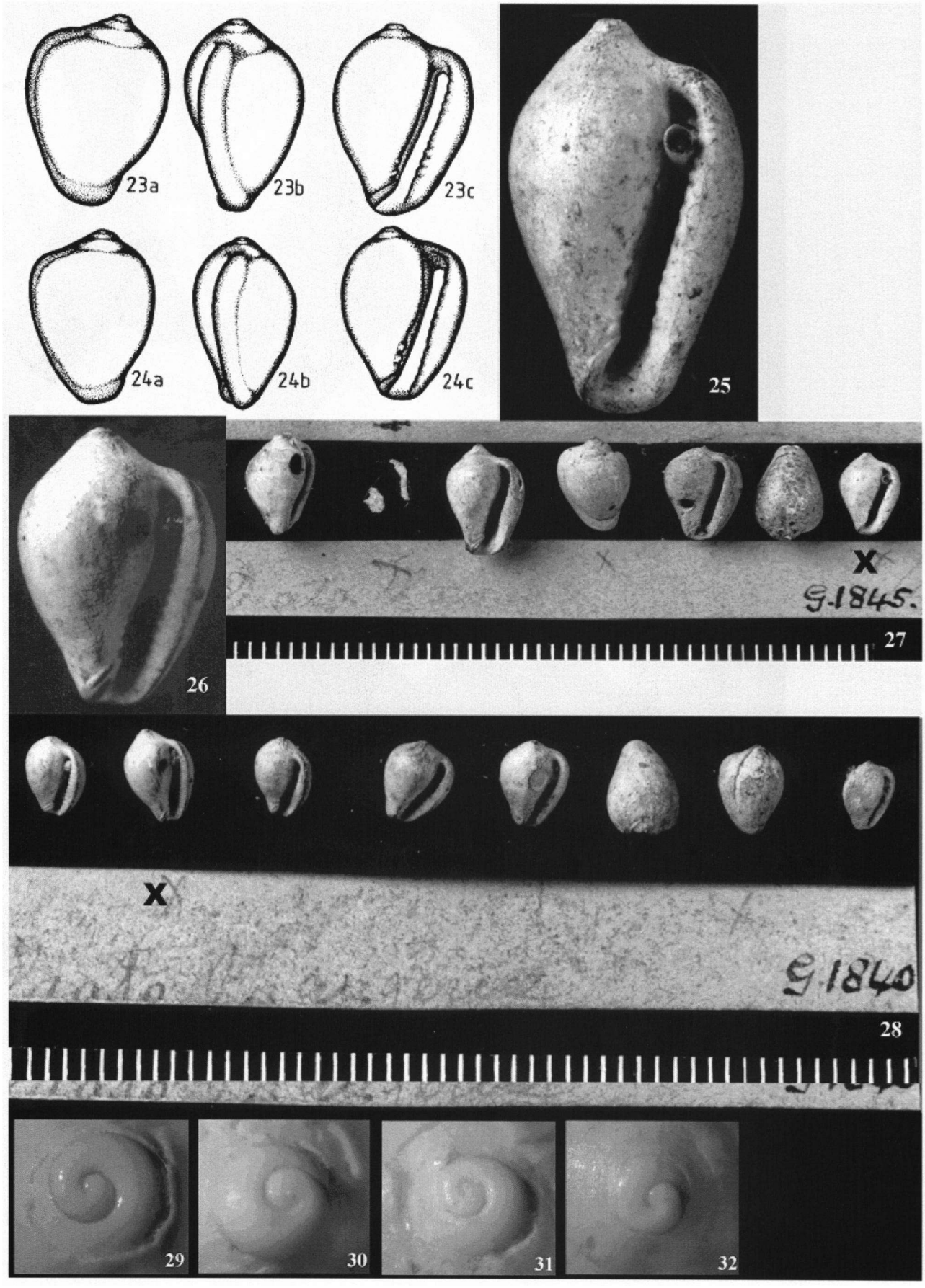
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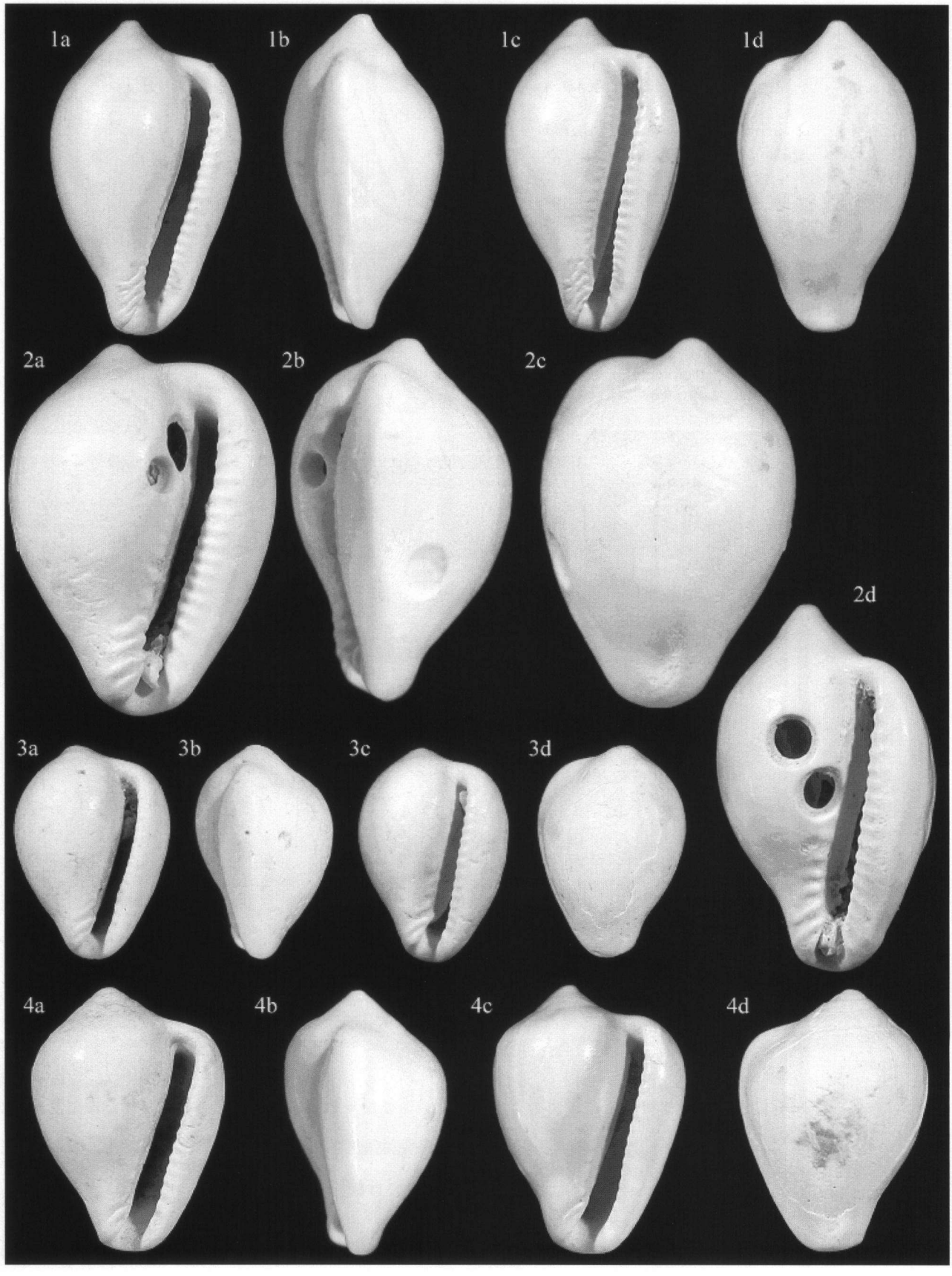

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Conclusions

The relative paucity at Sceaux d'Anjou of species representing the superfamilies Cypraeoidea and Trivioidea, as compared to the Middle Miocene of Touraine and the North Sea Basin, indicates an adaptation to colder waters, but with retention of some subtropical characteristics, *e.g.* the presence of the genus *Hespererato*. The number of taxa representing the families Triviidae and Eratoidae is much higher than present figures for the North Sea and northeast. *Hespererato marqueti* is yet another indication of a connection between the Caribbean and the eastern Atlantic, as discussed earlier by Dolin (1991) and Fehse (1999, in press).

In the present paper, we duly consider protoconch features, ignored by previous authors who have studied the Eratoidae. The protoconchs of all eratoids from Sceaux d'Anjou have fewer than 2 whorls. In other groups of gastropods, this would strongly suggest a planktotrophic development (Jackson *et al.*, 1996, fig. 9.6). Fretter & Graham (1981, p. 327) described the breeding pattern of the extant European *Erato voluta* as having a similar planktotrophic larval stage of the echinospira type.

Planktotrophic development tends to favour longevity and a wide geographical distribution. Unfortunately, exposures of Upper Miocene Atlantic deposits are limited. None of the species found at Sceaux d'Anjou are known from older Middle Miocene Atlantic deposits in France or from the Upper Miocene (Tortonian) of the more southerly Atlantic Iberian coast (Cacela, Algarve, Portugal).

Eratoids are highly abundant at Sceaux d'Anjou. 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). At Sceaux d'Anjou numerous other gastropod genera that favour rocky shores and hard bottoms are found, *e.g.* *Fissurella*, *Gibbula*, *Calliostoma* and *Trivia*. From the number of individuals and the large size attained, it may be concluded that the habitat was favourable. Finally, a high degree of predation amongst the specimens collected should be noted. Numerous naticid borings have been found, usually occurring on the base, but some are on the dorsum.

Acknowledgements

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