

Contributions to eratoid systematics (Mollusca, Gastropoda), 3. European Oligocene Eratoidae, with description of a new species

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European Oligocene eratoid faunas are revised systematically and compared with assemblages recorded from elsewhere. The material comes from the Lower Oligocene (Rupelian) of Gaas-Espibos (France), the Upper Oligocene (Chattian) of Abbesse (Aquitaine, France) and the Upper Oligocene (Kasseler Meeressand, Chattian) of Glimmerode (Germany). One new species, *Erato dolini* n. sp., is described, and possible evolutionary trends and migrations, as based on shell morphology, are outlined.

KEY WORDS: Mollusca, Gastropoda, Eratoidae, Rupelian, Chattian, NE Atlantic, France, systematics, new taxon.

Introduction

The present paper continues our series on the taxonomy of the Eratoidae, and is devoted to a discussion of eratoids from Oligocene strata in Europe. Although Oligocene molluscan faunas are very rich, eratoid diversity is surprisingly limited, with only three species described so far, viz. *Erato prolaevis* Sacco, 1894, *E. transiens* Boettger, 1884 and *Hespererato rhenana* Schilder, 1933. The well-preserved Chattian molluscan faunas from Abbesse, near St-Paul-lès-Dax (France) have now yielded a fourth species, *E. dolini* n. sp.

Faunas from the Oligocene of France have recently received much attention (Lozouet, 1998, 1999), yielding numerous new species, especially from Chattian strata at Abbesse, Peyrehorade, St-Etienne-d'Orthe and other localities. However, no eratoids have so far been recorded from these deposits. Our material stems from Abbesse, Gaas-Espibos (near Dax, of 'Stampian' [= Rupelian] age) and Glimmerode (near Kassel, of Chattian age; see Janssen, 1978b).

Systematic palaeontology

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

BLP B. Landau Colln, Albufeira;
CS F.A. Schilder Colln, provisionally deposited at

the Museum für Naturkunde der Humboldt Universität, Berlin;

DFB D. Fehse Colln, Berlin;

HNC Haus der Natur, Cismar;

IRScNB Institut royal des Sciences naturelles de Belgique, Brussels;

NHM The Natural History Museum, London;

NHMB Natural History Museum Budapest, Geological-palaeontological collections;

SMF Senckenberg Museum, Frankfurt am Main.

To describe eratoid shell morphology the following abbreviations are used:

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. 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

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 percent) 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 prolaevis Sacco, 1894

Figures 1/1a-c, 2a-c; 2/1d; 3/1a-c

1862 *Erato laevis* Don. — Speyer, p. 106, pl. 18, fig. 16a-c (non Donovan, 1804).

*1894 *Erato prolaevis* Sacco, p. 58.

1929 *Erato* cf. *prolaevis* Sac. — Schilder, p. 7, text-fig. 1.

1932b *Erato* (*Archierato*) *prolaevis* Sacco — Schilder, p. 82.

1933 *Erato* (*Eratopsis*) *prolaevis* Sacco, 1894 — Schilder, pp. 249, 254, 270.

1952 *Hesperato prolaevis* Sacco - Görge, p. 82, pl. 2, figs 59, 60.

1967 *Erato gaasensis* Vergneau, p. 206.

1968 *Erato gaasensis* Vergneau-Saubade, p. 202, text-fig. 12.

1971 *Erato* (*Eratopsis*) *prolaevis prolaevis* Sacco, 1894 — Schilder & Schilder, p. 13.

1973 *Erato prolaevis* Sacco, 1894 — Báldi, p. 279, pl. 34, fig. 5.

1978b *Erato* (*Eratopsis*) *prolaevis prolaevis* Sacco 1894 — Janssen, p. 196.

Distribution — Hohenkirchen, Harleshausen, Ahnetal (Germany; Janssen, 1978b); Eger (Chattian), Hungary (Báldi, 1973); Gaas-Espibos ('Stampian') and Abbesse (Chattian), SW France.

Material studied — In addition to NHMB M69/224, 5 specimens from Abbesse and 7 specimens from Gaas-Espibos (BLP Colln), 10 and 30 specimens from Abbesse and Gaas-Espibos, respectively (DFB Colln).

Description — Shell small to medium sized, relatively fragile, elongated pyriform, with an elevated, slightly pointed spire. Protoconch mostly covered by callus, but visible in several specimens, consisting of 2¾, the first 1½ depressed, becoming convex below, with a very small nucleus; suture clearly marked and incised, and junction with teleoconch indistinct. Teleoconch consisting of about 2¼ whorls; spire covered by very thick callus which covers the suture. Body whorl 80% of total height, shouldered adapically, with maximum diameter ¼ distance from adapical suture, evenly tapered below and only faintly constricted at the base. Dorsum usually smooth, but some specimens show surface pustules, rounded, with dorsal sulcus represented by a dimple behind the anterior extremity in fully-adult specimens. Entire shell surface covered by thick, glossy callus. Aperture comprising about 75% of total height, straight and narrow adapically, becoming wider in anterior half. Outer lip thickened, smooth, evenly rounded, bearing 10-18 strong to weak denticles which extend onto the lip at a variable distance. Siphonal canal short, rounded and straight. Columella sinuous, with a well-developed carinal edge. Dentition on outer edge of columella varies from a row of c. 20 weak denticles to almost smooth. The anteriormost 2-4 denticles are developed into folds which run obliquely across the base. Fossula marked by a shallow concavity, not delimited from the columella. Terminal ridge simple.

Range of variation — This species is characterised by having an elongated shape with an elevated spire; other features are remarkably variable. Specimens from the 'Stampian' of Gaas-Espibos generally are half the size of Chattian material from Abbesse. Pustules are seen in 10% of and a dorsal dimple in all Chattian-age specimens, whereas 'Stampian' material shows no pustules and only 30% have a dimple.

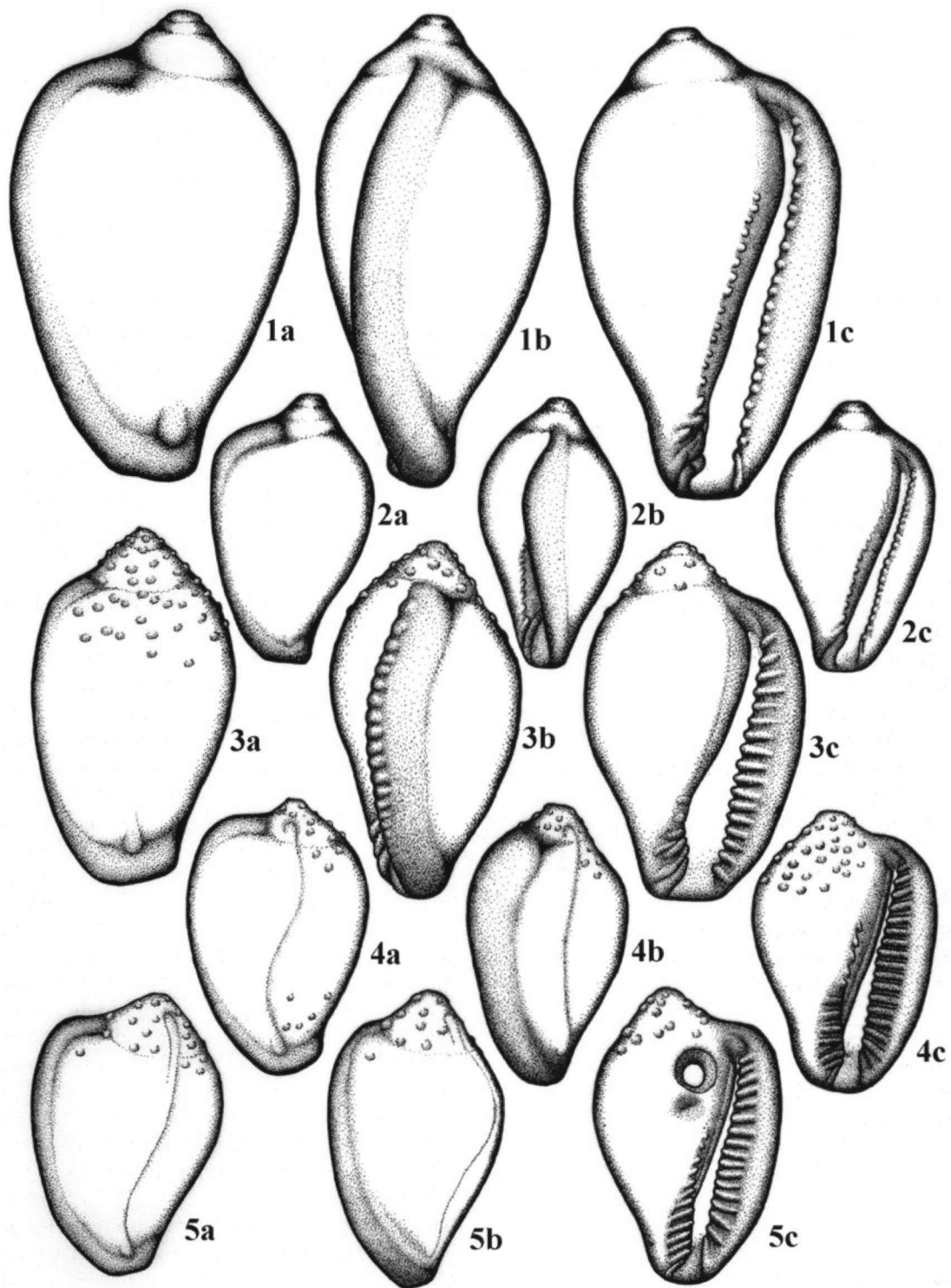


Figure 1. Oligocene eratoid species from SW France (drawings: D. Fehse):

1a-c, 2a-c. *Erato prolaevis* Sacco, 1894; 1 - Abbesse, Upper Oligocene (Chattian) (DFB Colln); original height = 8.8 mm; 2 - Gaas-Espibos, Middle Oligocene ('Stampian') (DFB Colln); original height = 5.0 mm.
3a-c. *Erato* cf. *transiens* Boettger, 1884, Abbesse, Upper Oligocene (Chattian) (DFB Colln); original height = 6.7 mm.
4a-c, 5a-c. *Erato dolini* n. sp.; 4 - HNC 57308 (**holotype**), Abbesse, Upper Oligocene (Chattian); original height = 5.2 mm; 5 - HNC 57309 (**paratype**), Abbesse, Upper Oligocene (Chattian); original height = 5.4 mm.

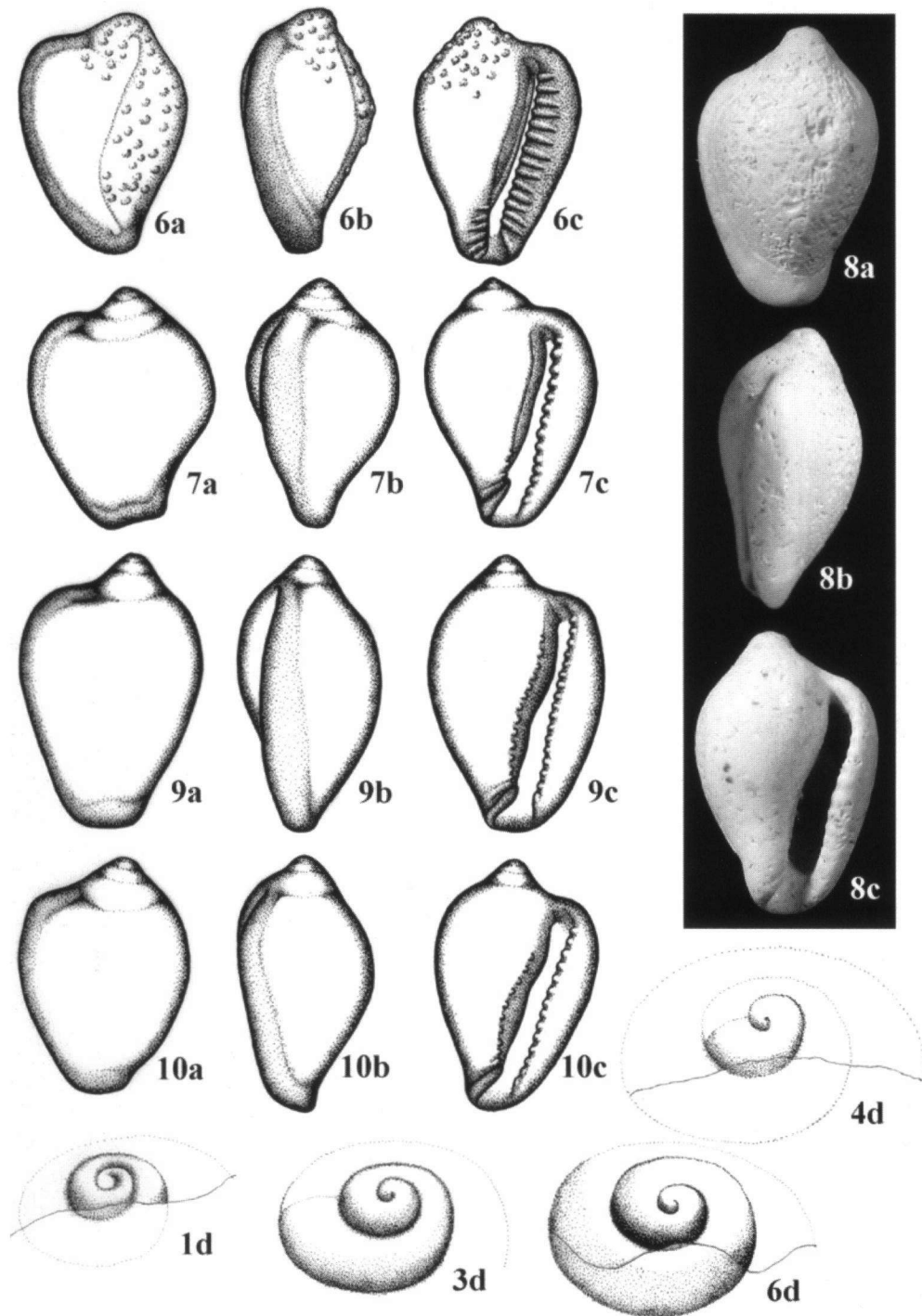


Figure 2. Oligocene eratoid species from SW France (drawings: D. Fehse; photograph: B. Landau):

- 1d. *Erato prolaevis* Sacco, 1894, Abbesse, Upper Oligocene (Chattian) (DFB Colln), protoconch (x 18).
 3d. *Erato* cf. *transiens* Boettger, 1884, Abbesse, Upper Oligocene (Chattian) (DFB Colln), protoconch (x 18).
 4d, 6. *Erato dolini* n. sp.; 4 - HNC 57308 (**holotype**), Abbesse, Upper Oligocene (Chattian), protoconch (x 18); 6 - HNC 57310 (**paratype**), Abbesse, Upper Oligocene (Chattian), protoconch (x 18).
 7a-c, 8a-c, 9a-c, 10a-c. *Hespererato rhenana* Schilder, 1933; 7 - Abbesse, Upper Oligocene (Chattian) (DFB Colln); original height = 4.6 mm; 8 - same locality and stratigraphy (BLP Colln); original height = 5.0 mm; 9 - same locality and stratigraphy (DFB Colln); original height = 5.1 mm; 10 - same locality and stratigraphy (DFB Colln); original height = 4.6 mm.

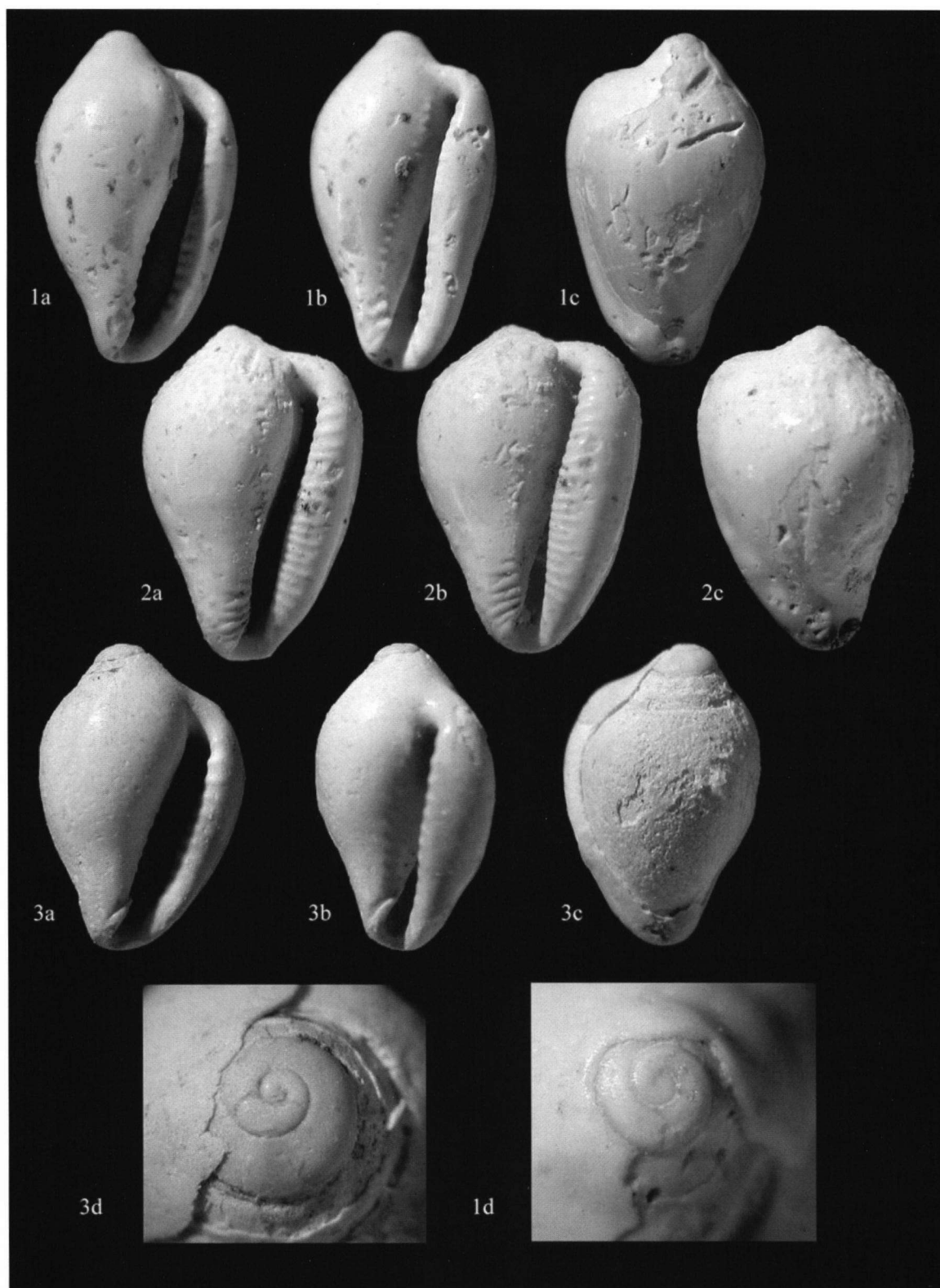


Figure 3. Oligocene eratoid species from SW France (Photographs: B. Landau):

1a-d, 3a-d. *Erato prolaevis* Sacco, 1894; 1 - Abbesse, Upper Oligocene (Chattian) (DFB Colln); original height = 6.7 mm; 3 - Gaas-Espibos, Middle Oligocene ('Stampian') (BLP Colln); original height = 5.2 mm.
2a-c. *Erato dolini* n. sp., Abbesse, Upper Oligocene (Chattian) (BLP Colln); original height = 4.9 mm.

The number and strength of denticles on the outer lip may vary from strongly developed, extending onto the lip, to subobsolete teeth confined to the inner border. Similarly, the columella may have a complete row of fine denticles or be almost smooth.

Discussion — The present taxon is widely distributed in the Oligocene (France, Germany and Hungary). It was first illustrated by Speyer (1862), who assigned it to *E. laevis* (Donovan, 1804). Sacco (1894) considered Speyer's material to be specifically distinct from extant *E. laevis*, a senior synonym of *E. voluta* (Montagu, 1803). Unfortunately, the type material could not be traced; should turn out that the originals are lost, a shell contained in the geological-palaeontological collections of the Natural History Museum Budapest (registration no. M69/224) might be designated neotype.

Erato transiens Boettger, 1884, a similarly widely distributed, Early Miocene species (possibly also known from the Oligocene at Abbesse, see below and Figures 1/3a-c; 2/3d), differs in being slightly less elongated, with a shorter spire, an outer lip which is less thickened and a greater number of oblique ridges on the anterior part of the base. The protoconch in *E. transiens* is smaller, consisting of 1½ whorls, and more elevated than that in *E. prolaevis*.

Erato dolini n. sp.

Figure 1/4a-c, 5a-c; 2/4d, 6; 3/2a-c

Types — Holotype is NHC 57308; paratypes are HNC 57309-57312.

Stratum typicum — Chattian (Upper Oligocene).

Locus typicus — Abbesse, near St Paul-lès-Dax, SW France.

Derivatio nominis — In honour of Luc Dolin, who contributed much to our knowledge of Cypraeoidea and Trivioidea.

Distribution — Known only from the type locality.

Material studied — In addition to the types (see above), eleven specimens in BLP Colln and 80 specimens in DFB Colln.

Description — Shell medium sized, relatively fragile, inflated pyriform, with a short, broad, conical spire. Protoconch and teleoconch covered by thick callus in all specimens, obscuring the number of whorls and outer spire characteristics. Body whorl 90% of total height, shouldered adapically, with maximum diameter ¼ distance from adapical suture, concave below and constricted at the base. Dorsum covered in pustules which are densest around spire and behind the anterior extremity. Dorsal sulcus present on

posterior part, curving to left and becoming obsolete on mid-portion, reappearing on anterior part, ending in a strong dimple. Entire shell surface covered by thick, glossy callus. Aperture comprising about 80% of total height, straight and narrow. Outer lip greatly thickened, keeled, with inner half tapering towards aperture and outer half outwards; 14-20 very strong, fold-like denticles extend across inner half of keel. Siphonal canal short, rounded and straight. Columella sinuous, with a well-developed carinal ridge which ends adaxially in a small, distinct sinus. Dentition on outer edge of columella consisting of six strong, elongated, oblique folds, above which there may be a row of up to 12 denticles, but usually these are subobsolete. Fossula deeply concave, not delimited from columella. Terminal ridge simple and subobsolete.

Range of variation — Typical features of this species are the keeled outer lip with strong, fold-like teeth on the inner part, the strong folds on the base, the deep fossula and the carinal edge ending in a sinus. As in Miocene eratoids with pustules and a dorsal sulcus, these features are highly variable in presence and development; some of the specimens are slightly more inflated.

Measurements (in mm) —

	Total length	Length of lip	Width	ps	pd
HNC 57308	5.2	4.9	3.4	15	16
HNC 57309	5.4	5.0	3.5	18	16
HNC 57310	3.6	3.5	2.4	-	14
HNC 57311	5.9	5.4	4.0	15	16
HNC 57312	5.1	4.9	3.5	15	16

Discussion — Shell shape in *Erato dolini* n. sp. is unique amongst Oligocene eratoids in Europe, in having a deep, sinuous dorsal furrow and strong columellar dentition, with relatively numerous denticles elongated as ventral folds and covering almost the entire anterior portion of the base. This last-named feature is seen in extant Indo-Pacific species of the genus *Alaerato* Cate, 1977, whose most typical feature is, however, the 'exaggerated, wing-like extension of the acute angular portion of the posterior outer lip' (Cate, 1977, p. 345), absent in *E. dolini* n. sp., and thus clearly different from the extant species. *Eratoena sulcifera capensis* (Schilder, 1933), an extant South African form, has a similar dentition as well. However, *E. dolini* n. sp. is easily distinguished in having a differently shaped aperture and fossula, a more depressed spire and a curved dorsal sulcus.

Erato dolini n. sp. differs from *E. prolaevis* in having a more inflated shell, with a shorter spire, a much thicker outer lip with stronger denticles and more numerous and stronger folds on the base; the fossula is more concave and the carinal ridge better developed.

The present species appears directly ancestral to *E.*

subcypraeola (d'Orbigny, 1852) from SW France, of Miocene (Aquitanian and Burdigalian) age, which it resembles, but from which it differs in having a keeled outer lip which is not quite as thickened as that of the Miocene congener, in which it is more rounded. There are fewer folds on the anterior end of the columella (at least 6 in *E. dolini* n. sp., 3 in *E. subcypraeola*) and the fossula is more deeply concave. Pustules in the latter species are evenly distributed on the dorsum, whereas in *E. dolini* n. sp. these are much denser in the area around the spire and immediately behind the anterior end.

Erato transiens has a similar shape, but a much wider aperture, a less thickened outer lip with weaker dentition, fewer folds on the base and a very shallow fossula.

***Erato* cf. *transiens* Boettger, 1884**

Figures 1/3a-c; 2/3d

compare

- 1879 *Eratopsis barrandei* (Varietät A) Hoernes & Auinger, pl. 8, fig. 9a-c.
- 1879 *Eratopsis barrandei* (Varietät B) Hoernes & Auinger, pl. 8, fig. 10a-c.
- *1884 *Erato transiens* Boettger, p. 137.
- 1894 *E. transiens* Boettger, 1884 — Sacco, p. 62.
- 1929 *Erato transiens* Boettg. — Schilder, p. 12.
- 1932a *Erato transiens* — Schilder, p. 44.
- 1932b *Erato (Erato) transiens transiens* Boettg. — Schilder, p. 89.
- 1933 *Erato (Erato) transiens* Boettg. — Schilder, pp. 250, 254, text-figs 69-71.
- 1971 *Erato (Erato) transiens transiens* Böttger, 1884 — Schilder & Schilder, p. 14.
- 1977 *Erato transiens transiens* — Cate, text-fig. 32, 32a.
- 1995 *Erato transiens* Boettger, 1884 — Baluk, p. 190.
- 1995 *Erato (Eratopsis) barrandei* Hoernes & Auinger — Baluk, pl. 13, fig. 4.
- 2001 *Eratopsis subcypraeola* (d'Orbigny, 1852) — Lozouet et al., p. 42, pl. 16, fig. 3.

Distribution — Austria and Romania (Schilder, 1932b).

Material studied — CS 22, 26 and 3626; > 50 specimens, St Martin d'Oney (France), Lower Miocene (Aquitanian) (BLP Colln); 7 specimens from Abbese, Chattian; 4 specimens from St Martin d'Oney; 1 specimen from Thenay (France), Middle Miocene (Langhian); 1 specimen from Rhoznik (Slovakia), Middle Miocene ('Badenian'), all in DFB Colln.

Description — Shell medium sized, relatively fragile, elongated pyriform, with an elevated, slightly pointed spire. Protoconch mostly covered by callus, but visible in several specimens, consisting of 2 to 2½ depressed whorls, with well-marked lines and a minute nucleus. Suture clearly marked and incised; junction with teleoconch indistinct. Teleoconch consisting of about 3¼ whorls; spire covered by very thick callus which covers the suture. Body whorl

almost 90% of total height, shouldered adapically, with maximum diameter ¼ distance from adapical suture, evenly tapered below and only slightly constricted at the base. Dorsum usually covered with minute to large pustules, mostly concentrated around spire. Dorsum rounded and bearing a dorsal sulcus represented by at least a dimple behind the anterior extremity in fully-adult specimens. Entire shell surface covered by thick, glossy callus. Aperture comprising c. 85% of total height, slightly sinuous and narrow. Outer lip thickened, smooth, flattened and sloping slightly into the aperture, rounded at the outer margin, bearing 17 to 21 strong teeth which extend onto the lip to a variable distance. Siphonal canal short, rounded and straight. Columella sinuous, with weakly developed inner carinal ridge and a thickened parietal lip. Denticles on parietal lip varying in number from 17 to 22; anteriormost 3-5 denticles developed into folds which run obliquely across the base, the remaining weakly developed. Fossula marked by a shallow concavity, not delimited from columella. Terminal ridge simple.

Range of variation — The present species is characterised by an elongated shape, a surface bearing pustules and an elevated spire with pustules. Strength and extension of pustules vary considerably. The dorsal sulcus varies from a distinct dimple behind the anterior extremity to a straight, well-marked line extending from the anterior extremity to the suture, where a similar dimple may be visible. The columellar teeth may be well developed and distinct to almost obsolete.

Discussion — It appears that *E. transiens* has often been misidentified as *Eratopsis barrandei* or *Erato subcypraeola* (see synonymy above); the species possibly originated in the Atlantic Upper Oligocene and extended its range into the 'Badenian' and Langhian (Middle Miocene) in the Vienna and North Sea basins.

Material of *E. cf. transiens* from Abbese closely resembles the Middle Miocene specimens but has somewhat stronger labial teeth which are extended into folds on the lip. In addition, the outer lip is slightly sinuous. However, the plication on the anterior base, the elevated spire, the fossula, pustules and dorsal sulcus are all similar to those seen in Middle Miocene material. In view of these small differences in morphology and stratigraphic age, we prefer a record in open nomenclature.

Yet again, the type material could not be traced. Specimens were not present amongst Boettger's originals at the Senckenberg Museum (Frankfurt am Main). Specimen 22 in the F.A. Schilder Colln (CS), from Steinabrunn (Austria) might serve as a neotype, in case Boettger's types should turn out lost.

Genus *Hespererato* Schilder, 1932b

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

***Hespererato rhenana* Schilder, 1933**

Figures 2/7a-c, 8a-c, 9a-c, 10a-c; 3/3a-d

- *1933 *Hespererato rhenana* Schilder, pp. 248, 254, 271, text-fig. 42.
- 1941 *Erato laevis* Donovan — Görge, p. 137.
- 1952 *Hespererato rhenana* Schilder — Görge, p. 83, pl. 2, figs 61, 62.
- 1978a *Hespererato (Hespererato) rhenana* Schilder 1933 — Janssen, p. 85.
- 1978b *Hespererato rhenana* Schilder, 1933 — Janssen, p. 196, pl. 14, fig. 85.
- 1996 *Hespererato rhenana* Schilder, 1933 — Moths *et al.*, p. 27, pl. 13, fig. 1.

Distribution — Krefeld, Hohenkirchen, Niederkaufungen, Harleshausen, Ahnetal, Rumeln (Germany; Janssen, 1978b); 'Steinberger Gestein', Kobrow, Segrahner Berg (Germany; Moths *et al.*, 1996); Glimmerode and Meerbusch-Osterath (Germany) and Abbesse (France).

Material studied — SMF 250434a; 1 specimen from Krefeld and 2 specimens from Abbesse (BLP Colln); 2 specimens from Glimmerode, 4 four Meerbusch-Osterath and 15 from Abbesse (DFB Colln).

Description — Shell small, fragile, inflated, pyriform with a short, conical spire. Protoconch consisting of 2½ whorls, the first depressed, somewhat elevated below and rapidly expanding, with a very small nucleus. Suture distinct and incised; junction with teleoconch not clearly defined. Teleoconch comprising 2½ flat-sided whorls, originally covered by very thick callus, most of which is eroded. Body whorl *c.* 80% of total height, inflated, shouldered adapically, with maximum diameter just below adapical suture, slightly convex below and weakly constricted at the base. Dorsum smooth, rounded, without any dorsal sulcus and not constricted behind the anterior extremity. Aperture narrow for genus and straight, 70-75% of total height. Outer lip weakly thickened, bearing 10-11 subequal denticles on inner border which do not usually extend onto the lip. Siphonal canal short, rounded and straight. Columella smooth, slightly sinuous, bordered internally by a weak carinal ridge; ridge slightly stronger in the fossular area and slightly protruding. Outer border delimited by a ridge bearing up to 13 weak denticles, becoming obsolete in posterior portion. Fossula marked by a weak concavity. Terminal ridge simple and strong, running along border of siphonal canal.

Table 1. Differences in shell morphology of eratoid species discussed in the present paper (after Schilder, 1933, p. 254)

	L	Sp	BL	D	SD	pd	ps	PT	psp	F
<i>H. rhenana</i>	33-40	117	68	-	-	14	18	A	100	s
<i>H. marqueti</i>	43-50	114	79	-	-	13	+	A	0	v
<i>E. s. capensis</i>	35-47	103	67	(g)	vs	23	21	DC	100	n
<i>E. dolini</i>	35-54	106	70	g	s	16	16	D	90	p
<i>E. subcypraeola</i>	41-56	109	73	Gg	vs	15	18	F	28	ns
<i>E. prolaevis</i>	41	122	79	-	-	13	+	E	(0)	?
<i>E. transiens</i>	64-80	113	69	gG	v-	16	16	F	69	s
<i>E. cf. transiens</i>	52-66	109	70	gG	vs	18	17	F	100	s
<i>E. barrandei</i>	30-36	100	80	G	n	12	11	EB	100	np

Identification key for Oligocene eratoid species

- 1. Adult shell usually with pustules +/- dorsal sulcus or dimple, well-developed teeth and folds on base
Adult shell fragile, no dorsal sulcus or pustules and weak dentition 2
Hespererato rhenana
- 2. Adult shell with strong dentition, > 5 folds on base
Adult shell with strong to weak dentition, < 5 folds on base 3
Erato prolaevis
- 3. Squat shell, very callused, dorsal sulcus curved
Shell slender, elongated, dorsal sulcus obsolete *Erato dolini*
Erato cf. Transiens

Range of variation — Schilder (1933, p. 271) noted that shells vary from inflated with short spire to slender with an elongated spire; the width of the aperture varies considerably as well.

Discussion — The present species is not typical of the

genus *Hespererato*, since it is more elongated, with a narrower aperture than usual and with a stronger dentition and terminal ridge. It does, however, have a weak fossula and simple terminal ridge which probably led Schilder to assign it to the genus.

Until now, *H. rhenana* was recorded from Chattian

strata in the North Sea Basin only, invariably rare (Janssen, 1978b). At Abbesse, it appears to be fairly common (D. Fehse, pers. obs.).

The next member of the genus to appear in European fossil faunas is *H. marqueti* Fehse & Landau, 2002b from France, of Late Miocene ('Early Redonian') age. It is distinguished from the present species by having a larger, wider shell. The posterior columellar teeth are absent and density and strength of labial teeth are slightly less, the fossula even weaker, the columellar edge almost straight and the spire even more depressed. *Hespererato rhenana* has little in common with *H. marqueti*, and a wide stratigraphic gap separates the two taxa. It may be that this thermophilic genus disappeared at the end of the Oligocene, only to reappear during the Late Miocene, possibly migrating in from the Caribbean where the genus is well represented throughout the Miocene (Fehse & Landau, 2002b).

Conclusions

Of the faunas so far revised by us (Fehse & Landau, 2002a, b), the present is the least diverse one, both in numbers of individuals and species. The genus *Hespererato*, at present found only in the warmer waters of the Caribbean and tropical eastern Pacific, is represented by a single species in the Upper Oligocene of the North Sea Basin, where it is invariably rare and in the Upper Oligocene of the NE Atlantic, where it appears to be commoner. Of the other three species described in the present paper, *E. prolaevis* is widely distributed while the remaining two seem to have been endemic to the Atlantic coast of France during the Late Oligocene.

The protoconch of *E. prolaevis* consists of only 1½ whorls. In other gastropod groups this would strongly suggest a planktotrophic larval development (Jackson *et al.*, 1996, pp. 242-243, fig. 9.6). Fretter & Graham (1981, p. 327) described a similar breeding pattern in the extant *E. voluta* in Europe, which would explain the wide geographical and stratigraphical distribution of the species. *Hespererato rhenana*, with a protoconch of 2½ whorls, could have had a planktotrophic or lecithotrophic development. In *E. dolini* n. sp., the protoconch is invariably covered by callus, so that the number of whorls cannot be determined.

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