

The earliest cowries: the origin of cypraeoid gastropods

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Cowries, the family Cypraeidae, form a diverse and conspicuous group of gastropods living in tropical to subtropical seas. Their shell is convolute (last whorl covers all previous ones) with a narrow, slit-like siphonate aperture bearing denticles (“teeth”). When extended, a large part of their shell surface is covered by a soft fleshy mantle. The earliest cowries were reported from the Upper Jurassic of Sicily: *Cypraea tithonica* and *Cypraea gemmellaroi*. Subsequently, these species had been assigned to various cypraeid genera. Examination of the type material of *Cypraea tithonica* reveals that this species represents a new genus: *Coffeacypraea* Nützel & Schneider. *Cypraea gemmellaroi* also belongs to this new genus and is potentially synonymous with *Coffeacypraea tithonica*. The Upper Jurassic caenogastropod genera *Colombellina* and *Zittelia* (family Colombellinidae) also have narrowly elongated siphonate apertures and are closely related to Cypraeidae but their shells are not convolute. The origination of Cypraeidae and Colombellinidae contributed considerably to the Mesozoic–Cenozoic caenogastropod radiation.

Key words: Gastropoda, Cypraeoidea, Jurassic, taxonomy, systematics, evolutionary relationships, Sicily, Italy.

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Introduction

Cowries, the family Cypraeidae Rafinesque, 1815, comprise approximately 400 living species and subspecies, and have a rich Cenozoic and sparse Cretaceous fossil record (e.g., Schilder and Schilder 1971; Lorenz 2017, 2018; MolluscaBase 2025). Two species of latest Jurassic (Tithonian) age, *Cypraea tithonica* and *C. gemmellaroi*, were first described from Sicily (Italy) by Di Stefano (1882) and later also reported from coeval strata on Capri (Italy) (Parona 1919); they represent the earliest cowries known to date. The present contribution revises the taxonomy and systematic placement of these early cypraeids, based on re-study of the type series of *Cypraea tithonica* Di Stefano, 1882.

Cowries are conspicuous in having a convolute shell, with the last whorl enclosing all previous whorls and form-

ing a narrowly elongate, slit-like aperture with anterior and posterior canals. Cypraeids can cover their entire shell with a fleshy mantle, which enables them to produce a spotlessly smooth, glossy outer shell surface. While most of the modern diversity of Cypraeidae is located in the tropical Indo-Pacific, the family as a whole has a pantropical distribution between 35° N and S (Riedel 2000; Passamonti 2015; Lorenz 2017, 2018).

Juveniles of the type genus of the family, *Cypraea*, are herbivorous grazers, and are carnivorous or omnivorous grazers as adults, feeding on sponges and other sessile invertebrates (Tay et al. 2023 and references therein). All species of which early ontogeny and protoconchs are recorded have planktotrophic larval development. They have relatively large larval shells, generally approximately 1 mm high, but some reaching up to 1.5 mm, with a reticulate ornament (Bandel et al. 1997; Riedel 2000; Tay et al. 2023) (Fig. 1).

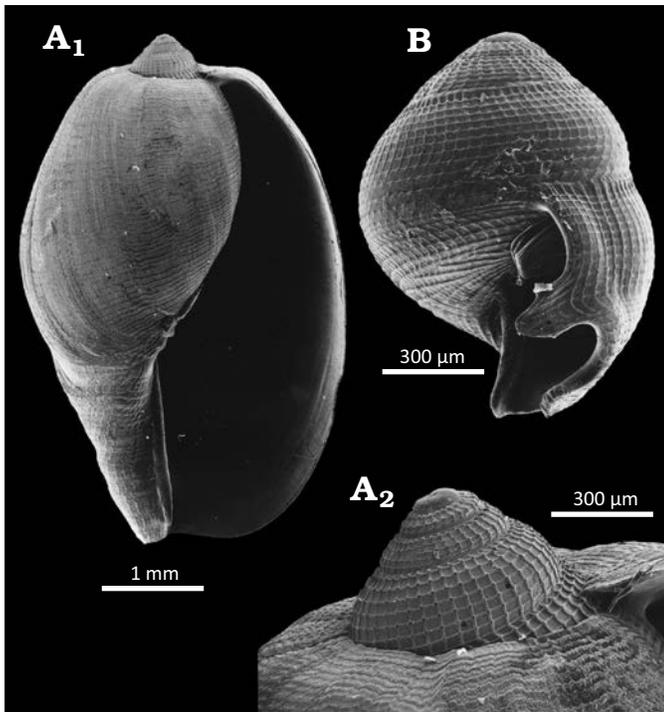


Fig. 1. Early ontogenetic shells of Cypraeidae (from seagrass meadow at Bira, Sulawesi, Indonesia), housed at SNSB-BSPG. **A.** Juvenile cypraeid with protoconch, SNSB-BSPG 2025 I 1. **A₁**, specimen with the last whorl, overgrowing all previous ones, not yet developed; the aperture, while already elongated, is not yet slit-like; **A₂**, lateral view of earliest whorl including larval shell with reticulate ornament. **B.** Isolated larval shell of a Recent cypraeid with sinusigera notches and cancellate ornament, SNSB-BSPG 2025 I 2. This larval shell of the planktotrophic type is typical of modern cypraeids, but is not visible in full-grown specimens, due to overgrowth by the last whorl and diagenetic alteration.

Cypraeidae have a taenioglossate radula and were placed in the traditional Mesogastropoda (e.g., Wenz 1938–1944). They are now assigned to the “higher” Caenogastropoda within Latrogastropoda (e.g., Bouchet et al. 2017; Ponder et al. 2020; Li et al. 2024), which are characterized by an inhalant flow, commonly associated with the development of an anterior siphonal canal. While family-level phylogeny and systematics of the Cypraeidae within Gastropoda is relatively well resolved and stable (Meyer 2003, 2004), subdivision at the genus level is still under debate. So far, cypraeid genus-level systematics is largely based on shell morphology, which is rather conservative in this family, and modern anatomical and molecular studies are lacking (e.g., Passamonti 2015). More than 150 genus-level names have been proposed for extant and fossil Cypraeidae, and approximately 80 of these are currently considered valid (Schilder and Schilder 1971; Riedel 2000; MolluscaBase 2025).

The aim of this study is to revise the available cypraeid materials from the Upper Jurassic of Italy and attempt to relate them to other caenogastropods which have narrowly elongated siphonate apertures.

Institutional abbreviations.—MGUP, Museo Geologico G.G. Gemmellaro, Università di Palermo, Sicily, Italy;

MSTC, Museo di Paleontologia, Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Catania, Sicily, Italy; SNSB-BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in Zoobank: urn:lsid:zoobank.org:pub:3FC4C848-4D6B-4554-AB84-1EB2125A6D01.

Historical background

As highlighted above, the earliest Cypraeidae have been described from the uppermost Jurassic of Sicily (Di Stefano 1882; Tracey et al. 1993; Groves and Landau 2021; Capasso 2024). However, the type material of *Cypraea tithonica* Di Stefano, 1882, and *Cypraea gemmellaroii* Di Stefano, 1882, has never been restudied, and Zamberlan and Checchi (2014) and Capasso (2024) considered these specimens as lost. Thus, it came as a surprise that during a visit to the Museo di Geologia G.G. Gemmellaro in Palermo, two of the authors (AN and SS) re-discovered the type series of *Cypraea tithonica*, which forms the base for the present contribution. The original material of *Cypraea gemmellaroii* was not found.

Besides their type locality, Termini Imerese near Palermo, both species were reported to occur in Tithonian strata on the island of Capri south of Naples, Italy by Parona (1919); as far as we are aware, his specimens were never illustrated. However, Zamberlan and Checchi (2014) figured a specimen from the Tithonian of Capri, which is part of the Viglino Collection (MSTC no. 186vi0950) curated at the Museo di Paleontologia, Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Catania, and was assigned to *Cypraea gemmellaroii*; they further stated that the same collection also contained specimens of *Cypraea tithonica* (MSTC no. 186vi0949). Recently, Capasso (2024) figured both specimens from Capri.

Cypraea tithonica was assigned to *Cyproglobina* De Gregorio, 1880, by Schilder (1927), a genus now placed in the Ovulidae (Fehse 2013). Later, Schilder and Schilder (1971) transferred the species to *Palaeocypraea* Schilder, 1928, where it was retained by Groves (1990, 1992, 1994), Tracey et al. (1993) and most recently Capasso (2024). Based on re-study of the type material of *C. tithonica*, this assignment is erroneous, as will be outlined below.

The second, larger species introduced by Di Stefano (1882), *Cypraea gemmellaroii*, was assigned by Schilder (1927) to his new subgenus *Bernaya* (*Protocypraea*), but later transferred to *Bernaya* Jousseaume, 1884 sensu stricto (Schilder and Schilder 1971). Again, Groves (1990, 1992, 1994), Zamberlan and Checchi (2014) and Capasso (2024) retained this combination. This assignment is equally untenable, and *Cypraea gemmellaroii* is congeneric with *Cypraea tithonica*.

Material and methods

The material studied herein is housed at the Museo Geologico G.G. Gemmellaro in Palermo, Sicily, Italy. Only the type series of *Cypraea tithonica* Di Stefano, 1882, consisting of seven syntypes, which are archived under accession numbers MGUP-20-368a–g, was found during a visit in March 2017. The type series of *Cypraea gemmellaro* Di Stefano, 1882, could not be traced.

The specimens come from an isolated limestone outcrop on the castle mountain of Termini Imerese (Palermo region, Sicily; coordinates: 37.9886, 13.6979, WGS1984). The castle mountain succession is part of a series of originally African structural domains (Sicilian-Maghrebide units; Fig. 2) that were obducted onto the European part of Sicily during Neogene times (Catalano et al. 2010, 2011). The strata that yielded the cypraeids are assigned to the informal *Ellipsactinia* breccias member of the Crisanti Formation (Catalano et al. 2010; Basilone 2018), which comprises thick-bedded limestone breccias and conglomerates. The components of these rocks are characterised by shallow-water carbonate platform facies containing abundant corals and molluscs; the latter were monographed by Gemmellaro (1869a–d, 1871a–d, 1875) and Gemmellaro and Di Blasi (1874). The rocks are classically attributed to the Tithonian, but may partly be Berriasian (earliest Cretaceous) in age, based on calpionellid biostratigraphy (Catalano et al. 2010; Basilone 2018).

All seven specimens were coated with ammonium chloride, and photographs from those views deemed taxonomically informative were taken. The higher classification of the Gastropoda is adopted from Bouchet et al. (2017), Ponder et al. (2020) and MolluscaBase (2025). The descriptive terminology follows Groves and Squires (2023).

In 2024, SB and AK analysed the type material of the colombellid *Zittelia cipraeiformis* Gemmellaro, 1869d from the Gemmellaro collection stored at the same museum,

which comprises nine syntypes (SB and AK unpublished data). All of them are stored under the inventory number MGUP-20-361.

The Recent specimens depicted in Fig. 1 are stored at the Bayerische Staassammlung für Paläontologie, München (SNSB-BSPG).

Systematic palaeontology

Class Gastropoda Cuvier, 1795

Infraclass Caenogastropoda Cox, 1960

Cohort Sorbeoconcha Ponder & Lindberg, 1997

Megaorder Hypsogastropoda Ponder & Lindberg, 1997

Superorder Latrogastropoda Riedel, 2000

Order Cypraeida Rafinesque, 1815

Superfamily Cypraeoidea Rafinesque, 1815

Family Cypraeidae Rafinesque, 1815

Genus *Coffeacypraea* Nützel & Schneider nov.

Zoobank LSID: urn:lsid:zoobank.org:act:C0956AF7-1075-4294-8F6F-14EC45D48245.

Type species: *Cypraea tithonica* Di Stefano, 1882, by original designation herein.

Species included: *Coffeacypraea tithonica* (Di Stefano, 1882) and *Coffeacypraea gemmellaro* (Di Stefano, 1882).

Etymology: A combination of the Latin genus names *Coffea*, which includes the coffee plant, and *Cypraea*, which is the type genus of the Cypraeidae, referring to the rather simple shell shape of the new genus, which resembles an oversized coffee bean.

Diagnosis.—Relatively small (up to 25 mm long), smooth-shelled Cypraeidae; short-ovate to almost circular in outline in dorsal view; basal side of shell widely flattened; dorsal side more or less evenly arched and inflated. Aperture slit-like, narrow, in almost central position, straight, with-

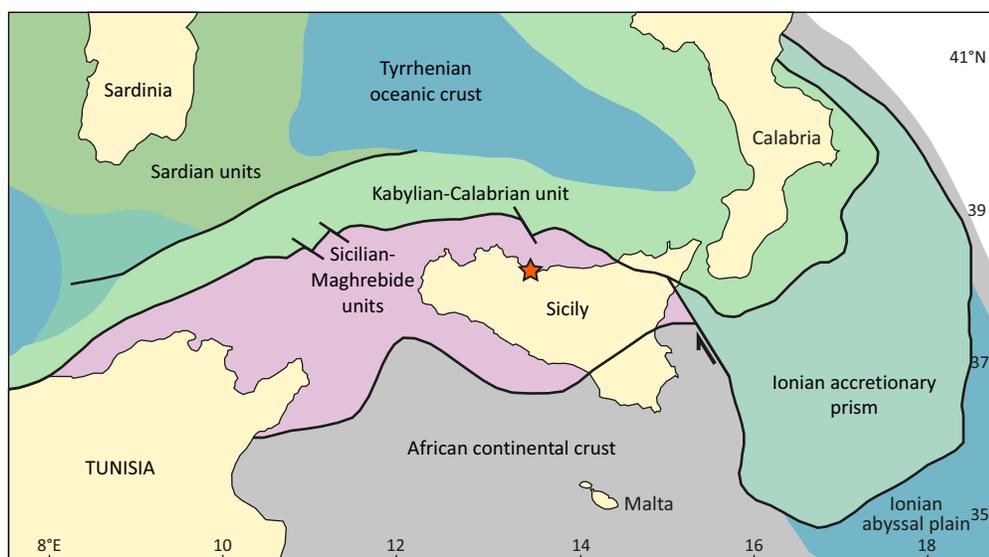


Fig. 2. Overview of structural domains in the central Mediterranean (modified from Catalano et al. 2010). The location of Termini Imerese is indicated by a red star.

out widened anterior and posterior notches; columellar and labral denticles evenly sized and spaced (barely visible due to limited preservation). Anterior (siphonal) and posterior canals indistinct or very short.

Stratigraphic and geographic range.—Tithonian, Upper Jurassic of Italy and potentially Czechia.

Coffeacypraea tithonica (Di Stefano, 1882)

Figs. 3A–D, 4A–G, 5.

1882 *Cypraea tithonica*, Di Stef.; Di Stefano 1882: 76, pl. 4: 4, 5.

?1911 *Cypraea tithonica* di Stef.; Blaschke 1911: 162.

?1919 *Cypr. tithonica* Di Stef.; Parona 1919: 475.

1927 [*Cyproglobina*] *tithonica* di Stef.; Schilder 1927: 71.

1971 *Palaeocypraea (Palaeocypraea) tithonica*; Schilder and Schilder 1971: 24.

1990 *Palaeocypraea (P.) tithonica* (Stefano, 1882); Groves 1990: 273.

1992 *Palaeocypraea (Palaeocypraea) tithonica* (Stefano, 1882); Groves 1990: 101.

1993 *Palaeocypraea tithonica*; Tracey et al. 1993: 148.

1994 *Palaeocypraea (Palaeocypraea) tithonica* (Steffano 1882) [sic!]; Groves 1994: 26, figs. 5, 6 [reproduced from Di Stefano 1882].

2014 *Bernaya gemmellaroi* (Di Stefano, 1882); Zamberlan and Checchi 2014: 21, fig. 8 [not fig. 7].

2021 *Palaeocypraea tithonica* (Stefano, 1882); Groves and Landau 2021: 8.

2024 *Palaeocypraea tithonica* (Di Stefano, 1882); Capasso 2024: 165, figs. 1, 2.

2024 *Bernaya gemmellaroi* (Di Stefano, 1882); Capasso 2024: 166, fig. 4 [not fig. 3].

Emended diagnosis.—Small (up to 13 mm long), smooth-shelled Cypraeidae; short-ovate to almost circular in outline in dorsal view; basal side of shell widely flattened; dorsal side more or less evenly arched and inflated. Aperture slit-like, in almost central position, straight, without widened an-

terior and posterior notches; columellar and labral denticles evenly sized and spaced (barely visible due to limited preservation). Anterior (siphonal) and posterior canals very short.

Material.—Seven syntypes, curated under catalogue numbers MGUP-20-368a–g; relatively well preserved shells. The specimen in Fig. 4D (Di Stefano 1882: pl. 4: 4a, b; MGUP-20-368a) is designated as the lectotype herein, while the remaining six specimens become paralectotypes (MGUP-20-368b–g). All specimens come from the castle mountain of Termini Imerese, Palermo Region, Sicily; *Ellipsactinia* breccias member, Crisanti Formation, Tithonian, Upper Jurassic. Two additional specimens not examined by the authors come from Tithonian strata on the island of Capri (MSTC no. 186vi0949 and MSTC no. 186vi0950); see Zamberlan and Checchi (2014) and Capasso (2024).

Description.—Shell up to 13 mm long, 12.5 mm wide and 8 mm high; convolute, cypraeid in shape, with last whorl overgrowing all previous whorls; very short ovate to almost circular in outline in dorsal view; moderately and evenly inflated in lateral view, with basal (apertural) side flattened. Outer shell surface smooth. Aperture narrow, slit-like, in almost central position, straight, without widened anterior and posterior notches. Columellar and labral sides of aperture with numerous teeth, in most specimens barely visible due to limited preservation.

Remarks.—The studied specimens of *Coffeacypraea tithonica* generally are similar to modern cypraeids with regard to shell morphology, but differ sufficiently from younger taxa to be placed in their own genus. The specimens illustrated in Fig. 4A and B show that the last whorl overgrows the low-spired previous whorls and produces the typical cypraeid convolute shape. However, as noted by Capasso (2024), the

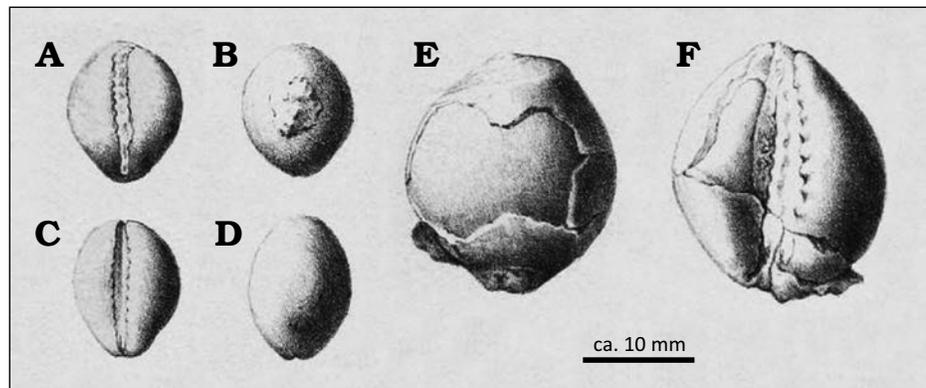
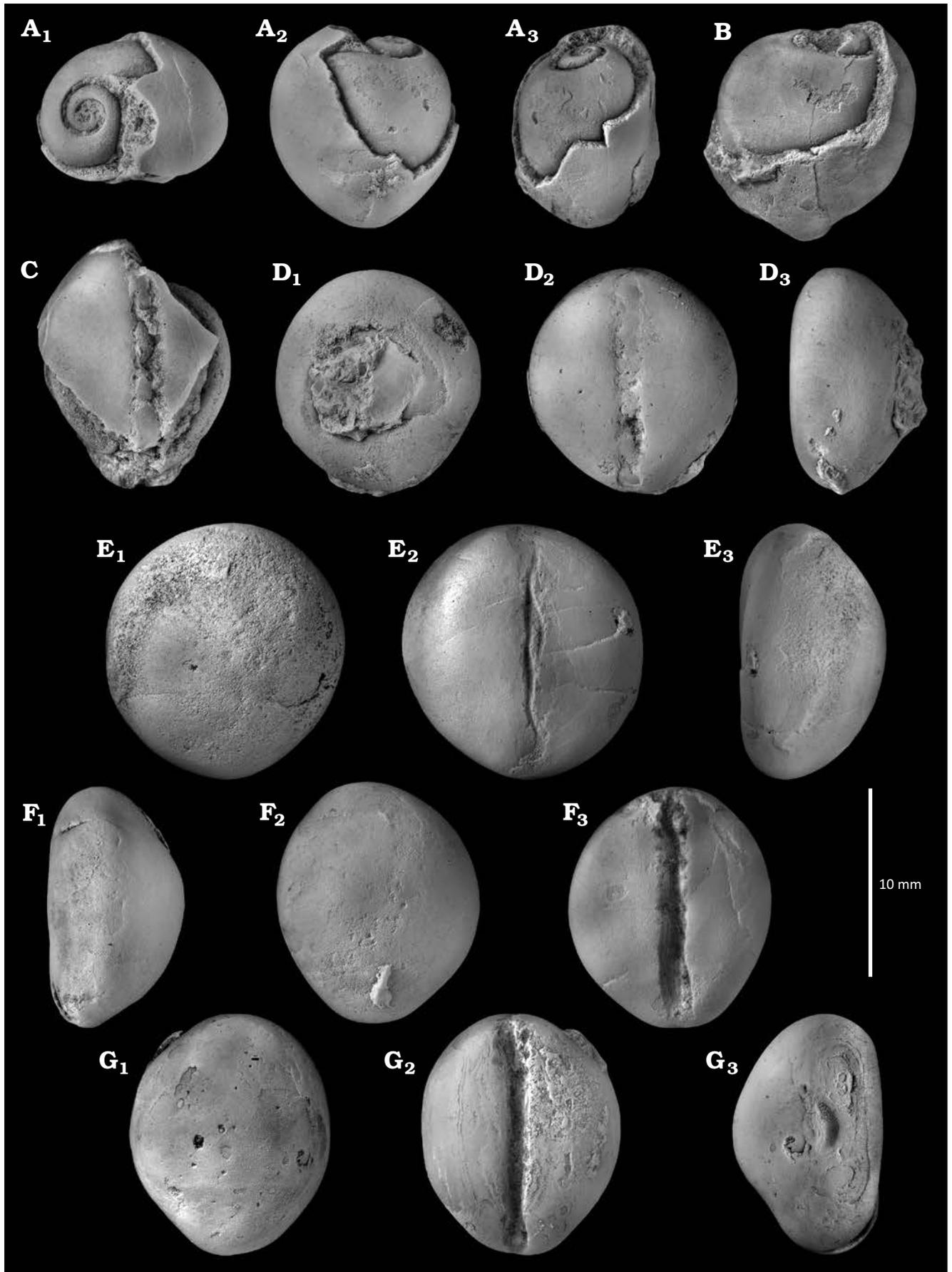


Fig. 3. Reproduction of Di Stefano's (1882) drawings of "*Cypraea tithonica* Di Stefano, 1882" (A–D) and *Cypraea gemmellaroi* Di Stefano, 1882 (E, F), illustrating the significant difference in size. A, C, F, apertural view; B, D, E, dorsal view. An approximate scale bar is added.

Fig. 4. Cypraeid gastropod *Coffeacypraea tithonica* (Di Stefano, 1882) from the Tithonian, Upper Jurassic, of the castle mountain of Termini Imerese, Sicily, Italy. Type series of *Cypraea tithonica* Di Stefano, 1882: lectotype (D), paralectotypes (A–C, E–G). A, B. Specimens with broken last whorl, exposing the earlier whorls. A. MGUP-20-368b, in apical (posterior) (A₁), dorsal (abapertural) (A₂), and lateral (A₃) views. B. MGUP-20-368c, in dorsal view. C. MGUP-20-368d, fragmentary specimen showing part of the aperture with some of the denticles visible, in apertural view. D. MGUP-20-368a, specimen with denticulate aperture, in dorsal (abapertural) (D₁), apertural (D₂), and lateral (D₃) views. E. MGUP-20-368e, largest and roundest specimen of the type series with poorly preserved aperture, in dorsal (abapertural) (E₁), apertural (E₂), and lateral (E₃) views. F. MGUP-20-368f, faintly asymmetric specimen, in lateral (F₁), dorsal (abapertural) (F₂), and apertural (F₃) views. G. MGUP-20-368g, slightly irregularly shaped specimen with a faint dent on the dorsal side, seen best in G₃, in dorsal (abapertural) (G₁), apertural (G₂), and lateral (G₃) views.



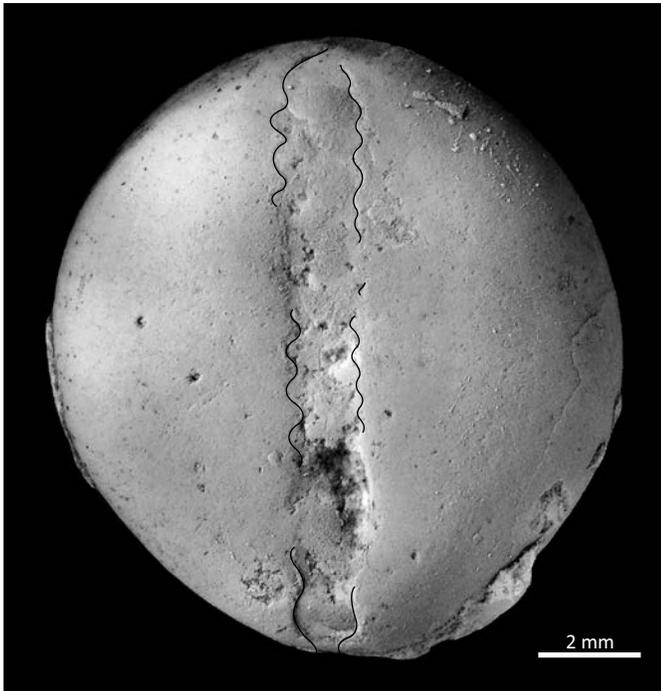


Fig. 5. Cypraeid gastropod *Coffeacypraea tithonica* (Di Stefano, 1882) from the Tithonian, Upper Jurassic of the castle mountain of Termini Imerese, Sicily, Italy. The designated lectotype of *Cypraea tithonica*, with apertural denticles traced as far as visible; MGUP-20-368a.

shells are much shorter and more circular than in any other genera, with length/width ratios of 1.04 to 1.18 for *C. tithonica* and approximately 1.12 to 1.15 for *C. gemmellaroi* (measured from Fig. 3E, F). *Coffeacypraea* Nützel & Schneider gen. nov. also differs from the other genera of the Cypraeidae by having a straight, rather narrow aperture in central position, which lacks the widened anterior and posterior notches seen in their Cretaceous and younger descendants. Moreover, the anterior and posterior canals are barely developed. Although the preservation of the specimens is not ideal, this is not a result of erosion, but a genuine feature. By far most other Cypraeidae have more or less curved apertures, which are opisthocyrt inclined and the siphonal (anterior) and posterior canals are usually much more pronounced.

Two specimens from the island of Capri, figured by Zamberlan and Checchi (2014) and Capasso (2024) under the names *Bernaya gemmellaroi* (Di Stefano, 1882) and *Palaeocypraea tithonica* (Di Stefano, 1882), fall into the size range and morphological variability of the type series of *C. tithonica*. MSTC no. 186vi0950 is slightly tapered posteriorly and has a shallow dent in its anterior part. However, similar features occur in the paralectotypes (Fig. 4B, C, G₃) and should be attributed to intraspecific variability.

Whether the single specimen from the Tithonian–Berrasian of Štramberk (Czech Republic) reported by Blaschke (1911) should be assigned to *Coffeacypraea tithonica* is unconfirmed. The specimen was not illustrated and could not be traced among Blaschke's (1911) material, which only comprises the figured specimens (personal communication Thomas Nichterl, January 2025).

In his first major revision of the Cypraeoidea, Schilder (1927) assigned *Cypraea tithonica*, the type species of *Coffeacypraea* Nützel & Schneider gen. nov., to *Cyproglobina* De Gregorio, 1880, a genus that is based on an Eocene type species from southeastern France and is presently placed in the family Ovulidae (see Fehse 2013 for subsequent type designation and taxonomy). Subsequently, *Cypraea tithonica* was assigned to the genus *Palaeocypraea* Schilder, 1928, by several authors (see synonymy above), which is based on a type species from the Danian (Paleogene) of Denmark, *Cypraeacites spiratus* Schlotheim, 1820. While comparable in size, *Palaeocypraea spirata* is significantly more elongated and has a distinctly curved aperture in a less central position. It also differs by having widened posterior and anterior canals. Owing to the curvature of the aperture, the apertural denticles vary in strength and inclination in *Palaeocypraea*, while they are apparently equal in size and orientation in *Coffeacypraea* Nützel & Schneider gen. nov. *Coffeacypraea tithonica* was not originally included when Schilder (1928) introduced *Palaeocypraea*, but was later transferred to that genus (Schilder and Schilder 1971).

Stratigraphic and geographic range.—Tithonian, Upper Jurassic of Italy and potentially Czechia.

Coffeacypraea gemmellaroi (Di Stefano, 1882)

Fig. 3E, F.

- 1882 *Cypraea Gemmellaroi*, Di-Stef.; Di Stefano 1882: 75, pl. 4: 3.
 ?1919 *Cypraea Gemmellaroi* Di Stef.; Parona 1919: 475.
 1927 [*Bernaya (Protocypraea)*] *gemmellaroi* di Stef.; Schilder 1927: 88.
 1928 [*Protocypraea*] *gemmellaroi* di Stef.; Schilder 1928: 23.
 1971 [*Bernaya (Bernaya)*] *gemmellaroi* Stefano 1882; Schilder and Schilder 1971: 27.
 1990 *Bernaya (B.) gemmellaroi* (Stefano, 1882); Groves 1990: 273.
 1993 *Bernaya gemmellaroi* Stefano, 1882; Tracey et al. 1993: 148.
 1994 *Bernaya (Protocypraea) gemmellaroi* (Steffano 1882) [sic!]; Groves 1994: 26, figs. 3, 4 [reproduced from Di Stefano 1882].
 non 2014 *Bernaya gemmellaroi* (Di Stefano, 1882); Zamberlan and Checchi 2014: 21, fig. 8.
 2021 *Palaeocypraea gemmellaroi* (Stefano, 1882); Groves and Landau 2021: 8.
 non 2024 *Bernaya gemmellaroi* (Di Stefano, 1882); Capasso 2024: 166, fig. 4.

Emended diagnosis.—Relatively small (approximately 25 mm long), smooth-shelled Cypraeidae; rounded short-ovate in outline in dorsal view, with slightly tapering anterior and posterior portions; basal side of shell widely flattened, slightly subsiding towards the apertural slit; dorsal side evenly arched and inflated. Aperture slit-like, in almost central position, straight, seemingly slightly widened in central part, without widened anterior and posterior notches; apertural denticles seen on columellar lip only, presumably due to limited preservation, evenly sized and spaced. Anterior (siphonal) and posterior canals very short.

Material.—The type material of *Cypraea gemmellaroi* was not found during our visit to Palermo in 2017. From

Di Stefano's (1882) description, it is unclear whether there were more specimens than the figured one. However, the expression "height of the figured specimen" may be read as a hint that there were several syntypes. The type material comes from the castle mountain of Termini Imerese, Palermo Region, Sicily, Italy; *Ellipsactinia* breccias member, Crisanti Formation, Tithonian, Upper Jurassic.

Description.—Shell up to 25 mm long; convolute, cypraeid in shape, with last whorl overgrowing all previous whorls; rounded short-ovate in outline in dorsal view; anterior and posterior ends slightly tapering, the posterior one more so than the anterior one (note that the posterior end is facing upward in Fig. 3E, F). Shell considerably and evenly inflated in lateral view, with basal (apertural) side widely flattened, probably slightly subsiding towards the apertural slit. Outer shell surface smooth. Aperture relatively narrow, slit-like, in almost central position, slightly widened (?) in central part, straight without widened anterior and posterior notches. Apertural denticles evenly sized and spaced, clearly visible on columellar lip only, presumably due to limited preservation. Anterior (siphonal) and posterior canals very short; posterior canal more clearly marked than siphonal canal.

Remarks.—*Cypraea gemmellaroi* is also included in *Coffeacypraea* Nützel & Schneider gen. nov., which has a more bulbous shell than *Coffeacypraea tithonica* and is also significantly larger, almost twice the size. According to the original illustration by Di Stefano (1882), its slit-like aperture is also straight; the anterior and posterior canals are more distinct than in *Coffeacypraea tithonica* but still not very pronounced. In modern cypraeids, shell size is highly variable, and in some species, the largest individuals are three times the size of the smallest ones (e.g., Poppe and Goto 1991). This means that *Coffeacypraea tithonica* and *C. gemmellaroi* may represent a single species, based on their sizes alone. However, in view of the slight differences noted above, while relying only on Di Stefano's (1882) figures and description, both species are considered valid.

As mentioned above, *Coffeacypraea gemmellaroi* was assigned to *Bernaya* (*Protocypraea*) Schilder, 1927, with the original description of the subgenus (Schilder 1927; type species: *Cypraea orbignyana* Vredenburg, 1920; Upper Cretaceous, southern India); Groves (1994) reverted to this assignment without discussion, but subsequently transferred the species to *Bernaya* Jousseau, 1884 sensu stricto (Schilder and Schilder 1971), which is based on a type species from the Eocene of France, *Cypraea media* Deshayes, 1835. Species of *Bernaya* differ from *Coffeacypraea gemmellaroi* by having a curved aperture that is widened posteriorly, while that of *C. gemmellaroi* is straight and lacks a widened posterior part. Moreover, species of the genus *Bernaya* are broadly pyriform in dorso-ventral view. In contrast, *Coffeacypraea gemmellaroi* is rounded short-ovate in outline. Besides the morphological differences, Eocene species of *Bernaya* are also significantly larger than these

of *Coffeacypraea* Nützel & Schneider gen. nov., ranging between 37 and 62 mm in length (e.g., Pacaud 2018).

Stratigraphic and geographic range.—Tithonian, Upper Jurassic of Italy.

Discussion

Evolutionary relationships.—The new genus *Coffeacypraea* Nützel & Schneider in the Cypraeidae and the genera *Zittelia* and *Colombellina* in the Colombellinidae, all from the Upper Jurassic of southern and central Europe, are among the oldest caenogastropods that share an elongated, slit-like aperture, although some Paleozoic subulitoids also have narrow apertures. Furthermore, elongated apertures occur in several Triassic, Jurassic, and younger heterobranchs (e.g., Gründel and Nützel 2013; Hausmann and Nützel 2015). This feature has been interpreted as a convergent anti-predatory adaptation, which evolved repeatedly in the course of the Mesozoic Marine Revolution (Vermeij 1977, 1987).

With the exception of certain bellerophonitoids, which are, however, isostrophically coiled, convolute gastropod shells (last whorl covering all previous ones) are unknown from the Paleozoic and the Triassic. Convolute shells with elongate aperture are also known from the Late Jurassic onward in Heterobranchia (genus *Volvocylindrites* Cossmann, 1895, see Gründel and Nützel 2013). So far known, *Coffeacypraea* Nützel & Schneider gen. nov. represents the earliest record of this type of convolute shell in Caenogastropoda and clearly is the earliest member of the Cypraeidae and the Cypraeoidea, as was assumed previously.

The relationship between the Jurassic colombellinid *Zittelia* and the Recent *Cypraea* was initially discussed by Sayn (1932), and later, Colombellinidae were considered the stem group of Cypraeoidea by Taylor and Morris (1988). This hypothesis, however, has never been critically assessed and Gemmellar's (1869d) type material had not been revised since the original description. Moreover, the characteristics of *Zittelia* and *Colombellina* have not been clearly demarcated. As a result, species have commonly been misplaced in either of these genera and taxa with entirely different characteristics were included in the family Colombellinidae (SB and AK unpublished data).

Colombellina is similar to *Zittelia* both with regard to its aperture morphology and its coarse nodular ornamentation (Fig. 6A, B). However, in *Colombellina*, the outer and inner lips are rather narrow, and the majority of the spire is not covered by them, whereas in *Zittelia* the lips are expanded over the spire and cover more than half of it (Fig. 6B₂). This indicates that the mantle of *Zittelia* could envelop a significant portion of the shell. The spire, therefore, is not visible on the ventral side of the shell, as it is covered by the expansion of the lips.

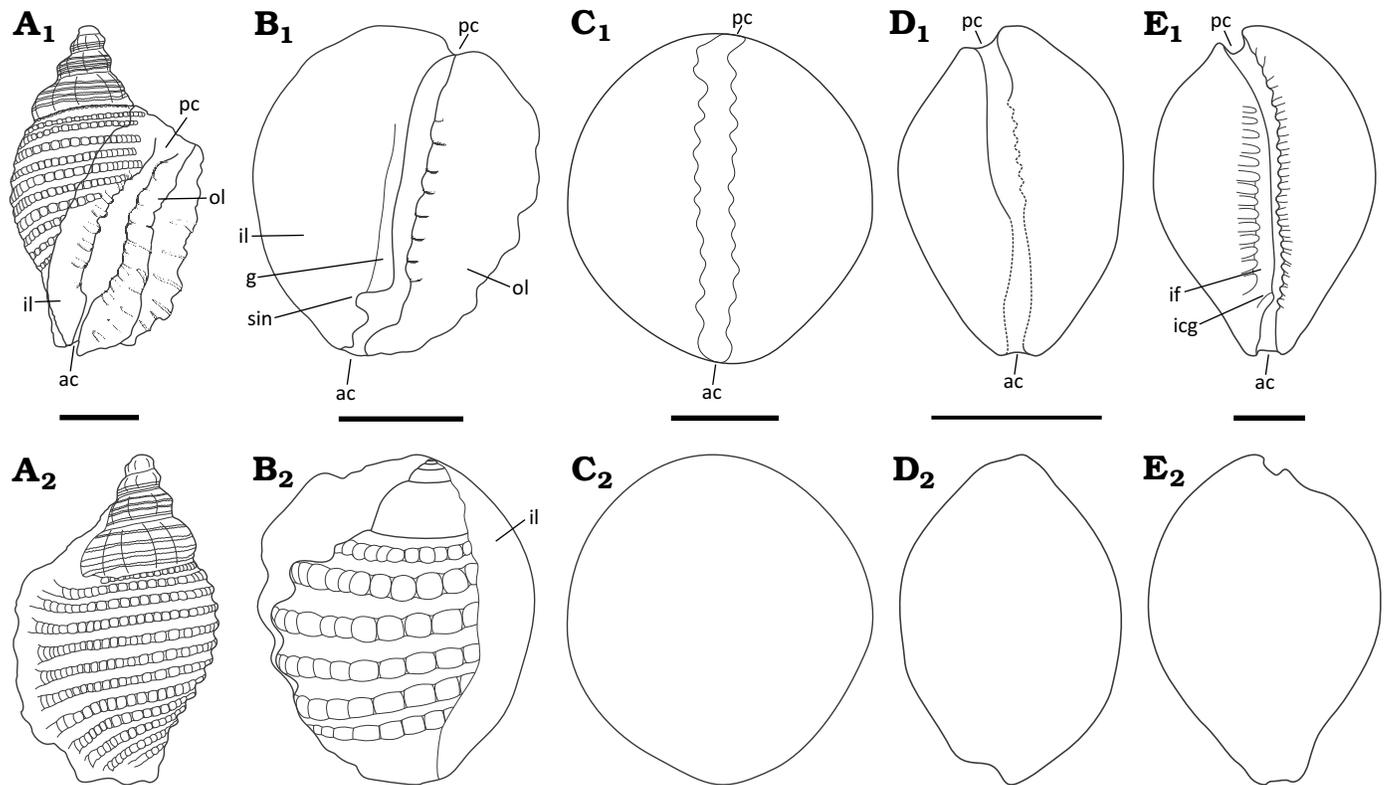


Fig. 6. Comparison between colombellinids and cypraeids showing the morphological gradient from *Colombellina* through *Zittelia* and *Coffeacypraea* to *Cypraeorbis* (modern Cypraeidae). **A.** *Colombellina corallina* (Quenstedt, 1852), Tithonian, Upper Jurassic of Štramberk, Czechia. Redrawn from unpublished specimens GP101101 and GP101102 in the collection of the Department of Geological Engineering, VSB – Technical University of Ostrava, Czechia. **B.** *Zittelia cipraeaeformis* Gemmellaro, 1869, Tithonian, Upper Jurassic of Carini near Palermo, Sicily, Italy. Redrawn from the type material, MGUP-20-361A. **C.** *Coffeacypraea tithonica* (Di Stefano, 1882), Tithonian, Upper Jurassic of the castle mountain of Termini Imerese near Palermo, Sicily, Italy. Redrawn from the type material, MGUP-20-368A (Fig. 5). **D.** *Cypraea antiqua* Sayn, 1932, Barremian, Lower Cretaceous of Barcelonne, Drôme, France. Redrawn from Sayn (1932: pl. 3: 1, 1a, b, c). **E.** *Cypraeorbis ventripotens* (Cossmann, 1903), Moodys Branch Formation, Upper Eocene of Town Creek, Jackson, Mississippi, USA. Redrawn from Darragh (2011: fig. 3A, B). In apertural (A_1 – E_1) and lateral (A_2 – E_2) views. Scale bars 5 mm. Abbreviations: ac, anterior canal; g, groove; icg, infracolumellar groove; if, incipient flange; il, inner lip; ol, outer lip; pc, posterior canal; sin, sinuosity.

According to Gemmellaro (1869d), one of the diagnostic characteristics of *Zittelia*, which distinguishes it from *Colombellina*, is its very narrow and slightly curved aperture, terminating both anteriorly and posteriorly in a notch or canal (Fig. 6B₁). The similarity of *Zittelia* and *Cypraea* was highlighted by Gemmellaro (1869d) through the naming of one of the new species, *Zittelia cypraeaeformis*, which was subsequently designated as the type species of *Zittelia* by Cossmann (1904). Other Jurassic species of *Zittelia*, i.e., those described by Zittel (1873) and Brösamlen (1909) are still awaiting revision. In Cretaceous Cypraeidae, the notches seen in *Zittelia* have not been mentioned nor depicted (Sayn 1932; Roman and Mazeran 1920; Groves 1990, 2004; Groves et al. 2011). In the Eocene cypraeid *Cypraeorbis*, Darragh (2011: fig. 1) noted a similar structure, termed infracolumellar groove, located at the anterior end of the aperture (Fig. 6E₁), which might be a homologous to the anterior sinuosity.

In the Late Jurassic forms of *Colombellina*, *Zittelia*, and *Coffeacypraea* Nützel & Schneider gen. nov., the position of the posterior canal is on the right (labral) side of the shell axis (Fig. 6A, B, C, Table 1). In Early Cretaceous cypraeids, the posterior canal has already shifted to the left (Fig.

6D), where it also occurs in Recent representatives of the Cypraeidae. It might be, therefore, hypothesized that a gradual shift of the posterior canal from the right side of the shell axis to its left side occurred between the Tithonian (Late Jurassic) and Barremian (Early Cretaceous).

Furthermore, the infracolumellar groove at the anterior end of the aperture observed in some Cenozoic and Recent Cypraeidae may have evolved from the sinuosity or notches in *Zittelia* and may thus represent a derived trait. However, this characteristic does not consistently appear within all cypraeids. Nevertheless, its repetitive occurrence, along with the strongly expanded lips in *Zittelia*, may be considered as a strong support of the relationship between these genera. Their co-occurrence in the uppermost Jurassic of Sicily, Italy, and potentially also Czechia, may indicate that the Late Jurassic reefs and associated lagoons of the Tethys were a centre of diversification of the Colombellinidae. In the same environments, decapod crustaceans underwent a remarkable diversification during Late Jurassic times (e.g., Klompmaker et al. 2013) and, as potential predators of the gastropods, may have indirectly contributed to the evolution of convolute shells with restricted apertures.

Table 1. Comparison of morphological characteristics of some species of Colombellinidae and Cypraeidae.

Species	<i>Colombellina corallina</i>	<i>Zittelia cipraeaeformis</i>	<i>Coffeacypraea tithonica</i>	<i>Cypraea antiqua</i>	<i>Cypraeorbis ventripotens</i>
Age	Tithonian	Tithonian	Tithonian	Barremian	Eocene
Aperture	expanded in the central part and prosocyrt oblique	narrow and prosocyrt oblique	narrow and straight	narrow and opisthocyrt oblique	narrow and opisthocyrt oblique
Anterior canal (ac)	short	absent, only notch present	absent, notch also absent	weakly developed notch	prominent notch
Groove (g)	absent	present	absent	?	absent
Infracolumellar groove (icg)	absent	absent	absent	?	present
Incipient flange (if)	absent	absent	absent	?	present
Inner lip	present only on the last whorl, usually denticulated	covers more than half of the spire	covers the entire spire, denticulated	covers the entire spire	covers the entire spire, denticulated
Outer lip	narrow and separated from inner lip, usually denticulated	wide but separated from inner lip, denticulated	merged with inner lip, denticulated	merged with inner lip, denticulated	merged with inner lip, denticulated
Position of the posterior canal relative to the shell axis	right	right	right	left	left
Angle between shell axis and posterior canal	30°	20°	7°	10°	25°
Sinuosity	absent	present	?	?	absent

The origination of Cypraeidae with the new genus *Coffeacypraea* Nützel & Schneider and the diversification of Colombellinidae in the Middle to Late Jurassic contributed considerably to the Mesozoic–Cenozoic caenogastropod radiation. Both taxa represent “higher” caenogastropods (Neomesogastropoda sensu Bandel 1991 and Latrogastropoda sensu Riedel 2000). At approximately the same time, the family Purpurinidae likely gave rise to Neogastropoda (Bakayeva et al. 2024). Therefore, the Middle to Late Jurassic was a pivotal time for the evolution of Caenogastropoda, one of the most diverse animal clades.

Conclusions

Based on the restudy of the type material of *Cypraea tithonica* from the Tithonian of Sicily, this species is placed in the new genus *Coffeacypraea* Nützel & Schneider gen. nov. *Coffeacypraea tithonica* and *Coffeacypraea gemmellaroi* from the same formation represent the earliest undoubted members of Cypraeoidea. As was previously suggested, cypraeoids are closely related (possibly sister-group) to coeval Colombellinidae which also have narrow, elongate apertures but are not convolute. The origination of Cypraeidae and the diversification of Colombellinidae in the Middle to Late Jurassic contributed considerably to the Mesozoic–Cenozoic caenogastropod radiation.

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