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Article

The Origin of the Mangrove and Saltmarsh Snail *Ellobium* (Eupulmonata, Ellobiidae) [†]

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Abstract: The pulmonate gastropod genus *Ellobium* has its greatest diversity in the modern Indo-West Pacific Region (IWP). Its origin, however, is traced to the Early Oligocene of the Northeastern Atlantic and the Western Tethys Region. Two *Ellobium* species are documented from the Rupelian of France and Italy and a new species is recorded from the Chattian of Hungary: *Ellobium kervaensis* nov. sp. The first records in the IWP are known from the Early Miocene, suggesting an eastward range expansion of the genus around the Oligocene/Miocene boundary, when *Ellobium* became extinct in the European seas. Extant *Ellobium* species are bound to habitats above the high tide line in salt marshes and mangroves. Comparable environmental requirements are expected for the fossil congeners. *Ellobium* may derive from Eocene ancestors, such as the Bartonian *Eoellobium heberti* from the Northeastern Atlantic. *Eoellobium* is introduced in this paper as a new genus.

Keywords: Ellobiidae; Western Tethys; Paratethys Sea; Oligocene; mangrove; salt marsh



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1. Introduction

Ellobium is an air-breathing, amphibious pulmonate gastropod of the tropics [1,2]. These animals are detritivorous, feeding on mangrove litter [3]. Several species of the genus are critically endangered due to anthropogenic habitat degradation [4,5]. Eleven extant species are currently listed by MolluscaBase eds. [6]. Eight of these species, including the type species *Ellobium aurismidae* (Linnaeus, 1758) [7] (Figure 1(A1–A3)) and species, such as *Ellobium aurisjudae* (Linnaeus, 1758) (Figure 1(B1–B3)), *Ellobium chinense* (L. Pfeiffer, 1855) [8] and *Ellobium scheepmakeri* (Petit de la Saussaye, 1850) [9], are confined to the IWP Region. *Ellobium gaziense* (Preston, 1913) [10] is found along East Africa, *E. stagnale* (d’Orbigny, 1835) [11] is restricted to the Eastern Pacific [11,12] and only *Ellobium dominicense* (Férussac, 1821) [13] is described from the Western Atlantic Caribbean Sea and the Gulf of Mexico [13–15]. No molecular data exist to confirm this disjunct distribution. Due to the glossy shell and thin outer lip seen in the Caribbean species, which differs from the typical *Ellobium* as understood herein, we would not be surprised if the Western Atlantic species were to belong to a distinct genus. Moreover, we have not found the fossil *Ellobium* species in the Caribbean during our own research (B.M.L.).

1.1. The Habitat of *Ellobium*

Ellison et al. [2] and Groh [16] discussed *Ellobium* as a mangrove-associated gastropod genus. Whilst a general affinity to the mangrove ecosystem can be stated for the genus, an

obligate relationship with mangrove trees is not obvious for most of the species. *Ellobium aurisjudae* is found in estuaries on saltmarshes above high tide, under logs, and within mangrove swamps [17]. It is also found on mangrove trunks [18] but not higher on mangrove trees [19]. Similarly, *E. aurismidae* dwells in salt marshes above the high tide line and may be associated with the *Nypa* trunks [17]. In the *Avicennia* mangroves of Sumatra, *E. aurismidae* and *E. aurisjudae* were found to be rare compared to typical mangrove-dwelling species, such as *Cerithidea cingulata* (Gmelin, 1791) [20] and *Nerita balteata* (Reeve, 1855) [21,22]. Setyadi et al. [23], found *Ellobium aurisjudae* to be among the most frequent gastropods in the *Rhizophora* and the *Bruguiera* mangroves of Papua, Indonesia. *Ellobium scheepmakeri* is found in the saltmarshes of estuaries between long grass and under logs above the high tide line and in the dry *Nypa* mangrove forests at salinities of 6–7 ppt [17,24]. Similarly, *E. tornatelliforme* (Petit de la Saussaye, 1843) [25] prefers the saltmarshes and occurs between the long grasses and among the rotting logs above the high tide line [17]. *Ellobium gangeticum* (Pfeiffer, 1855) was recorded from the salt marshes and the estuaries among the mangrove roots [26]. *Ellobium chinense* occurs between the stones in freshwater tidelands and on the halophytes such as *Zoysia* saltmarshes [27,28] and is also found on the trunks of the mangrove trees [29]. The Western Atlantic '*Ellobium*' *dominicense* also lives in embayments, mangrove creeks and estuaries at low salinities [30,31] but is mainly buried in the humic sediment and under rotting logs [14]. Thus, the lowest common denominator for the IWP-species of *Ellobium* in terms of habitat, is an occurrence in the saltmarshes above the high tide line in close vicinity of the mangroves. We propose comparable habitat requirements for the fossil species. This is also supported by the co-occurrence of *Nerita* and Potamididae at the type locality of *Ellobium kerwaense* (author's data, NHMW collection).

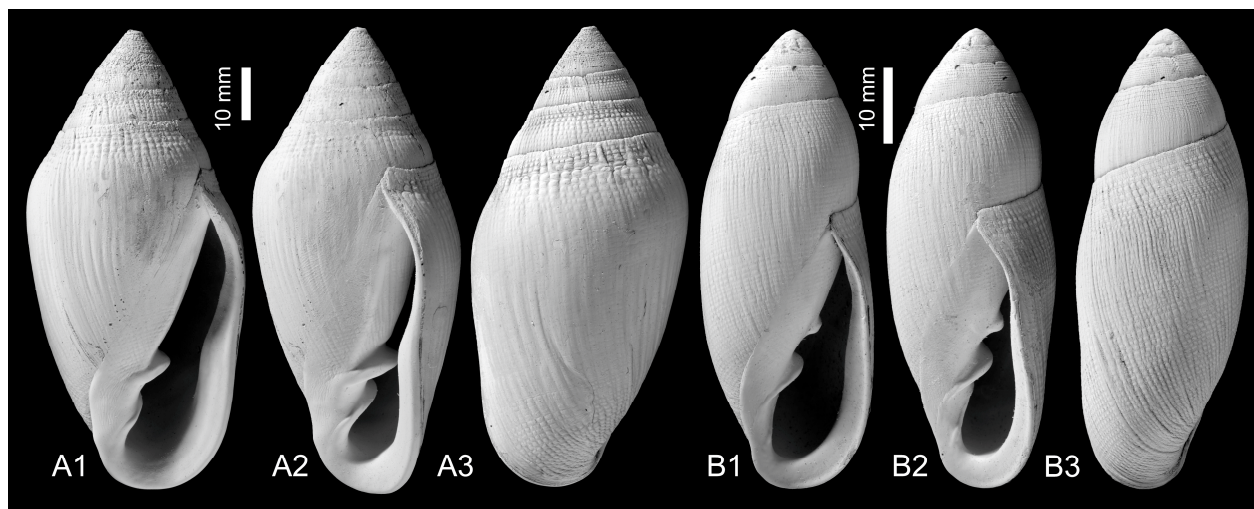


Figure 1. Recent *Ellobium* species: (A1–A3) *Ellobium aurismidae* NHMW-MO-83901/G/19, Moluccas; (A1) apertural view, (A2) oblique apertural view, (A3) dorsal view; (B1–B3) *Ellobium aurisjudae* NHMW-MO-75000/E/9194, New Guinea, (B1) apertural view, (B2) oblique apertural view, (B3) dorsal view.

1.2. The Fossil Record of *Ellobium*

The last complete synopsis of the fossil record of *Ellobium* was published by Wenz [32], who listed 13 species and subspecies from the Lutetian to the Pliocene of Europe. Glibert [33,34] provided another overview with eight fossil species from the Eocene and Miocene of Europe, and one fossil species from the Paleocene (Danian from Belgium) but did not consider the Oligocene species. Since then, several new species have been described, which are still placed in *Ellobium* by MolluscaBase eds. [6], e.g., '*E.*' *boriesi* (Plaziat, 1970) [35]. The census of 23 species, listed by MolluscaBase eds. [6], however, must not be read as a critical revision and comprises Jurassic ('*E.*' *koerti* Huckriede, 1967 [36])

and Danian (*E. olivaeforme* (Briart & Cornet, 1887) [37]) species sharing rather superficial similarities with *Ellobium*. Species such as the Eocene *E. scotinum* (Cossmann, 1902) [38], *E. namneticum* (Vasseur, 1881) [39], the Miocene *E. strangulatum* (de Morgan, 1917) [40], *E. roberti* (de Morgan, 1917) [40], *E. grateloupi* (Tournouër, 1871) [41], *E. grateloupi tournoueri* (Degrange-Touzin, 1892) [42] and the Pliocene *E. pyramidale* (J. de C. Sowerby, 1822) [43] differ from *Ellobium* in their small and relatively delicate shells and different apertural features (see [38,40,41,44]), and should be removed from *Ellobium*. Similarly, *E. oblongum* (Deshayes, 1830) [45] differs from *Ellobium* in its smooth and glossy shell surface and the strongly twisted columellar fold, which persists on the columellar callus and passes into the basal margin. Such shells should most likely be placed in *Pythiopsis* Sandberger, 1870 [46] or related genera. It is beyond the scope of this paper to clarify the generic placement of all of these species and therefore, we focus only on the few species listed by Wenz [32,47] and MolluscaBase eds. [6], which are accepted herein as *Ellobium*. These are *Ellobium subjudae* (d'Orbigny, 1852) [48] from the Rupelian (Early Oligocene of France), *E. vicentinum* (Fuchs, 1870) [49] from the Rupelian (Early Oligocene) of Italy, a species described herein from the Chattian (Late Oligocene) of Hungary and *E. mizutanii* Kawase & Ichihara, 2021 [50] and *E. yatsuoense* Tsuda, 1959 [51] from the Early Miocene of Japan. The Eocene *E. heberti* (Vasseur, 1881) [39], *Melampus britannus* Vasseur, 1882 [52] and *E. simplex* (Cossmann, 1895) [53] differ considerably from the extant *Ellobium* species in conchological features and are placed herein in the newly described genus *Eoellobium*. Overall, our knowledge on the history of *Ellobium* is clearly biased towards European occurrences.

2. Material and Methods

All specimens are stored in the collections of the Natural History Museum Vienna (Austria), the Muséum national d'Histoire naturelle, Paris (France) and the Naturalis Biodiversity Center, Leiden (The Netherlands). For conchological terminology see [54].

3. Systematics

Superorder Eupulmonata Haszprunar & Huber, 1990 [55]

Order Ellobiida L. Pfeiffer, 1854 (1822) [56]

Family Ellobiidae L. Pfeiffer, 1854 (1822) [56]

***Eoellobium* nov. gen.**

Figure 2(A1–B3)

Type species. *Auricula heberti* Vasseur, 1881 [39].

Etymology. A combination of *Eo-* (after Eos, the ancient Greek goddess of the dawn) and *Ellobium*.

Diagnosis. Large sized, ovate to elongate ovate shell with conical spire, convex spire whorls and occasional varices. Prominent subsutural collar, delimited by deep spiral groove. Sculpture of close-set, rugose axial ribs, crossed by weak spiral threads, resulting in irregularly granulose sculpture. Aperture moderately wide. Columellar callus forming sharply delimited, moderately thickened callus rim in adapical half of aperture, detached from base; callus becoming thinner adapically. Columellar fold moderately prominent, twisted; parietal fold weak. Outer lip slightly thickened without prominent palatal swelling. Differing from *Ellobium* in the convex spire whorls, the presence of varices and the prominent subsutural cord.

Description. As for type species.

Stratigraphic and geographic range. Middle Eocene, Bartonian; Northeastern Atlantic.

Included species. *Auricula heberti* Vasseur, 1881 [39], *Melampus britannus* Vasseur, 1882 [52] (MNHN.F.J03969, <http://coldb.mnhn.fr/catalognumber/mnhn/f/j03969> accessed on 27 January 2023) and *Auricula simplex* Cossmann, 1895 [53] (MNHN.F.J04903, <http://coldb.mnhn.fr/catalognumber/mnhn/f/j04903> accessed on 27 January 2023). The latter two species derive from the same locality as the type species.

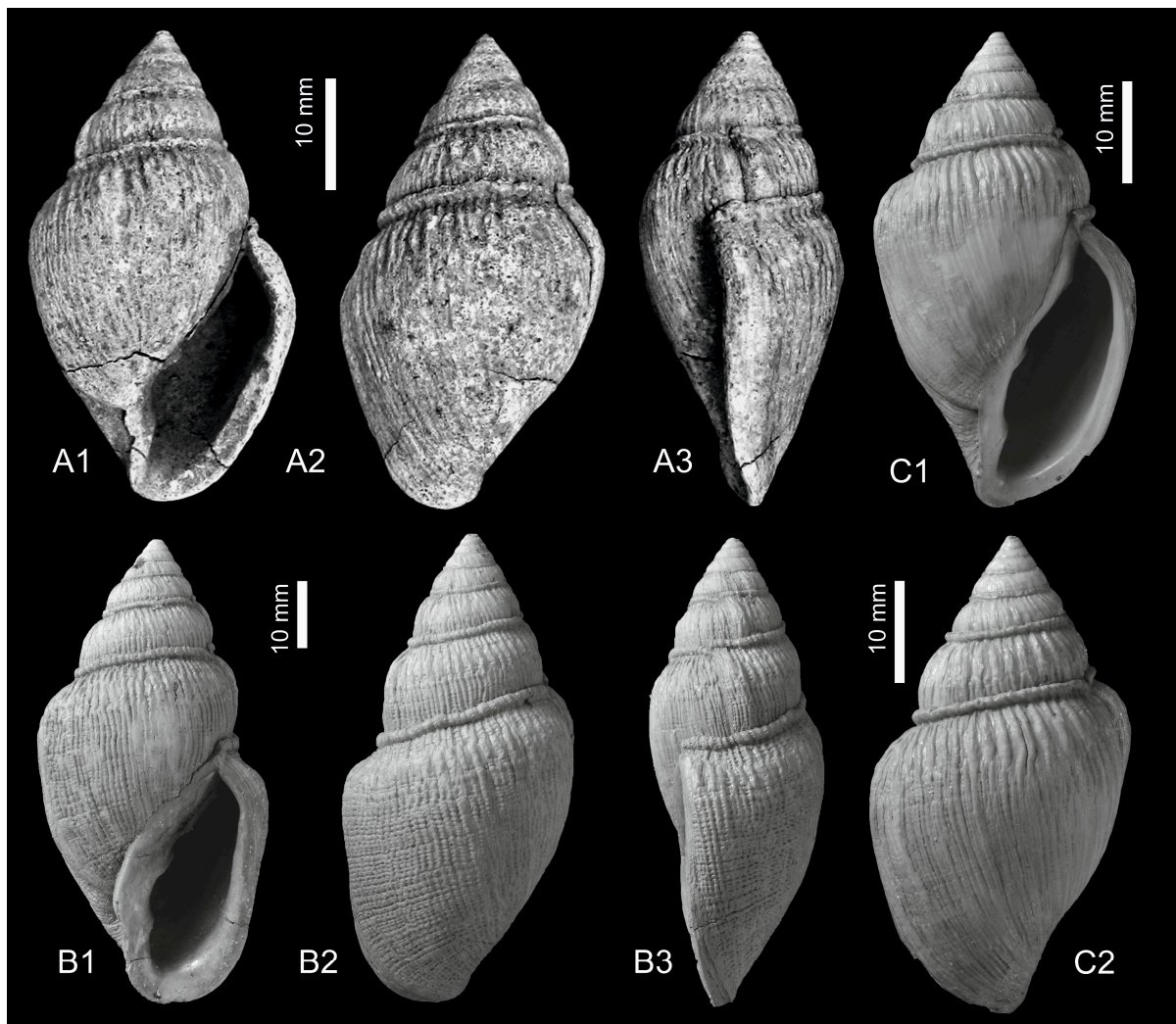


Figure 2. (A1–A3) *Eoellobium heberti* (Vasseur, 1881), lectotype MNHN.F.J04020 (Vasseur coll.) designated herein, Bartonian (Middle Eocene), Bartonian; Bois-Goüet at Saffré, Loire-Atlantique, France; (A1) apertural view, (A2) dorsal view, (A3) lateral view; (B1–B3) MNHN.F.A87734 (Pacaud coll.), Bartonian (Middle Eocene), Bartonian; Bois-Goüet at Saffré, Loire-Atlantique, France, (B1) apertural view, (B2) dorsal view, (B3) lateral view; (C1,C2) MNHN.F.A87733 (Pacaud coll.), Bartonian (Middle Eocene), Bartonian; Bois-Goüet at Saffré, Loire-Atlantique, France, (C1) apertural view, (C2) dorsal view.

Discussion. *Eoellobium* nov. gen. differs from *Ellobium* in the convex spire whorls, the presence of varices and the prominent subsutural cord. In addition, the weak columellar and parietal fold and the less thickened outer lip distinguish it from *Ellobium*. Crosse (1896: 107) wrote: “*A. Heberti*, Vasseur, grande et belle espèce, de la taille de l’*A. auris-Midae*, mais ne lui ressemblant d’ailleurs en aucune façon” [= *A. heberti*, Vasseur, a large and beautiful species, the size of *A. auris-Midae*, but in no way resembling it] [57]. Moreover, *Ellobium* does not develop such prominent axial ribs. In particular, the presence of varices suggests a different mode of ontogeny for *Eoellobium*. Nevertheless, *Eoellobium heberti* might represent an early representative of the Ellobiidae-lineage from which *Ellobium* developed around the Eocene/Oligocene boundary. Among the modern *Ellobium* species, *E. scheepmakeri* is morphologically closest to *Eoellobium heberti* concerning the convex spire whorls and the relatively wide aperture. *Ellobium scheepmakeri*, however, lacks the prominent subsutural collar and develops a prominent parietal fold.

Ecology. The mollusk assemblage from Bois-Gouët at Saffré (France) is very diverse and comprises more than 1000 species [58] derived from terrestrial, freshwater, brackish water and shallow marine paleoenvironments. Therefore, it is difficult to interpret the preferred habitat of *Eoellobium*.

***Eoellobium heberti* (Vasseur, 1881) nov. comb.**

Figure 2(A1–B3)

* *Auricula Heberti*—Vasseur 1881a: pl. 19, fig. 4 [39].

Auricula Heberti—Vasseur 1881b: 176, 251 [59].

Auricula Heberti—Vasseur 1882: pl. 9, figs 36–38, pl. 10, fig. 38 [52].

Auricula Heberti Vasseur—Cossmann 1895: 174, textfig. B [53].

Auricula Heberti Vasseur—Doncieux 1908: 33 [60].

Ellobium (*Ellobium*) *heberti* (Vasseur)—Wenz 1923: 1116 [32].

Ellobium (s. str.) *heberti* (Vasseur 1881)—Lebrun et al. 2012: 95, pl. 1, fig. 1 [58].

Illustrated material. Figure 2(A1–A3): lectotype MNHN.F.J04020 (Vasseur coll.) designated here, shell height: 41.0 mm, diameter: 24.0 mm (photo: Jacques Mouchart); Figure 2(B1–B3): MNHN.F.A87734 (Pacaud coll.), shell height: 69.4 mm, diameter: 33.4 mm (photo: Philippe Loubry, MNHN/CNRS); Figure 2(C1,C2): MNHN.F.A87733 (Pacaud coll.), shell height: 44.4 mm, diameter: 24.3 mm (photo: Philippe Loubry, MNHN/CNRS).

Material. Lectotype MNHN.F.J04020 (Vasseur coll.) designated here, shell height: 41 mm, diameter: 24 mm, (Figure 2(A1–A3)). Paralectotypes (3 ex.), MNHN.F.J17612 (Vasseur coll.). The designation of a lectotype before the year 2000, using the term “type” (CINZ 1999: Art. 74.5), by Cossmann (1895) [53] (175) for *Auricula heberti*, based on a specimen in the Dumas collection, is invalid; this specimen does not belong to the type series. Largest specimen (Dumas coll.): shell height 78 mm (illustrated in Cossmann, 1895), 4 ex., MNHN.F.A87735–A87738, one of which, with the only preserved last whorl measuring 65.6 mm (Pacaud coll.), 4 ex., MNHN.F.J16371 (Cossmann coll.), 2 ex., MNHN.F.A79882 (Pons coll.), 1 ex., MNHN.F.A77975 (Houdas coll.), Middle Eocene, Bartonian; Bois-Gouët at Saffré, Loire-Atlantique, France.

Revised description. Large sized, ovate to elongate ovate shells with conical spire; apical angle c. 65°. Protoconch and early teleoconch whorls unknown. Spire of more than seven convex whorls. Suture narrowly incised. Prominent subsutural collar, delimited by deep spiral groove. Last whorl convex with high-placed, rounded shoulder, passing into weakly convex base. Occasional varices. Sculpture of close-set, rugose axial ribs, crossed by weak spiral threads, resulting in irregularly granulose surface. Axial ribs most prominent along and below subsutural collar. Aperture moderately wide, posteriorly angulated, with faintly incised basal margin. Columellar callus forming sharply delimited, moderately thickened callus rim in abapical half of aperture; callus narrowing adapically. Columellar fold very weak to subobsolete. Parietal fold weak, placed roughly mid-aperture. Outer lip slightly thickened without marked palatal swelling. Fasciole broad, convex with prominent growth lines.

Discussion. This species was placed in *Ellobium* by Wenz 1923 [32] and Lebrun et al. 2012 [58] but the similarity in outline, sculpture and size with this genus is superficial. *Melampus britannus* Vasseur, 1882 and *Auricula simplex* Cossmann, 1895 are both found also at Bois-Gouët together with *Eoellobium heberti*. *Eoellobium britannus* and *E. simplex* represent shells with strongly reduced sculpture and weak spiral groove below the subsutural collar. ‘*Auricula*’ *boriesi* Plaziat, 1970, from the Ypresian of France, differs from *Eoellobium heberti* in its stronger, thicker columellar and parietal folds, by the presence of a third posterior parietal fold and by the strongly thickened outer lip, which has a prominent palatal swelling. Moreover, it lacks a subsutural collar. Similarly, ‘*Ellobium*’ *viai* Calzada & Urquiola, 1995 [61] from the Priabonian of Spain, lacks a subsutural collar and has a sculpture of prominent axial ribs.

Northeastern Atlantic. Middle Eocene, Bartonian; Bois-Gouët, Saffré, Loire-Atlantique, France.

***Ellobium* Röding, 1798 [62]**

Type species: *Ellobium midae* Röding, 1798, accepted as *Ellobium aurismidae* (Linnaeus, 1758) [7], subsequent designation by Gray (1847) [63] (179). Present-day, South-East Asia.

Diagnosis. “Shell moderately large and thin (25 mm) to large and thick (100 mm) and covered with pale brown periostracum. Spire low to moderately high, sculptured with granular spiral lines crossed by more or less conspicuous axial cords. Body whorl about 80% shell length, with same sculpture as spire, sometimes weakly depressed dorsoventrally. Aperture about 80% length of body whorl; small, very oblique, twisted columellar tooth, stronger anterior parietal tooth; posterior parietal tooth sometimes present; outer lip thin to thick, sharp to weakly reflected.” Martins (1996) [14] (178). Inner shell walls partly resorbed in [17] and figs 9.2c–d in [64]. For anatomical data see Martins (1996) [14].

***Ellobium kerwaense* nov. sp.**

Figure 3(A1–E3)

Ellobium sp.—Báldi & Cságoly 1975: 137 [65].

Ellobium n. sp. ex aff. *vicentina* Fuchs—Báldi 1976: 410 [66].

Ellobium (*Ellobium*) cf. *subjudae* (d’Orbigny, 1852)—Janssen 1984: 134, pl. 4, figs 16 and 17 [67].

Ellobium cf. *subjudae* (d’Orbigny)—Réka 1996: 24, n° 38 [68].

Ellobium cf. *subjudae* (d’Orbigny)—Harbeck 1996: 121, pl. 33, figs 502 and 503 [69].

Ellobium cf. *subjudae* (d’Orbigny, 1852)—Vicián et al. 2019: 158 [70].

Ellobium subjudae (d’Orbigny)—Harzhauser & Piller 2007: 24 [71] [non *Ellobium subjudae* (d’Orbigny 1852)].

Holotype. NHMW 2022/0285/0001, shell height: 38.7 mm, diameter: 20.4 mm (Figure 3(A1–A3)).

Paratypes. NHMW 2022/0285/0002, shell height: 38.9 mm, diameter: 19.8 mm (Figure 3(B1–B3)); NHMW 2022/0285/0003, shell height: 40.0 mm, diameter: 23.0 mm (Figure 3(C1–C3)); NHMW 2023/0036/0001, shell height: 44.0 mm, diameter: 21.5 mm; NHMW 2023/0036/0002, shell height: 36.7 mm, diameter: 19.1 mm; NHMW 2023/0036/0003, shell height: 42.7 mm, diameter: 23.1 mm; NHMW 2023/0036/0004, shell height: 34.0 mm, diameter: 18.6 mm. MNHN.F.A87731, shell height: 32.3 mm, diameter: 17.6 mm (Figure 3(D1–D3)). MNHN.F.A87732, shell height: 39.8 mm, diameter: 23.9 mm (Pl. 1. Figure 3(E1–E3)); RGM 224052, shell height: 44 mm, diameter: 23 mm, illustrated in Harbeck (1996, pl. 33, fig. 502) [69]; RGM 224052, shell height: 40 mm, diameter: 24 mm, illustrated in Harbeck (1996, pl. 33, fig. 503) [69].

Diagnosis. Medium sized, solid, ovate shells with prominent axial sculpture of granulose ribs. Moderately narrow aperture with broad, strongly thickened, smooth columellar callus, relatively weak columellar fold and prominent parietal fold. Outer lip thickened, broad with prominent palatal swelling.

Type locality. Sandpit at Máriahalom in the NE part of the Transdanubian Mountains in Hungary (47°37′56.39″ N, 18°43′29.51″ E).

Type stratum. Coastal sand of the Mány Formation, Upper Oligocene, Egerian (=Chattian).

Etymology. Referring to the old name ‘Kerwa’ of the type locality Máriahalom.

Description. Large, solid, ovate shell with conical spire; apical angle 65–80°. Protoconch and early teleoconch whorls unknown. Spire consisting of more than six weakly convex whorls. Last whorl ovoid, moderately convex with periphery usually in adapical third (but may be below mid-whorl in some specimens). Suture narrowly canaliculate. Base slowly contracting. Sculpture of prominent, slightly irregular, faintly sigmoidal, finely granulose axial ribs separated by narrower interspaces. Weak spiral threads most distinct on base separating slightly better defined, subquadratic granules. Aperture moderately narrow, posteriorly angulated with convex basal margin. Columellar callus very prominent, broad, thickened, well demarcated from base, forming broad, thickened callus detached at base and with distinct chink with base. Fasciole broad, indistinct. Columellar fold not very prominent, slightly twisted, fading out on columellar callus. Parietal fold prominent, raised,

moderately narrow, in abapical third of aperture, fading out on columellar callus. Outer lip strongly thickened, very broad with prominent palatal swelling slightly above midwhorl.

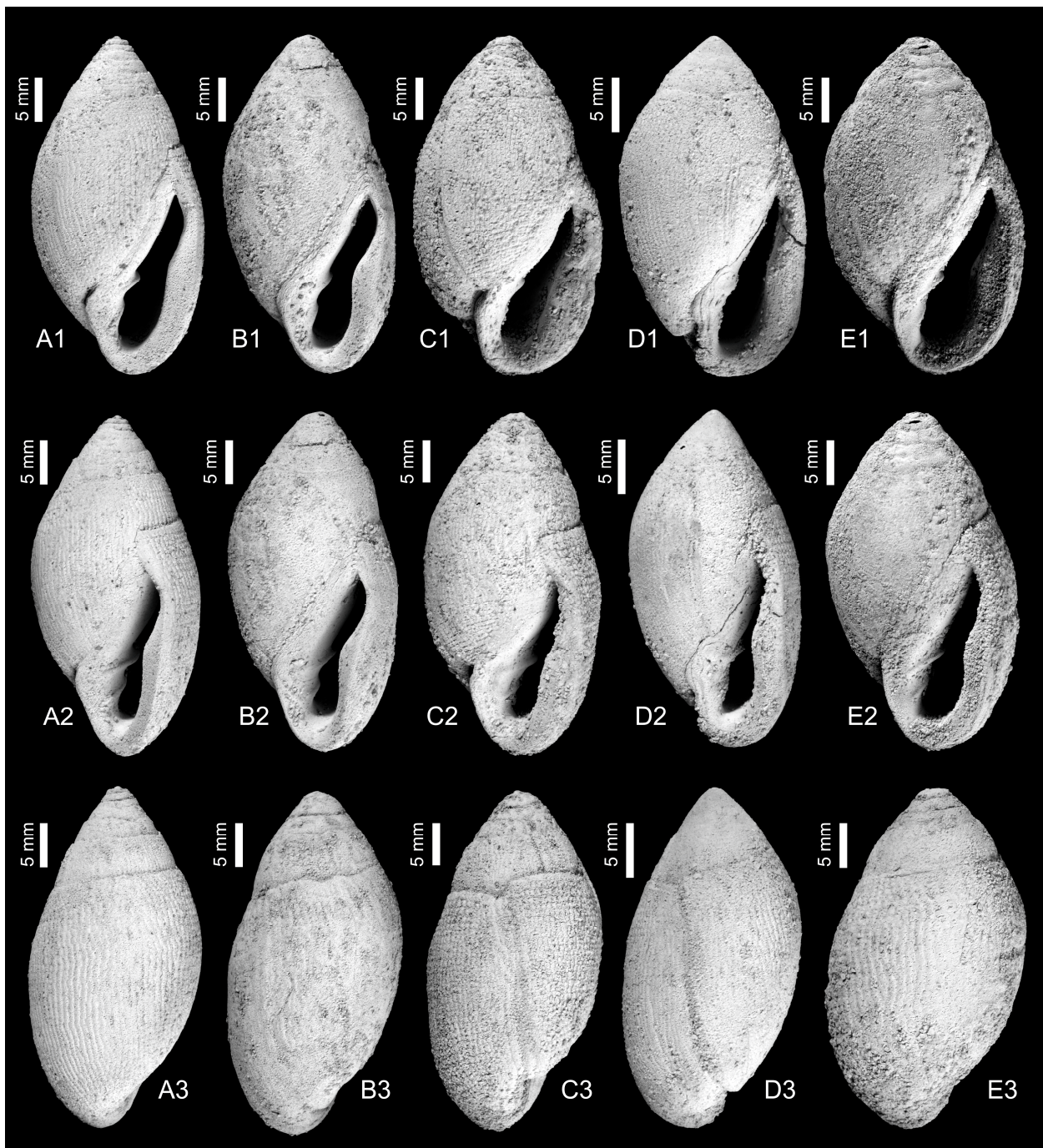


Figure 3. Chattian (Late Oligocene) *Ellobium* species: (A1–E3). *Ellobium kerwaense* nov. sp. (A1–A3). NHMW 2022/0285/0001, holotype, (A1) apertural view, (A2) oblique apertural view, (A3) dorsal view; (B1–B3). 2022/0285/0002, paratype, (B1) apertural view, (B2) oblique apertural view, (B3) dorsal view; (C1–C3). 2022/0285/0003, paratype, (C1) apertural view, (C2) oblique apertural view, (C3) dorsal view; (D1–D3). MNHN.F.A87731, paratype, (D1) apertural view, (D2) oblique apertural view, (D3) dorsal view; (E1–E3). MNHN.F.A87732, paratype, (E1) apertural view, (E2) oblique apertural view, (E3) dorsal view; all specimens Máriahalom, Hungary.

Discussion. *Ellobium kerwaense* nov. sp. was compared with or confused with *Ellobium subjudae* and *E. vicentinum* [66,71]. *Ellobium vicentinum* differs in its smaller size, slenderer outline, higher spire, more adapical position of the parietal fold and distinctly less thickened outer lip. *Ellobium subjudae* is distinguished by its much higher spire and the wider aperture, which lacks a palatal swelling. Moreover, the outer lip and columellar callus are much more thickened in *E. kerwaense* nov. sp. *Ellobium mizutanii* Kawase & Ichihara, 2021, from the Early Miocene of Japan [50], is similar in outline but is even more inflated, has a wider aperture and a less thickened outer lip, which lacks a palatal swelling. The Early Miocene *E. yatsuoense* Tsuda, 1959, from Japan [52], is similar to *E. kerwaense* in outline but has slightly higher spire whorls and its sculpture is weaker [51] (pl. 7, figs 4a,b). Among the extant *Ellobium* species, *E. aurismidae* is reminiscent of the Paratethyan species in its general shell shape. However, *E. aurismidae* has a much larger shell, with flat spire whorls bearing more prominent granules, and a much weaker palatal swelling than that seen in *E. kerwaensis*. Moreover, below the shoulder the whorls in *E. aurismidae* are usually smooth and not finely granular as seen in *E. kerwaensis*.

Concerning the prominent palatal swelling, *E. kerwaense* nov. sp. is morphologically closer to the extant *E. aurisjudae*, which is far more elongate and bears a second parietal fold.

Ellobium kerwaense occurs in dense, nearly rock-forming coquinas composed mainly of shells of the potamidids *Mesohalina margaritacea* (Brocchi, 1814) [72], *Ptychopotamides cinctus* (Bruguière, 1792) [73] and *Granulolabium plicatum* (Bruguière, 1792) [73] along with melongenids and the bivalves *Polymesoda* and *Isognomon* [67]. Although we are not aware of palaeobotanical data on Máriahalom, this mollusk assemblage is indicative for the presence of mangroves and coastal mudflats [74].

Distribution. Central Paratethys Sea: Known so far only from Máriahalom and Esztergom in the Komárom-Esztergom district in Hungary [67,70].

Ellobium subjudae (d’Orbigny, 1852)

Figure 4(A1,A2)

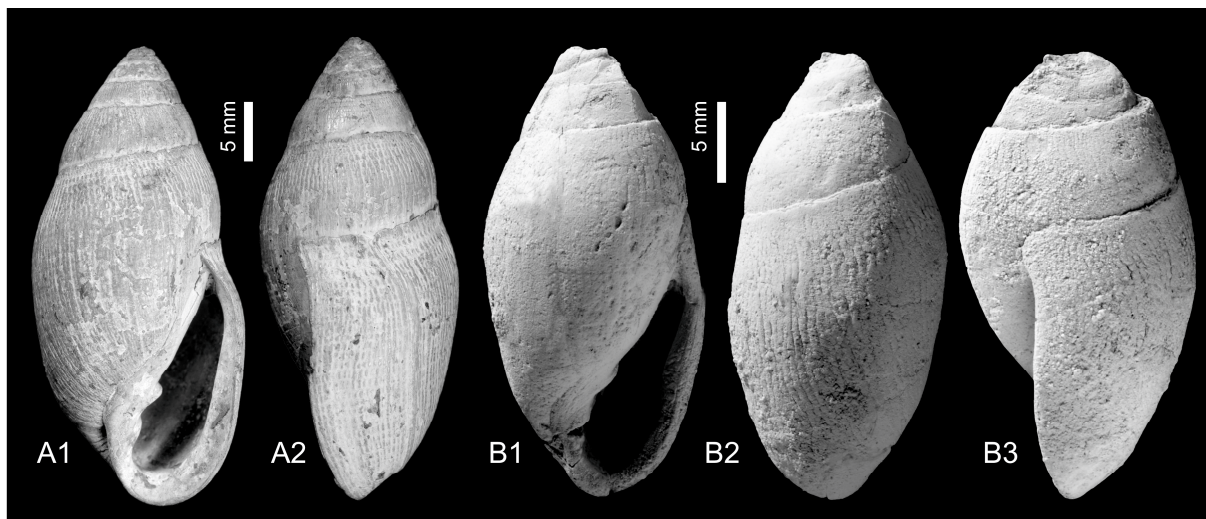


Figure 4. Rupelian (Early Oligocene) *Ellobium* species: (A1,A2) *Ellobium subjudae* (d’Orbigny, 1852), syntype, UB n° 65-2-153 (Grateloup collection), Lesbarritz, Gaas (Landes), France; (A1) apertural view, (A2) lateral view; (B1–B3) *Ellobium vicentinum* (Fuchs, 1870), lectotype, NHMW 2022/0286/0001, Soggio di Brin at Salcedo, Vicenza, Italy; (B1) apertural view, (B2) dorsal view, (B3) lateral view.

Auricula Judae Lamarck—Grateloup 1827: 6 [75] [non Linnaeus, 1758].

Auricula Judae Lamarck—Grateloup 1828: 103 [76] [non Linnaeus, 1758].

Auricula Judae Lamarck—Grateloup 1838: 254, pl. 6, fig. 1 [77] [non Linnaeus, 1758].

Auricula Judae Lamarck—Grateloup 1847: plate captions, pl. 1 (11), fig. 1 [78] [non Linnaeus, 1758].

* *Auricula subjudae*—d’Orbigny 1852: 2 [48].

Auricula subjudae Lamk.—Pictet 1855: 33, pl. 52, fig. 30 [79] [non Linnaeus, 1758].

Auricula sub-Judae Lamk.—Raulin 1856: 386 [80] [non Linnaeus, 1758].

Auricula aquitanica Sandberger—Sandberger 1871: 330, pl. 19, fig. 24 [46].

Auricula subjudae d’Orb.—Tournouër 1872: 97 [81].

Auricula Aquitanica Sandb.—Benoist 1875: 72 [82].

Auricula aquitanica Sandb.—Hoernes 1884: 286, textfig. 386 [83].

A[uricula]. Aquitanica Grat.—Zittel 1885: 229 [84].

Auricula Aquitanica Sandberger—Degrange-Touzin 1892: 204 [42].

Auricula Judae Lamk.—Raulin 1896: 552 [85] [non Linnaeus, 1758].

Auricula subjudae d’Orb.—Raulin 1896: 552 [85].

Auricula subjudae Grat., d’Orb.—Raulin 1900: 47 [86].

Auricula Aquitanica Sandb.—Raulin 1900: 52 [86].

Ellobium (Ellobium) subjudae (d’Orbigny)—Wenz 1923: 1120 [32].

Auricula subauris-judae [sic] d’Orbigny—Magne 1936: 37 [87].

non Ellobium subjudae (d’Orbigny)—Harzhauser & Piller 2007: 24 [71] [= *Ellobium kerwaense* nov. sp.].

Syntypes. Figure 4(A1,A2), UB n° 65-2-153 (coll. Grateloup), shell height: 37 mm, diameter: 17 mm. UB n° 65-2-154 (coll. Grateloup), stored in the Université de Bordeaux, France. Lesbarritz, Gaas (Landes), France, Early Oligocene (Rupelian).

Revised description. Medium-sized, elongate ovate, solid shell with conical spire, apical angle c. 60°. Protoconch and early teleoconch whorls unknown. Spire of more than six weakly convex whorls. Last whorl elongate ovoid, with faint subsutural concavity; base convex. Suture narrowly incised; suture on last whorl slightly oblique. Sculpture of rugose, faintly sigmoidal axial ribs, separated by narrow interspaces. Granules most distinct over subsutural ramp and on base. Aperture moderately wide, posteriorly angulated, with wide, convex basal margin. Columellar callus, moderately thickened, forming broad rim, well demarcated from base. Abapically, columellar callus becoming thick, demarcating narrow chink from base. Columellar fold relatively weak, broad fading out on smooth columellar callus. Parietal fold prominent, relatively narrow (compared to some of the extant species like *E. aurisjudae*), slightly oblique, fading out on columellar callus. Outer lip thickened with beveled edge, the inner beveled portion concave, without palatal swelling. adapically

Discussion. *Ellobium subjudae* is similar to the coeval *E. vicentinum* but differs in its much larger size and the more prominent parietal fold. Because *E. vicentinum* bears a palatal swelling, whereas *E. subjudae* lacks such feature, it is unlikely that *E. vicentinum* is based on a subadult specimen of *E. subjudae*. For a separation from *E. kerwaense* nov. sp. see discussion on that species. The extant *Ellobium aurisjudae* is reminiscent of *E. subjudae* in its elongate outline, but differs clearly in its higher last whorl, the narrower and high aperture, the presence of a second parietal fold, and broader folds.

Distribution. Northeastern Atlantic: Aquitaine Basin: Rupelian (Early Oligocene): Gaas, Lesbarritz (France); Chattian (Late Oligocene): Saint-Paul-lès-Dax (France).

Ellobium vicentinum (Fuchs, 1870)

Figure 4(B1,B2)

* *Auricula Vicentina* Fuchs—Fuchs 1870: 208, pl. 10, figs 9–10 [49].

Auricula vicentina Fuchs—Tournouër 1872: 97 [81].

Auricula vicentina Fuchs—Sandberger 1873: 330 [46].

Auricula vicentina Fuchs—Oppenheim 1900: 326 [88].

Ellobium (Ellobium) vicentinum (Fuchs)—Wenz 1923: 1121 [32].

Lectotype (designated herein). NHMW 2022/0286/0001, shell height: 28.1 mm, diameter: 14.7 mm, Soggio di Brin at Salcedo, Vicenza, Italy; Early Oligocene (Rupelian).

Revised description. Medium sized, moderately narrowly ovate with acute spire, solid. Spire conical, moderately high, of more than 5 weakly convex whorls; apical angle 63°. Protoconch and early teleoconch whorls unknown. Shell surface of spire abraded. Last

whorl moderately convex, attaining about 80% of total height, with periphery distinctly below suture. Suture narrowly canaliculate, slightly oblique on last whorl. Base slowly contracting. Sculpture on last two whorls of coarse, finely rugose, broad, low, irregular, faintly sigmoidal axial ribs with narrow interspaces, composed of coalescent subquadratic nodes. Sculpture persisting to base. Aperture moderately narrow with acute posterior angulation and convex basal margin. Columella with broad, not very thickened callus narrowing adapically. Columellar callus relatively weak, delimitating narrow chink on base. Columellar fold moderately prominent, weakening inside aperture. Parietal fold relatively weak for genus, not very broad, weakly oblique, slightly below middle of aperture. Outer lip thickened with palatal swelling above mid-whorl.

Discussion. The description of this species by Fuchs (1870) was misleading as he did not describe and illustrate the columellar fold. The mollusk fauna from Soggio di Brin is a rich assemblage typical for shallow sublittoral environments with cassid, cypraeid and marginellid gastropods but lacks genera typical for mudflats, saltmarshes and mangroves. Therefore, the single *Ellobium* shell is parautochthonous and transported.

Distribution. Western Tethys: Only known so far from the two close-by Early Oligocene (Rupelian) localities Soggio di Brin at Salcedo and Casa Privata at Bassano in the Vicenza Province (Italy) [88].

4. Discussion

The modern distribution pattern of *Ellobium*, with the greatest diversity being in the Indo-West Pacific-Region (IWP Region), suggests that this region was a center of origin of the genus. However, this hypothesis conflicts with the fossil record, as the oldest records are not from the IWP Region but from the Rupelian of the Western Tethys and the Northeastern Atlantic (Figure 5). A Rupelian first appearance of *Ellobium* is in excellent agreement with the molecular data [89], which includes *E. aurisjudae*, *E. chinense* and *E. scheepmakeri*. This molecular analysis suggested an origination of the genus during the Oligocene times. However, the taxonomic revision presented herein suggests older roots for the group, extending back to the Middle Eocene, represented by *Eoellobium* nov. gen. from the North Eastern Atlantic. The oldest fossil *Ellobium* species in the IWP Region post-dates the European occurrences. *Ellobium mizutanii* Kawase & Ichihara, 2007 and one unnamed species from Mizunami (Gifu Prefecture, Japan), *E. yatsuoensis* Tsuda, 1959 from Osa-wano-machi and Kaminiikawa-gun (Toyama Prefecture, Japan) and *E. cf. aurisjudae* from Ninohe City (Iwate Prefecture, Japan) were described from the Early Miocene [50,90–93]. After this first radiation in the IWP Region, the fossil record of the genus becomes rather poor. An unnamed species was recorded from the Middle Miocene of Java [94] and *Ellobium aurismidae* was reported from the Late Miocene or Early Pliocene of the Philippines [95]. Another unnamed Late Miocene *Ellobium* was reported from Japan [96]. *Ellobium aurisjudae* was documented from the Late Pliocene of Java [93] and from the Holocene of Malaysia [17] from where *Ellobium scheepmakeri* was also documented from the Late Pleistocene or Holocene [17]. The molecular data suggests *Ellobium chinensis* was present at least since the Pleistocene [28]. Despite this fragmentary record, it can be stated that *Ellobium* was established in the IWP Region represented by several species since the Early Miocene. *Ellobium* aff. *pellucens* (Menke) [=‘E.’ aff. *dominicense*] from the Lower Miocene of Panama [97] documents that the Western Atlantic lineage ‘E.’ *dominicense* can also be traced back to the Early Miocene but it is questionable if this lineage is directly related to *Ellobium*.

This pattern of stratigraphic occurrences would suggest the Northeastern Atlantic and the Western Tethys as the centers of origin from where *Ellobium* spread into the IWP Region. It is possible that the Western Atlantic ‘E.’ *dominicense* represents a Transatlantic offshoot of this radiation.

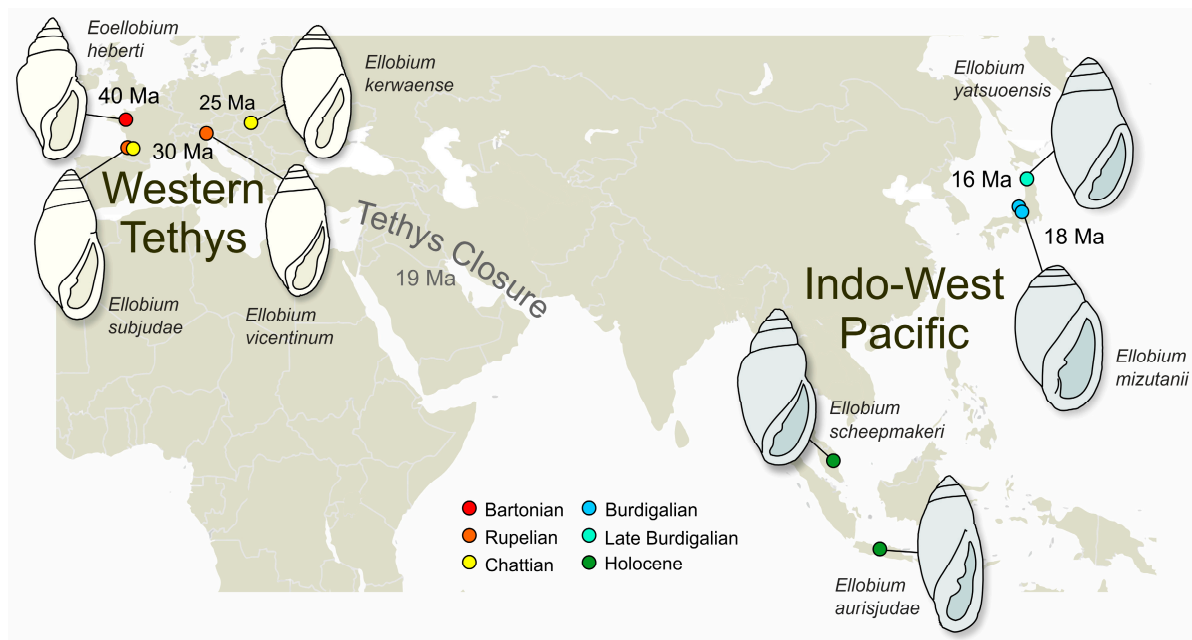


Figure 5. Middle Eocene to Holocene geographic and stratigraphic distribution of *Eoellobium* and *Ellobium*.

Similar range expansions were documented for some Western Tethyan strombids and for the tridacnine bivalves [98–100]. These taxa first appeared in the Northeastern Atlantic and Western Tethys and arrived during the Oligocene via the open Tethys Gateway in the IWP Region (Tridaninae) and in part also arrived in the Western Atlantic (e.g., *Persististrombus* Kronenberg & Lee, 2007 [101]). We note however, that the mode of dispersal of marine taxa, such as strombids and tridacnids, is clearly different from that of pulmonate ellobiids.

The Extinction of Ellobium in European Seas

Ellobium species are rare in the fossil record and the three European Oligocene species are known from only a few specimens. Nevertheless, we consider it unlikely that the genus was overlooked thus far in the well-known Early Miocene assemblages of the Northeastern Atlantic, the Western Tethys and the Central Paratethys Sea. This is especially true for the enormously rich mangrove fauna of the Korneuburg Basin, which has been systematically screened by citizen scientists for nearly 30 years resulting in a significant amount of material [102,103]. Similarly, the Aquitanian and Burdigalian faunas from the Aquitaine Basin are well documented and extensively collected. Therefore, we assume that *Ellobium* vanished from this region at the end of the Chattian. It would be tempting to explain this extinction by the cooling around the Oligocene/Miocene boundary, which coincided with the M1 glaciation, due to a major expansion of Antarctic ice shields [104,105]. Other species of the Oligocene mangrove assemblage, however, persisted into the Early Miocene. The potamidids *Mesohalina margaritacea* (Brocchi, 1814), and *Ptychopotamides cinctus* (Bruguière, 1792) and the bivalve *Polymesoda subarata* (Schlotheim, 1820) [106] occur in Rupelian and Chattian assemblages of the Western Tethys and passed the Oligocene/Miocene boundary [107]. Therefore, the correlation with the M1 glaciation might be too simplistic.

5. Conclusions

The tropical pulmonate genus *Ellobium* has its highest diversity in the Indo-West Pacific Region and does not occur in the modern Mediterranean Sea and the Eastern Atlantic. Its origin can be traced back to the Early Oligocene in the Northeastern Atlantic and Western Tethys, where it is documented by two species. During the Late Oligocene, *Ellobium* also reached the Central Paratethys Sea, from where it is documented by the newly described *Ellobium kerwaense* nov. sp. No *Ellobium* species are known from the European Miocene

suggesting an extinction around the Oligocene/Miocene boundary. The radiation in the IWP Region started during the Early Miocene. Since then, the genus is documented by fragmentary fossil records in the entire IWP Region. The Oligocene appearance of *Ellobium* is in excellent agreement with the proposed age of the genus in a molecular phylogeny of the Ellobiidae [89]. The roots of *Ellobium* might be represented by the Middle Eocene genus *Eoellobium*, which is morphologically closely similar to *Ellobium* but differs in its prominent subsutural collar and weaker columellar and parietal folds. *Ellobium* is another example of an eastward range expansion of a mollusk group, as it originated in the Paleogene of the Western Tethys and subsequently spread into the Indo-West Pacific via the Tethys Gateway.

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Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

NHMW	Natural History Museum Vienna (Austria)
MNHN.F.	Muséum national d’Histoire naturelle, Paris (France)
RGM	Naturalis Biodiversity Center, Leiden (Netherlands)

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