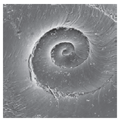
Filling the gap in knowledge of early Miocene continental molluscs of southwest Europe: gastropods from Ribesalbes-Alcora Basin (Spain)

Joaquín Albesa, José María López & Vicente D. Crespo



We present the results obtained in the study of the fifteen early Miocene sites of Campisano Ravine, a sector of the Ribesalbes-Alcora Basin. This work contributes to filling a gap in the knowledge of continental molluscs from the early Miocene of the Iberian Peninsula. The studied assemblage contains eight species, four aquatic and four terrestrial. One of the aquatic species, *Pseudamnicola roblesi*, is new to science. The registered fauna mainly shows affinities to the early and middle Miocene faunas of Central Europe. The ecological requirements for the fauna, as derived from recent relatives, in combination with the presence of different depositional environments allowed a reconstruction of the local palaeoenvironment. The assemblage is consistent with the existence of a shallow oligohaline palaeolake with macrophytic vegetation and the possibility of a littoral reed belt. This palaeolake would have been located in an area with diverse vegetal coverage, in a subtropical to tropical climatic context. Extent and depth of the lake varied over time in relation to the changes in climatic conditions and alluvial input, which may have been the result of episodical storms. • Key words: continental molluscs, systematics, palaeoecology, palaeobiogeograhy, Aragonian, Iberian Peninsula.

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The Iberian Peninsula accommodates large endorreic basins such as those of Vallés-Penedés, Ebro, Calatayud-Daroca, Teruel, Duero and Tajo, as well as smaller ones such as Cabriel, Fortuna, Guadix-Baza and Granada (Agustí 2018). Continental sediments of Aragonian age (end of the early Miocene to middle Miocene; mammal biozones MN4 to MN7/8) are represented in many of these basins (Agustí 2018). While mammal associations have been studied extensively in several palaeontological sites, the malacological record is comparatively poor documented. The few studies carried out on the malacological assemblages recorded in sediments today attributed to an Aragonian age are to some extent outdated (Vilanova y Piera 1859; Royo Gómez 1922, 1926, 1928; Jodot 1959). Also, many of sites and faunas documented in these works could not be precisely located. The available references accurately located and dated correspond to sites attributed to the middle Aragonian of the Tajo Basin (Truc 1977) and the upper Aragonian of the Duero Basin (González Delgado *et al.* 1986, Civis *et al.* 1989). The references from the early Aragonian are practically inexistent and correspond to isolated cites or recent multidisciplinary studies in the Ribesalbes-Alcora Basin (Peñalver *et al.* 2016, Álvarez-Parra *et al.* 2021).

In line with the above, the available data on the malacological content of the sediments of the Ribesalbes-Alcora Basin (Fig. 1A) are mostly old and very scarce. The first one corresponds to Vilanova y Piera (1859) who studied the materials in the "Balsa de Fanzara" (the classical name for the Cenozoic sediments of the basin) and the nearby area of Alcalá. He cited the generic presence of "lymneas", "planorbis" and "helices" (Vilanova y Piera 1859: p. 44), and more specifically a single specimen of *Planorbis rotundatus* Brongniart, 1810 from the "Balsa de Fanzara", which is shown on a plate alongside with four species belonging to the Alcalá area. Royo Gómez (1922) included a brief reference to the sediments of the studied area correcting the determination of *Planorbis rotundatus* to

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Planorbis thiollierei [sic] Michaud, 1855 [= *Planorbarius thiollieri*]. Hahne (1930) indicated the presence of three taxa determined by Wilhelm Wenz as *Gyraulus* sp., *Amnicola* sp. and *Lymnaeus* sp. in the vicinity of Alcora. Sos Baynat (1981) made an erroneous compilation of the previous information citing for the site of the "Balsa de Fanzara" the species *Planorbis rotundatus*, *Lymnae palustris* [sic] Grateloup, 1828 [= *Stagnicola palustris* (Müller, 1774)] and *Helix dufrenoyi* Matheron, 1843 [= *Leucochroopsis dufrenoyii*].

Recently, Peñalver *et al.* (2016) mentioned the presence of *Anisus* sp. and cf. *Cepaea* sp. in La Rinconada site, very close to the Campisano Ravine although possibly older than our sites. Álvarez-Parra *et al.* (2021), within the framework of a multidisciplinary study, analysed the malacological composition of Foieta la Sarra-A site, listing four freshwater mollusc taxa (Hydrobiidae indet., Lymnaeidae indet., *Ferrissia* sp. and *Gyraulus* sp.).

The scarce early-middle Miocene malacological record in the Iberian Peninsula constrasts with a diverse fauna in Central and Southeastern Europe. Numerous faunas have been described in Poland (Kadolsky & Piechocki 2000, Harzhauser & Neubauer 2018), Austria (Harzhauser *et al.* 2014b), Germany (Salvador *et al.* 2016, Höltke *et al.* 2018), Hungary (Kókay 2006), Czech Republic (Harzhauser *et al.* 2014a), Slovakia (Neubauer *et al.* 2015), Croatia (Neubauer *et al.* 2011, 2016a), Bosnia-Herzegovina (Neubauer *et al.* 2013a, 2016b, Mandic *et al.* 2020), Serbia (Neubauer *et al.* 2017), Ukraine (Gozhik & Prysjazhnjuk 1978), Greece (Vasileiadou *et al.* 2017) and France (Fischer 2000).

The current study of the assemblage detected in the Campisano Ravine sites aims to increase the knowledge

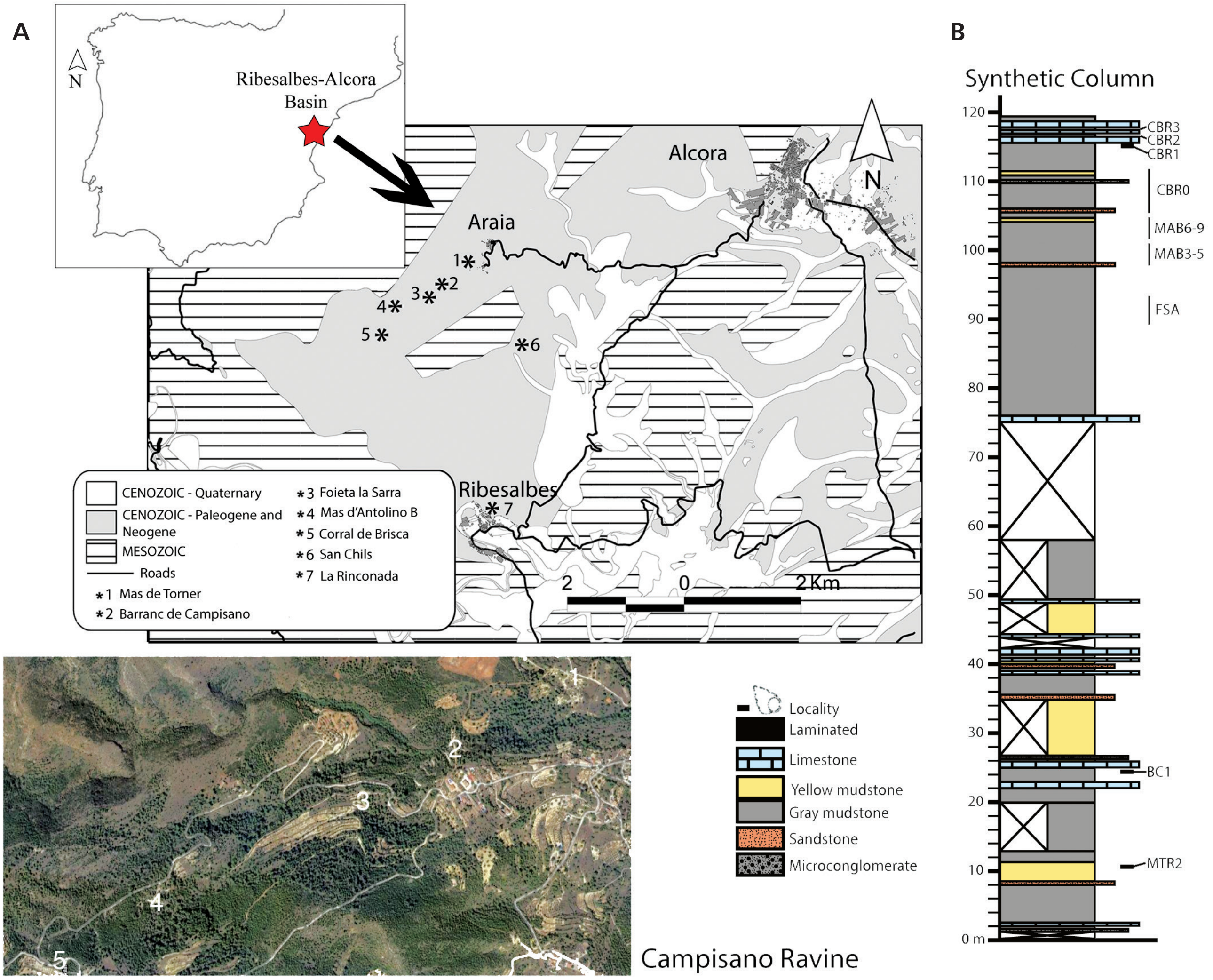


Figure 1. A – geographic and geological location of the Ribesalbes-Alcora Basin and the Campisano Ravine, with indication of the sites studieds in this work (map made from orthophoto of Google Maps). • B – synthetic stratigraphic column of the Campisano Ravine, also with indication of the sites studieds. All modified from Crespo *et al.* (2018).

of the continental mollusc fauna of the European early Miocene and of its southwestern area in particular. We collected data from a basin for which there is hardly any information and we provided the taxonomic analysis of the species located in fourteen of the sites studied by Crespo (2017) and that of Foieta la Sarra-A studied by Álvarez-Parra *et al.* (2021). In addition, a reconstruction of the palaeoenvironment prevailing at the time of deposition is proposed here on the basis of the species' ecological requirements. The study of the molluscs in this area complements the study of its small mammals, investigation which is being carried out by one of the authors of this work (Crespo *et al.* 2018; 2019a, b, c; 2020a, b; 2021a, b; 2022). At the same time, together the study of the lacustrine ecosystem of Foieta la Sarra's limestones carried out by Álvarez-Parra *et al.* (2021), constitutes the starting point of a combined study, wich in turn it will make possible the analysis of the evolution of the Basin from a collaborative perspective.

Geographic and geological setting

The Ribesalbes-Alcora Basin (SE Iberian Range, Spain) is a graben complex that encompasses 150 km^2 and bounded by ENE-WSW to NNE-SSW trending normal faults (Anadón *et al.* 1989, Barrón & Postigo-Mijarra 2011). According to Agustí *et al.* (1988) and Anadón (1994), the sediments of this basin are composed of detrital and carbonate materials deposited in alluvial and palustrine environments, divided into two sequences. The lower sequence crops out in the town of Ribesalbes, has a thickness of up to 600 metres and it is formed by sediments of alluvial and palustrine origin, with an estimated age of early to middle Miocene. The upper sequence, originally described in the town of Alcora, is formed by alluvial deposits, with a thickness of up to 200 metres and aged middle to late? Miocene.

In the Ribesalbes sequence, Anadón (1983) defined five depositional units (A to E), the sediments from Araia-Mas d'Antolino outcrops belonging to the unit C (Anadón 1983, Agustí *et al.* 1988, Crespo *et al.* 2019a). This unit is formed by detritic sediments interbedded with a few dolomitic and calcareous levels. Their sediments consist of narrow sandstone beds and thick massive mudstones that are interpreted as distal deltaic and shallow lacustrine environments (Anadón 1983, Crespo 2017, Crespo *et al.* 2019a).

The Araia-Mas d'Antolino's outcrops are characterised by being thicker than those described for unit C in the Ribesalbes sector, having a red detritic formation on the upper part. This last formation belongs to the sequence of Alcora and it is in concordance with the unit C deposits, which in turn, contain the sites studied in the Campisano Ravine (Agustí *et al.* 1988; Anadón *et al.* 1990, 2004).

Crespo *et al.* (2019a) studied 45 new sites with mammal remains found in the Campisano Ravine (Fig. 1A), in addition to those already described by Agustí *et al.* (1988). These sites are described in ten sections, from which they reconstructed a synthetic 140 metres's profile (Fig. 1B). The composite section is mainly formed by deposits of lutites, marls and carbonates with some sandstone layers and microconglomerates. These sites studied by Crespo *et al.* (2019a) can be correlated with the local biozone C (MN4, early Miocene) from the Calatayud-Montalbán Basin (Spain), the type area of the Aragonian stage, with an estimated age between 16.49 and 15.98 Myr ago (Van der Meulen *et al.* 2012, Crespo et *al.* 2019a). Fifteen of the sites contain a malacological record which is studied here.

According Crespo *et al.* (2019a), the lithogical characteristics of the sections where we found the mollusc remains are as follow:

1) Mas de Torner (MTR) is composed of three subsections that contain principally yellow, reddish and grey mudstones. The site MTR2 consists of grey mudstones, with intercalations of white and yellow mudstones.

2) Barranc de Campisano (BC) is composed of yellow and grey mudstones with sandstone and limestone intercalations, being located the site BC1 in the grey mudstone beds, under limestone deposits.

3) Foieta la Sarra (FS) is composed of grey mudstones on a laminated limestone bed (FSA), wich presents remains of flora and fauna (studied by Álvarez-Parra *et al.* 2021) at the base.

4) Mas d'Antolino B (MAB) is composed of greenish grey, yellow and grey mudstones, with intercalations of several terrigenous channels and some gypsum beds in the lower part. The sites MAB3, MAB4, MAB6, MAB7, MAB8 and MAB9 are located in thick beds of grey-dark mudstones; the site MAB5 includes multiple layers of black, grey or reddish (ferruginous) mudstones, with intercalations of gypsum.

5) Corral de Brisca (CBR) is composed of two short sub-sections. The first could correlate to the uppermost part of MAB, it contains the sites CBR0B and CBR0G and is composed of grey, black and reddish mudstones. The second sub-section contains the sites CBR1, CBR2, CBR3 and is composed by grey sandy mudstones with intercalations of limestones.

Material and methods

The studied material comes from the prospections done in fifteen of the palaeomastological sites located during the realization of the doctoral thesis of V.D. Crespo (Crespo 2017) in the sections of Mas de Torner (MTR), Barranc de Campisano (BC), Foieta la Sarra (FS), Mas de Antolino B (MAB) and Corral de Brisca (CBR). The specific sites studied in this work are MTR2, BC1, FSA, MAB5, CBR0B, CBR0G, CBR1, CBR2, CBR3 and the surface area between MAB3 and MAB4 (MAB3–4) and between MAB6 and MAB9 (MAB6–9).

The molluscs were obtained by two different methods depending on their size. The larger ones were directly collected by hand from the sediment, while the smaller ones were obtained from the disaggregation of the sediment in a solution of H_2O, H_2O_2 and NaOH, subsequently sifted using a 0.5 mm mesh sieve and finally separated under a stereomicroscope.

Apart from a few completely preserved snails, many of the found specimens are available as fragments, moulds and impressions only, which complicated determinations at species level. The shell parameters were measured according to Ramos *et al.* (2000). The number of whorls was estimated beginning at the initial suture, following the method proposed by Solem (1976) and Burch (1982).

The photographs of the smallest specimens were taken with a Hitachi H-4100 scanning electron microscope at the Servei Central de Suport a la Investigació Experimental (SCSIE) in the University of València Estudi General (UVEG). The larger specimens were photographed with a Nikon D90 camera attached to a Sigma AF 105mm f/2.8 EX DG macro lens and using an image stacking procedure. The treatment of the images and the assemblage of the figures were made by combining the programmes Ligthroom CC v. 2015.0.0 and Photoshop CC v. 2015.12.

All the specimens studied have been deposited at the Museu de la Universitat de València d'Història Natural (MUVHN), fomerly Museu de Geologia de la Universitat de València (MGUV), in Burjassot (Valencian Community, Spain).

Systematic palaeontology

The systematic classification follows Bouchet *et al.* (2017) and MolluscaBase (2021).

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Littorinoidea Children, 1834
Family Pomatiidae Newton, 1891 (1828)

Genus *Pomatias* Studer, 1789

Type species. – *Neritina elegans* Müller, 1774. Recent, Europe.

***Pomatias conicus* (Klein, 1853)**
Figure 2A–H

1853 *Cyclostoma conicum*; Klein, p. 217, pl. 5, fig. 14.
1981 *Pomatias conica* (Klein) [sic]. – Lueger, p. 10, pl. 1, figs 11, 12, pl. 6, fig. 3.
2002 *Pomatias conicus* (Klein, 1853). – Harzhauser & Kowalke, p. 70, pl. 10, figs 6–8.
2004 *Pomatias conicum* (Klein 1853) [sic]. – Harzhauser & Binder, p. 7, pl.1, figs 7–11.
2015 *Pomatias conicus* (Klein, 1853). – Salvador *et al.*, p. 253, fig. 3a.
2017 *Pomatias conicus* (Klein, 1853). – Salvador & Rasser, fig. 2a–c.
2018 *Pomatias conicus* (Klein, 1853). – Höltke *et al.*, p. 21, figs 3, 4.

Material. – Five moulds from the surface area of MAB3–4 (MGUV-39033 to MGUV-39037); three moulds from the surface area of MAB6–9 (MGUV-39038); sixteen apexes from CBR0B (MGUV-39039); three incomplete specimens from CBR0B (MGUV-39040); one operculum from CBR0B (MGUV-39041); eleven apexes from CBR0G (MGUV-39042); two incomplete specimens from CBROG (MGUV-39043); thirty apexes from CBR1 (MGUV-39044); one apex from CBR1 (MGUV-39045); several shell fragments and operculum fragments from CBR0B, CBR0G and CBR1 (MGUV-39046, MGUV-39047 and MGUV-39048).

Description. – Moderately large shell, conical trochiform with up to four preserved convex whorls with deep suture in the specimens studied. Protoconch smooth and rounded, with 2 whorls, a maximum diameter of 1.3 mm and a nucleus 400 μm wide (MGUV-39045, Fig. 2E). Transition to teleoconch abrupt, being marked by the appearance of ornamentation consisting of up to 7 spiral ribs, separated by a distance greater than its width, which intertwine with denser and very weak axial growth lines (MGUV-39045, Fig. 2F). As the shell grows, the number and width of spiral ribs increases, reaching up to 14 in the proximity of the aperture, where they are separated by a space equivalent to their thickness (MGUV-39040, Fig. 2H). The axial growth lines also increase in thickness as the whorls advance, being the characteristic reticulated ornamentation much more visible. The last whorl is around 70% of the total height of the shell. Subcircular aperture with a slight angularity at the top; slightly thickened peristome. The operculum has three spiral growth lines and a slight convexity on its outer side.

Dimensions: The two most complete specimens have up to 4 whorls and measure (height × width) 12.1 mm × 8.2 mm (MGUV-39033, Fig. 2A, B) and 13.8 mm × 10 mm (MGUV-39035, Fig. 2C, D), respectively. The operculum (MGUV-39041, Fig. 2G) has (height × width) 5.8 mm × 4.8 mm.

Remarks. – The fossil record of the genus *Pomatias* dates back to the Oligocene (Harzhauser & Neubauer 2021). The studied specimens in MAB sites correspond to incomplete internal moulds, which makes the comparison with other species and its specific identification difficult. However, the CBR sites have provided an operculum, numerous apexes and shell fragments (including some containing the last whorl), which have allowed the study of both morphology and ornamentation of the protoconch and teleoconch as well as the shape of the aperture.

Our material differs from *Pomatias schrammeni* (Andreae, 1902) from the middle Miocene of Poland (Harzhauser & Neubauer 2018), which has a wider shell with a more convex profile of whorls and a less elevated spire, as well as a different pattern of the teleoconch's ornamentation, consisting on the progressive appearance of new spiral ribs between the initial ones. *Pomatias consobrinus* (Sandberger, 1875) from the middle Miocene of Germany, Hungary and Austria (Schlickum 1976, Kókay 2006, Salvador 2014, Höltke *et al.* 2018) has similar ornamentation to our specimens. However, it also has a more globular shape and a more convex profile of the last whorl (although to a lesser extent than the previous discussed species) as well as a lower spire. According to Harzhauser & Kowalke (2002), it also has an operculum with up to 5 spiral lines as opposed to the 3 found on the operculum located in CBR0B. The more elongated shape and moderately convex profile of the whorls is somewhat consistent with *Pomatias bisulcatus* (von Zieten, 1830) from the early Miocene of Poland (Stworcevicz 1995). However, *P. bisulcatus* differs in its larger size, the oval aperture and its greater proportion in height compared to the total shell's height. *Pomatias conicus* (Klein, 1853) of the middle and late Miocene of Central Europe (Klein 1853; Schlickum 1976; Harzhauser & Kowalke 2002; Harzhauser & Binder 2004; Kókay 2006; Salvador *et al.* 2015; Salvador & Rasser 2016a, b, 2017; Höltke *et al.* 2018) is morphologically similar. The protoconch is rounded, the convexity of the whorls marked, the sutures are deep, the general aspect trochiform and the ornamentation of the teleoconch is reticulated, as the typical characteristics of *P. conicus* according to Salvador *et al.* (2015). In addition, the morphology of the operculum is consistent with that described by Harzhauser & Kowalke (2002) and Lueger (1981) for *P. conicus*. For these reasons, we can assign our specimens to that species.

Ocurrence. – This species, originally described in the middle Miocene of Southwest Germany, has been located in several sites in both the middle and late Miocene of Central Europe (Klein 1853; Schlickum 1976; Harzhauser & Kowalke 2002; Harzhauser & Binder 2004; Kókay 2006; Salvador *et al.* 2015; Salvador & Rasser 2016a, b, 2017; Höltke *et al.* 2018).

Superfamily Truncatelloidea Gray, 1840
Family Hydrobiidae Stimpson, 1865
Subfamily Pseudamnicolinae Radoman, 1977

Genus *Pseudamnicola* Paulucci, 1878

Type species. – *Bythinia lucensis* Issel, 1866. Recent, Tuscany (Italy).

***Pseudamnicola roblesi* sp. nov.**
Figure 2I–R

LSID. urn:lsid:zoobank.org:act:CAA70CF0-8671-452A-B215-0EC51F926D44

? 2021 Hydrobiidae indet. – Álvarez-Parra *et al.*, fig. 3d–g.

Types. – Holotype: MGUV-39049: height 2.32 mm, width 1.45 mm (Fig. 2I, N, O, P). Paratypes: MGUV-39050: height 2.22 mm, width 1.39 mm (Fig. 2J); MGUV-39051: height 2.26 mm, width 1.48 mm (Fig. 2K); MGUV-39052: height 2.14 mm, width 1.44 mm (Fig. 2L); MGUV-39053: height 2.30 mm, width 1.43 mm (Fig. 2M).

Type horizon and locality. – Grey sandy mudstones of Unit C of sequence Ribesalbes of Ribesalbes-Alcora Basin (Anadón 1983), early Miocene, early Aragonian, MN4. Corral de Brisca 1 (Araia d'Alcora, Alcora, Spain) (40º 3′ 24.56″ N; 0º 17′ 47.14″ W).

Material. – Ninety six specimens from CBR1 (MGUV-39054); forty six specimens from CBR2 (MGUV-39055); four specimens from CBR3 (MGUV-39056); one specimen from CBR1 (MGUV-39057, Fig. 2Q); one specimen from CBR1 (MGUV-39058, Fig. 2R). Fifteen specimens from FSA-9A, FSA-15, FSA-28AB, FSA-31C, FSA-41, FSA-42ABC and FSA-44ABCD are housed, pending registration, at MUVHN, indicating the sample in which they are located.

Etymology. – Dedicated to Fernando Robles, molluscs palaeontologist at the University of Valencia and thesis supervisor of the first author.

Diagnosis. – Very small shell, ovate-conic with convex whorls and deep sutures, last whorl relatively inflated and equivalent about three-quarters of the total length. Aperture tear shaped, ovate angled at the top and often vertical outer lip. Peristome continuous and slightly reflected.

Description. – Very small shell, ovate-conic with 4.5 spire convex whorls with deep sutures. Protoconch paucispiral with 1.4 whorls, approximately 240 µm wide and a nucleus around 120 µm long; microsculpture slightly granulated and passage to the teleoconch defined by the appearance of growth lines (MGUV-39049, Fig. 2P and MGUV-39057,

Fig. 2Q). Teleoconch with sculpture of prosocline lines those sometimes become particularly visible on the last whorl, forming fine varicose ribs in the vicinity of the aperture (MGUV-39058, Fig. 3R). Last whorl relatively inflated and attaining about 75% of the total length. Aperture frontal, subvertical in lateral view (MGUV-3049, Fig. 2N), attaining about 50% of the total shell's height, oval tear shaped, angled at the top and often vertical outer lip. Peristome complete, something thickened and slightly reflected, sometimes coming to weld in the adapical region with the body of the last whorl and also cover part of the umbilicus, which is narrow and fissure-shaped.

Remarks. – Even considering that many of the species attributed to *Pseudamnicola* may not belong to this genus, many are those described in the Neogene of Europe. In contrast, no species has been described from the Iberian Peninsula. Moreover, the few existing Iberian records, all at genus level, correspond exclusively to the late Miocene of the Cabriel Basin (Lacomba *et al.* 1986, García Flor 1996, Robles *et al.* 1991, Montoya *et al.* 2006) and, with some doubts concerning the determination, to the Villarroya Basin (Rodríguez-Lázaro *et al.* 1997). Only García Flor (1996) included descriptions of specimens attributed to this genus. In addition to the age difference, the two species discussed by this author differ from our specimens in the general shape and the shape of the aperture. According to this author, *Pseudamnicola* sp. A, from the late Miocene of Venta del Moro, has a more staggered profile of the whorls and a thickened peristome that is progressively reflexed from the basal edge towards the columellar edge and covers the umbilicus to a greater extent than in our specimens. *Pseudamnicola* sp. B, from the early Pliocene of Fuente del Viso, has, in spite the variability in the expansion rate of the last whorl, a more conical shape and a proportionally larger last whorl. Likewise, it has an aperture with a very marked angle at the adapical edge.

The general morphology of our species is reminiscent of *Pseudamnicola messapica* Esu & Girotti, 2010 from the late Oligocene of Otranto (Italy). However, the Italian species has a less convex turn profile and shallower sutures, as well as a slightly larger and more globose last whorl, resulting in a more elongated overall shape. In addition, *P. messapica* has a smaller, non-reflexed aperture with a more pronounced upper angle.

The new species is also similar to the French species *Pseudamnicola turonensis* (Sandberger, 1872) from the early-middle Miocene of Manthelan and *Pseudamnicola gerannensis* Rey, 1974 from the early Miocene of Chavroche. Both, however, have a somewhat more voluminous and ventrose last whorl. In addition, *P. turonensis* has a shorter and externally rounder aperture, while *P. gerannensis* has a proportionally larger last whorl.

The specimens from the FSA site, consisting of fragments of molds and impressions and initially determined as Hydrobiidae indet. (Álvarez-Parra *et al.* 2021), may correspond to this new species.

Occurrence. – Known from the type locality (CBR1) and the sites CBR2, CBR3, and FSA. Early Miocene (early Aragonian, MN4).

Subclass Heterobranchia Burmeister, 1837
Superorder Hygrophila Férussac, 1822
Superfamily Lymnaeoidea Rafinesque, 1815
Family Lymnaeidae Rafinesque, 1815
Subfamily Lymnaeinae Rafinesque, 1815

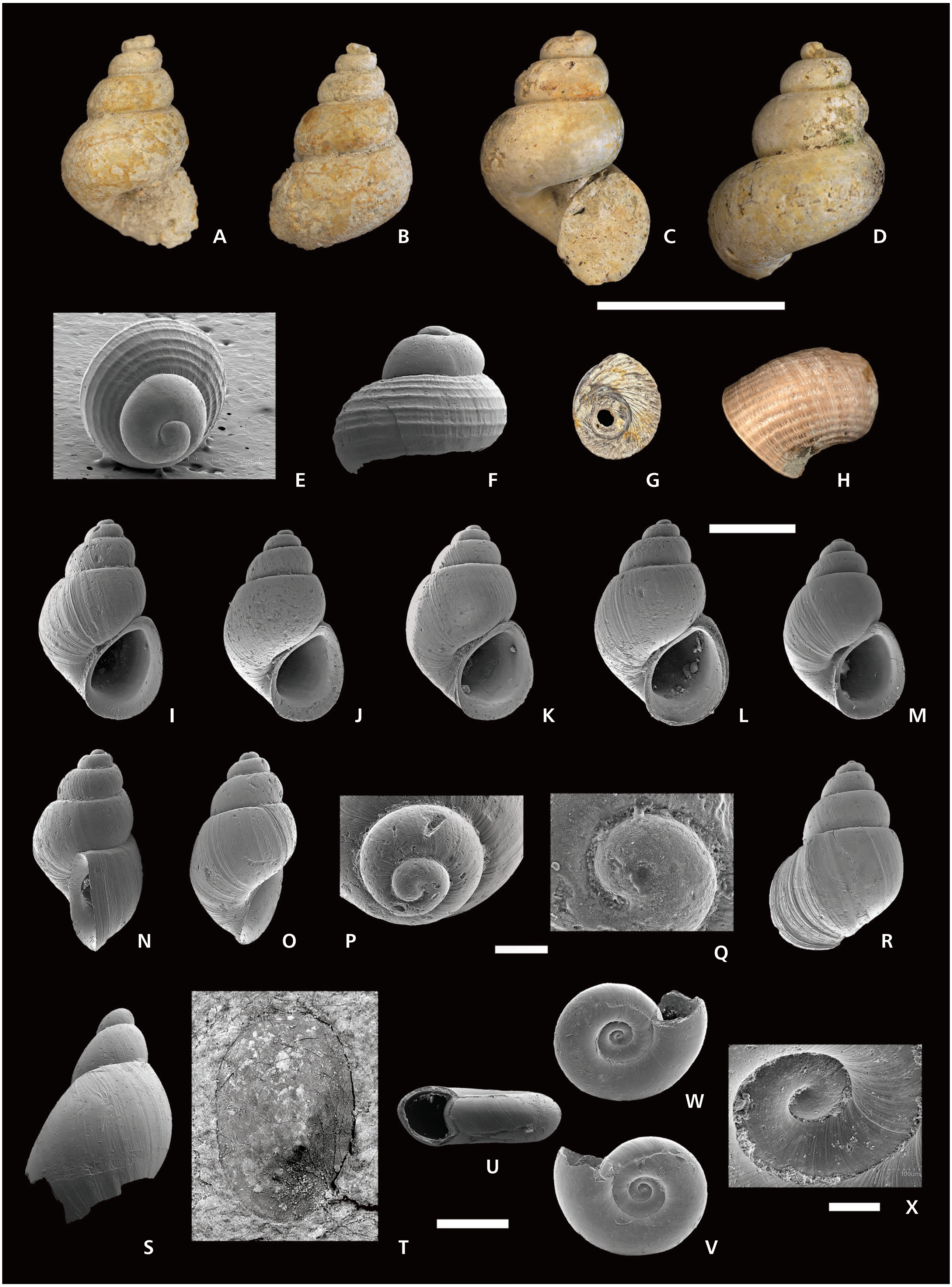
Genus *Stagnicola* Jeffreys, 1830

Type species. – *Lymnaea communis* Jeffreys, 1830 [= *Stagnicola palustris* (Müller, 1774)]. Recent, Europe.

Stagnicola cf. *armaniacensis* (Noulet, 1857)
Figure 2S

cf. 1857	*Limnea armaniacensis* nov. sp.; Noulet, p. 22.
cf. 2005	*S. armaniacensis* (Noulet, 1857). – Kowalke & Reichenbacher, p. 631, fig. 9.6, 9.7).
cf. 2014b	*Stagnicola armaniacensis* (Noulet 1857). – Harzhauser *et al.*, p. 11, pl. 2, figs 4–11.
cf. 2016	*Stagnicola armaniacensis* (Noulet, 1857). – Salvador *et al.*, p. 12, fig. 5b.
cf. 2021	Lymnaeidae indet. – Álvarez-Parra *et al.*, fig. 3d–g.

Figure 2. A–H – *Pomatias* cf. *conicus* (Klein, 1853); (A) frontal and (B) dorsal views of specimen MGUV-39033 from MAB3–6; (C) frontal and (D) dorsal views of specimen MGUV-39035 from MAB6–9; (E, F) apex-protoconch views of specimen MGUV-39045 from CBR1; (G) external side of operculum MGUV-39041 from CBR0B; (H) body whorl fragment of MGUV-39040 from CBR0B. • I –R – *Pseudamnicola roblesi* sp. nov.; (I) frontal view of holotype MGUV-39049 from CBR1; (J) paratype MGUV-39050 from CBR1; (K) paratype MGUV-39051 from CBR1; (L) paratype MGUV-39052 from CBR1; (M) paratype MGUV-39053 from CBR1; (N) lateral right view of holotype MGUV-39049 from CBR1; (O) lateral left view of holotype MGUV-39049 from CBR1; (P) protoconh of holotype MGUV-39049 from CBR1; (Q) protoconch ornamentation of specimen MGUV-39057 from CBR1; (R) dorsal view of specimen MGUV-39058 from CBR1. • S– *Stagnicola* cf. *armaniacensis* (Noulet, 1857), specimen MGUV-39060 from MTR2. • T – *Ferrissia* cf. *deperdita* (Desmarest, 1814), specimen from FSA. • U–X – *Gyraulus kleini* (Gottschick & Wenz 1916); (U) frontal, (V) umbilical, (W) apical and (X) protoconch view of specimen MGUV-39068 from CBR1. Scale bars equal 10 mm (A–H), 1 mm (I–O, R–W), 100 µm (P, X) and 50 µm (Q).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Material. – Only fragments and juvenile shells have been found: thirty specimens from MTR2 (MGUV-39059); one specimen from MTR2 (MGUV-39060, Fig. 2S); five specimens from BC1 (MGUV-39061); seven specimens from FSA-2, FSA-10, FSA-12, FSA28AB, FSA-39AB and FSA-40 are housed, pending registration, at the MUVHN, indicating the sample in which they are located; ten specimens from CBR1 (MGUV-39062); one specimen from CBR1 (MGUV-39063).

Description. – Slender elongate shell with up to 4 preserved whorls in the largest specimen. Protoconch smooth, bulbous with invisible transition to the teleoconch. Preserved whorls of teleoconch moderately convex and deep sutures. Sculpture of prosoclines lines. Last whorl of rapid growth, relatively wide and with growth constriction lines at the vicinity of the aperture. Aperture not preserved.

Dimensions: One of the more complete specimens from MTR2 (MGUV-39060) measures (height × width) 3.04 × 1.92 mm (Fig. 2S); juvenile specimen from FSA (FSA-28AB, pending registration at the MUVHN) measures 6.7 × 3.7 mm (Álvarez-Parra *et al.* 2021, fig. 3d–g).

Remarks. – Vilanova y Piera (1859) mentioned the presence of "Lymnaeas" in several areas of the province of Castellón, including the "Balsa de Fanzara" (classical name for the Cenozoic sediments of the Ribesalbes-Alcora Basin). The figure presented by Vilanova y Piera and determined as *Lymnaea palustris* Grateloup, 1828 [= *Stagnicola palustris* (Müller, 1774)] corresponds to a specimen from a nearby area. Lymnaeidae are generally characterized by a high degree of morphological variability (Vinarski 2013), which has led to an enormous inflation of species names in the palaeontological literature [*e.g*. see Harzhauser *et al.* 2014b for *Stagnicola armaniacensis* (Noulet, 1857) and Neubauer *et al.* 2017 for *Stagnicola palustriformis* (Gottschick, 1911)]. In addition, our specimens are only fragments of the first whorls, which make it even more difficult to determine at species level. They differ from *Stagnicola palustriformis* from the middle Miocene of Germany by the width and convexity of the whorls, being both smaller in that species and presenting, consequently, a more elongated aspect. *Stagnicola praebouilleti* Schlickum, 1970 from the early Miocene of the Molasse Basin (Burdigalian) has an even more elongated morphology, with even less wider and convex whorls. *Stagnicola subpalustris* (Thomä, 1845) from the early Miocene of the Mainz Basin (late Aquitanian–early Burdigalian) and *Stagnicola reinholdkunzi* Harzhauser & Neubauer, 2012 *in* Harzhauser *et al.* (2012) from the middle Miocene of the Aflenz Basin (Langhian) have some wider and more convex whorls. The combination of morphological characters observed in the larger specimens of MTR2, particularly the shape of the protoconch and the width and degree of convexity of the preserved whorls, are consistent with *Stagnicola armaniacensis*. The juvenile specimen and the fragments of the last whorl from FSA are also consistent in shape and size with this species. *Stagnicola armaniacensis* was described from the early–middle Miocene of France (late Burdigalian–Langhian) and occurs in many early to the middle Miocene European sites (Noulet 1857, Bourguignat 1881, Kowalke & Reichenbacher 2005, Harzhauser *et al.* 2014b, Salvador *et al.* 2016). Our specimens show enormous similarities with the Enzenbach specimen from the Rein Basin (early Langhian) figured by Harzhauser *et al.* (2014b) as well as with the Molasse Basin (Burdigalian) specimen figured by Salvador *et al.* (2016). In spite of some doubts because of the poor preservation, we tentatively attribute them to the same species.

Occurrence. – Recorded from the middle Miocene of Sansan in France (Noulet 1857, Bourguignat 1881), Silvana-Beds in South Germany and Switzerland (Sandberger 1875, Kowalke & Reichenbacher 2005, Salvador *et al.* 2016), Rein Basin and Graz Basin in Austria (Harzhauser *et al.* 2014b).

Family Planorbidae Rafinesque, 1815
Subfamily Ancylinae Rafinesque, 1815

Genus *Ferrissia* Walker, 1903

Type species. – Ancylus rivularis Say, 1817. Recent, North America.

Ferrissia cf. *deperdita* (Desmarest, 1814)

Figure 2T

cf. 1814 *Ancylus deperditus*; Desmarest, p. 19, pl. 1, fig. 14.
cf. 2014b *Ferrissia deperdita* (Desmarest 1814). – Harzhauser *et al.*, p. 17, pl. 5, figs 1, 2, 5, 12.
cf. 2017 *Ferrissia deperdita* (Desmarest, 1814). – Neubauer *et al.*, p. 736, fig. 3j, k, q.
cf. 2018 *Ferrissia deperdita* (Desmarest, 1814). – Harzhauser & Neubauer, p. 83, fig. 4b.

Material. – Forty-one specimens from FSA-2, FSA-8AB, FSA-11, FSA-13A, FSA-15, FSA-16, FSA-21AC, FSA-26, FSA-30AD, FSA-31C, FSA-37, FSA-38AB, FSA-39AB, FSA-41, FSA-43ABC and FSA-44ABC are housed, pending registration, at the MUVHN, indicating the sample in which they are located.

Description. – Limpet with an elliptical basal outline. Anterior shell portion is slightly broader and convex. Nearly straight or slightly convex flanks, posterior part convex. Apex slightly deflected to the right. In lateral view, the posterior portion is slightly concave and the anterior portion weakly convex. Poorly preserved ornamentation, with only a few visible growth lines.

Dimensions: Largest specimen (FSA-16-1) measures (length x width) 5.90 × 3.89 mm. Others specimens have 5.32 × 3.7 mm (FSA-16-3) and 5.28 × 3.65 mm (FSA-13A-1).

Remarks. – The specimens detected in FSA represent moulds and impressions, which complicate the determination on the species level. The specimens from middle Miocene *F. illyrica* (Neumayr, 1880) from the Dinaride System Lake (Neubauer *et al.* 2011, 2013a, 2016a) differs by its narrower contour. The early–middle Miocene *F. wittmanni* (Schlickum, 1964) from southern Germany and Austria (Harzhauser & Kowalke 2002, Kowalke & Reichenbacher 2005, Harzhauser *et al.* 2014b) also has a narrower profile as well as concave flanks and a cup-shaped apex. The late Miocene *F. truci* Wautier, 1975 from France (Wautier 1975) differs by having a more elongated contour and a apical region with a rounded apex located far back and strongly inclined to the right. The shape of the shell of our specimens is particularly similar to that of *F. deperdita* (Desmarest, 1814), a common species in the middle Miocene of Central Europe (Kókay 2006, Harzhauser *et al.* 2014b, Salvador *et al.* 2015, Salvador & Rasser 2016b, Neubauer *et al.* 2017, Harzhauser & Neubauer 2018). However, the general degree of preservation, and particularly of the ornamentation, prevents us from assigning the specimens to this species.

Occurrence. – Reported from several localities from the middle Miocene of Austria, southern France (Rhône Basin), southern Germany, Hungary, Poland, Serbia and Switzerland (Wenz 1923, Kókay 2006, Harzhauser *et al.* 2014b, Salvador & Rasser 2014, Salvador *et al.* 2015, Salvador & Rasser 2016b, Neubauer *et al.* 2017, Harzhauser & Neubauer 2018).

Subfamily Planorbinae Rafinesque, 1815

Genus *Gyraulus* Charpentier, 1837

Type species. – *Planorbis albus* Müller, 1774. Recent, Europe.

Gyraulus kleini (Gottschick & Wenz, 1916)

Figure 2U–X

1916 *Gyraulus multiformis kleini* n. (= *laevis* Klein.); Gottschick & Wenz, p. 101.
2014b *Gyraulus kleini* (Gottschick & Wenz, 1916). – Harzhauser *et al.*, p. 12, pl. 3, figs 1–4, 6, 14.
2015 *Gyraulus kleini* (Gottschick & Wenz, 1916). – Salvador *et al.*, p. 256, fig. 3d–f.
2017 *Gyraulus kleini* (Gottschick & Wenz 1916). – Neubauer *et al.*, p. 738, fig. 3f, i, l–o.

Material. – Eight specimens from MTR2 (MGUV-39064); seventy one moulds or from FSA-2, FSA-4, FSA-6, FSA-7AB, FSA-8AB, FSA-9E, FSA-10, FSA-12, FSA-13A, FSA-16, FSA-17, FSA-18AB, FSA-21AD, FSA-28AB, FSA-33C, FSA-35AB, FSA-38AB, FSA-41, FSA-42ABC, FSA-43ABC and FSA-44ABCD are housed, pending registration, at the MUVHN, indicating the sample in which they are located; twelve specimens from CBR0B (MGUV-39065); thirty five specimens from CBR0G (MGUV-39066); forty specimens from CBR1 (MGUV-39067); one specimen from CBR1 (MGUV-39068, Figs. 2U-X); seventy nine specimens from CBR2 (MGUV-39069); eighty specimens from CBR3 (MGUV-39070).

Description. – Small, planispiral shell with up to 4 whorls which increase rapidly in diameter. Upper and lower sides concave, slightly more apically, with initial whorls depressed respect to last whorl. Protoconch consisting of 1.5 whorls with spiral striae, not very pronounced, and with transition to teleoconch marked by the emergence of growth lines (MGUV-3068, Fig. 2X). Teleoconch with convex whorls separated by deep sutures and having more or less symmetrical profile, although some specimens show a slight asymmetry. Ornamentation consisting of growth lines, which are prosocline on umbilical side and prosocyrt on apical side. Aperture approximately as high as wide.

Dimensions: The largest specimen from FSA (FSA-42AB-1) has a maximum diameter of 5.18 mm. One of the largest specimen from CBR1 (MGUV-39068) has a diameter of 1.9 mm.

Remarks. – Some of the species of the genus *Gyraulus* are characterised by great morphological plasticity, which makes them difficult to determine (see Harzhauser *et al.* 2014a). The specimens collected by us at Campisano Ravine are characterised by the absence of a keel or angularity, an aspect that clearly differentiates them of many species from the European early and middle Miocene. *Gyraulus goussardianus* (Noulet, 1854) (*sensu* Fischer 2000) from the middle Miocene (Langhian) of Sansan (France) has a pronounced central keel, whereas *Gyraulus ludovici* (Noulet, 1854), from the same locality, has the keel in the adapical part. *Gyraulus applanatus* (Thomä, 1845) from the early Miocene of the Mainz Basin (Germany) shows a clear adapical angularity, as well as flatter apical and umbilical sides and a slower growth pattern. *Gyraulus albertanus* (Clessin, 1877) from the middle Miocene of the Molasse Basin (Germany) has more convex whorls and a greater circular aperture as a consequence of its more inflated profile. *Gyraulus dealbatus* Braun, 1851 *in* Walchner (1851), from the early Miocene of the Mainz Basin (Germany), has, according to Harzhauser *et al.* (2014a), a variable ontogeny-dependent profile, being very convex due to a last whorl clearly larger than the preceding ones, resulting in a relatively depressed apical and umbilical concavity. As a consequence of the allometric development in the final stages of ontogeny, the last whorl grows more in width than in height, generating a wider shell. On the other hand, Harzhauser *et al.* (2014b), following Gottschick (1920) and Nützel & Bandel (1993), point out the greater width of *G. dealbatus* in comparison with *G. kleini*, while highlighting the existence of a clear adapical angulation in the later stages of ontogeny. This also occurs in *Gyraulus krohi* Neubauer & Harzhauser, 2014 *in* Harzhauser *et al.* (2014b) from the Rein Basin (Austria), a species that also shows differences in the aperture, which is inclined, wider than high and elliptical in shape. The morphology of our juvenile or incomplete specimens closely resembles the description of young specimens of *G. dealbatus*. However, the larger specimens do not exhibit the growth in width mentioned above and the aperture remains with a similar height and width. Neither do they show, except very faintly in some specimens, the adapical angularity that characterises some of the adult specimens of *G. dealbatus*. The description of Harzhauser *et al.* (2014b) of *Gyraulus kleini* (Gottschick & Wenz, 1916) from the middle Miocene of the Rein Basin (Austria) is consistent with the morphology observed in our specimens. Also, the juvenile specimens from Vračević figured in Neubauer *et al.* (2017) bear a strong resemblance to ours.

Occurrence. – Recorded from several early and middle Miocene sites in Austria, Czech Republic, Germany, Hungary, Poland, Serbia, Switzerland and Ukraine (Wenz 1923, Gozhik & Prysjazhnjuk 1978, Piechocki 1997, Kókay 2006, Harzhauser *et al.* 2014b, Salvador *et al.* 2015, Neubauer *et al.* 2017).

Superorder Eupulmonata Haszprunar & Huber, 1990
Order Stylommatophora Schmidt, 1855
Suborder Helicina Rafinesque, 1815
Infraorder Oleacinoidei
Superfamily Oleacionoidea H. Adams & A. Adams, 1855
Family Oleacinidae H. Adams & A. Adams, 1855

Genus *Palaeoglandina* Wenz, 1914 *in* Fischer & Wenz (1914)

Type species. – *Limnaea gracilis* von Zieten, 1832. Miocene, Germany.

Palaeoglandina sp.
Figure 3A–D

Material. – Two incomplete specimens from surface of MAB3–4 (MGUV-39071, Fig. 3A, B and MGUV-39072, Fig. 3C, D); three body whorl fragments from MAB6–9 (MGUV-39073).

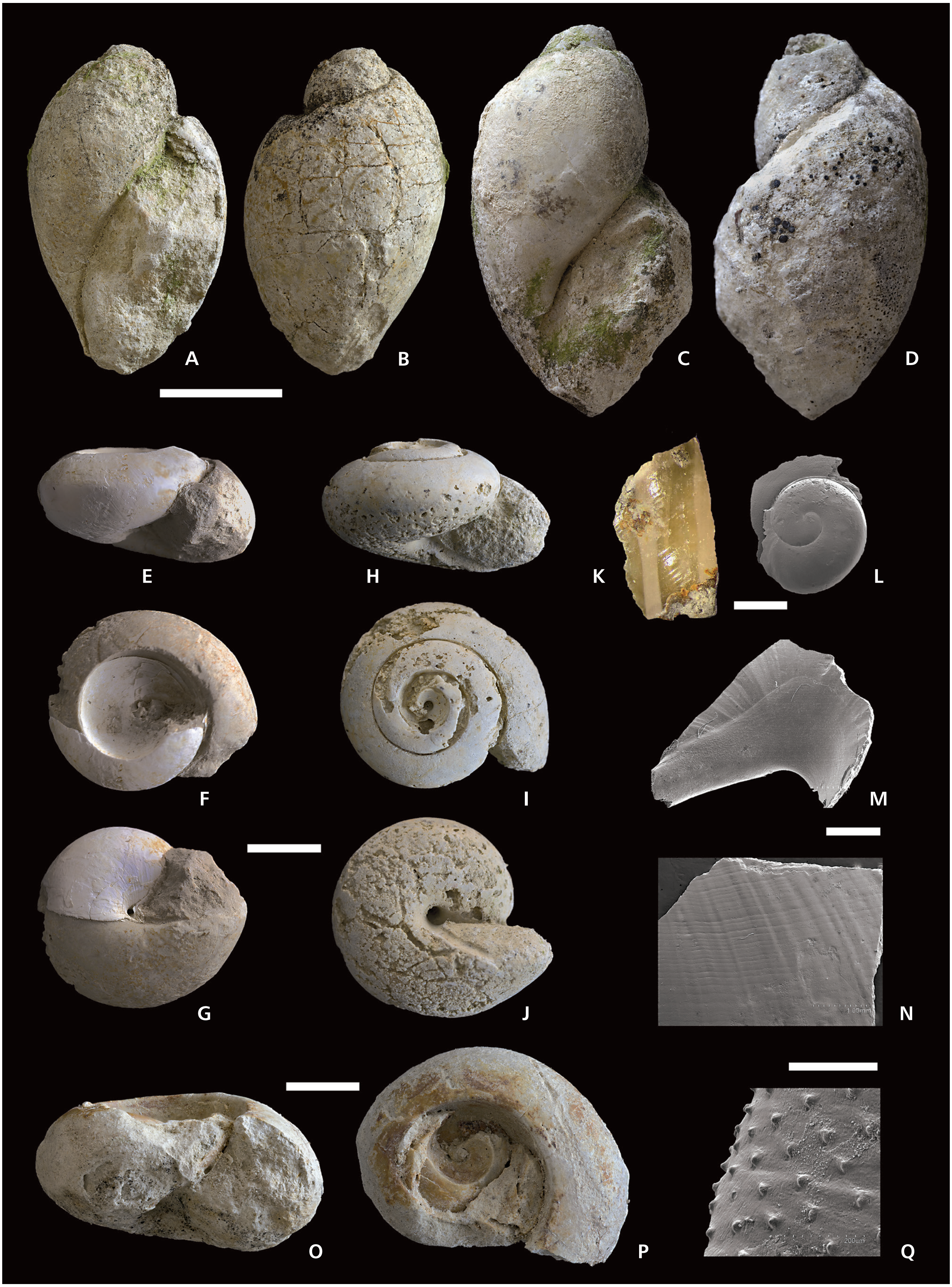
Description. – Large shell, moderately broad, fusiform, with bulbous apex and short spire and the last whorl of rapid growth. Elongated oval aperture poorly preserved.

Dimensions: The largest specimens (incomplete) have maximum dimensions (height × width) of 3.3 × 2 cm (MGUV-39071) and 2.8 × 1.8 cm (MGUV-39072).

Remarks. – The poor preservation and incompleteness of the specimens from MAB sites complicate the determination. However, the large size, the characteristical fusiform morphology, the length of the spire and the growth pattern of the last whorl suggest that the specimens should be attributed to the genus *Palaeoglandina*. This genus has a stratigraphic range from the Paleocene to the early Pleistocene (Esu *et al.* 1993, Harzhauser & Neubauer 2021).

Our material is similar to some of the Eocene species. *Palaeoglandina naudotii* (Michelin, 1832) from the Lutetian of the Paris Basin has a similar ratio between the last whorl's height and the total shell's height. However, in besides to being older, the French species has a more fusiform aspect as a consequence of having a lower ratio between the total width and the total height of the shell. The Priabonian species *Palaeoglandina alpina* (d'Orbigny, 1850) from Saint-André-de-Méouille (Alpes-de-Haute-Provence, France) has a similar ratio between the total width and the total height of the shell, but it has a lower ratio between the last whorl's height and the total shell's height. Among the species cited in the early and middle Miocene, our specimens differ from the early Miocene (Ottnangian) *Palaeoglandina dactylina* Binder, 2004 from Oberdorf (Steiermark, Austria) by the lesser convexity and

Figure 3. A–D – *Palaeoglandina* sp.; (A) frontal and (B) dorsal views of specimen MGUV-39071 from MAB3–4; (C) frontal and (D) dorsal views of specimen MGUV-39072 from MAB3–4. • E–N – *Palaeotachea* sp.; (E) frontal, (F) apical and (G) umbilical views of specimen MGUV-39074 from MAB3–4; (H) frontal, (I) apical and (J) umbilical views of specimen MGUV-39079 from MAB6–9; (K) fragment with coloured bands of specimen MGUV-39090 from CBR0B; (L) protoconch of specimen MGUV-39091 from MTR2; (M) fragment of peristome of specimen MGUV-39092 from MTR2; (N) fragment with reticulated ornamentation of specimen MGUV-39093 from MAB5. • O–Q – Klikiinae gen. et sp. indet.; (O) frontal and (P) views of specimen MGUV-39101 from MAB3–4; (Q) fragment with ornamentation of specimen MGUV-390102 from MAB5. Scale bars equal 10 mm (A–D), 5 mm (E–J, O, P), 1 mm (K–N) and 200 μm (Q).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width of last whorl that characterize this species, which gives it a more fusiform aspect than those located in MAB. *Palaeoglandina gracilis* (von Zieten, 1832), originally described from early Miocene of Ulm (Germany) and also located in others sites of Czech Republic, France, Germany and Switzerland (Wenz 1923, Harzhauser *et al.* 2014a), has a high spire and a less convex last whorl which also gives it a more fusiform appearance. Nevertheless, according to Harzhauser *et al.* (2014b), *P. gracilis* shows a variability that could allow us to attribute our material to this species. However, the degree of preservation does not allow a clear identification on the species level.

Infraorder Helicoidei
Superfamily Helicoidea Rafinesque, 1815
Family Helicidae Rafinesque, 1815
Subfamily Helicinae Rafinesque, 1815

Genus *Palaeotachea* Jooss, 1812

Type species. – *Helix crepidostoma* Sandberger, 1872.

***Palaeotachea* sp.**
Figure 3E–N

Material. – Five incomplete moulds from surface of MAB3–4 (MGUV-39074, Fig. 3E–G to MGUV-39078); eleven incomplete moulds from surface of MAB6–9 (MGUV-39079, Fig. 3H–J to MGUV-39089); one fragment with coloured bands from CBR0B (MGUV-39090, Fig. 3K); one protoconch from MTR2 (MGUV-39091, Fig. 3L); one fragment of the peristome from MTR2 (MGUV-39092, Fig. 3M); one fragment with reticulated ornamentation from MAB5 (MGUV-39093, Fig. 3N); several fragments, including apex and portions of whorls and aperture, from MTR2 (MGUV-39094), BC1 (MGUV-39095), MAB5 (MGUV-39096); CBR0B (MGUV-39097); CBR0G (MGUV-39098); CBR1 (MGUV-39099) and CBR2 (MGUV-39100).

Description. – Medium-sized shell, with up to about 4 preserved whorls. Protoconch flattened, smooth, with about 1.5 whorls and a poorly defined transition to teleoconch (MGUV-39091, Fig. 3L). Teleoconch with convex whorls, slow and regular growth, moderately deep sutures and ornamentation based on prosocline growth striae and spiral lines (MGUV-39093, Fig. 3N) as well as spiral bands of colouration (MGUV-39090, Fig. 3K). Last whorl slightly angular with a faint keel in smaller specimens. Peristome slightly thickened and reflexed. Umbilicus narrow and covered by the reflexion of the peristome.

Dimensions: The two largest specimens have diameters of 15.1 mm (MGUV-39074, Fig. 3C–E) and 14.7 mm (MGUV-39079, Fig. 3F–H), respectively.

Remarks. – The specimens found are mainly internal moulds with only a few shell fragments adhering to them. The general shape, the whorls' growth pattern and dimensions are compatible with some genera of the families Hygromiidae and Helicidae. However, the anomnphalous character of our specimens (MGUV-39092, Fig. 3M) suggests their attribution to the family helicidae. In addition, the reticulate ornamentation shown by some of the fragments (MGUV-39093, Fig. 3N), typical of the genus *Palaeotachea* according Nordsieck (2014), focuses the determination on this genus. *Palaeotachea* contains both large and medium-sized species (see Höltke & Rasser 2016). Within the medium-sized species, the specimens from Campisano Ravine differ from older species such as *Palaeotachea convexitesta* (Jooss, 1912) from the early Oligocene of Germany (Salvador *et al.* 2016) and *Palaeotachea subglobosa* (Grateloup, 1828) from the late Oligocene and early Miocene (MN1) of Germany (Schäfer & Kadolsky 2015) by having a more globular shape and a thicker peristome than the one observed in the fragments studied by us. Our specimens resemble to two middle Miocene (MN5) species from Germany, *Palaeotachea dentula* (Quenstedt, 1867) (Höltke & Rasser 2016) and *Palaeotachea renevieri* (Maillard, 1892) (Salvador *et al.* 2016). Höltke & Rasser (2016) differentiate these two species on the basis of, among others, the morphology of the peristome and the convexity of the last whorl. Although the indicators they provide are objective, the incomplete reconstruction of the peristome from the studied fragments complicates the comparison between these two especies and suggests determining the specimens as *Palaeotachea* sp.

Family Elonidae Gittenberger, 1979
Subfamily Klikiinae Nordsieck, 1986

Klikiinae gen. et sp. indet.
Figure 3O–Q

Material. – One incomplete mould from MAB3–4 (MGUV-39101, Fig. 3O, P); one fragment of MAB5 (MGUV-39102, Fig. 3Q); **s**ome fragments of MAB5 (MGUV-39103).

Description. – Medium-large shell. Teleoconch with convex whorls, slow and regular growth and ornamentation formed by dense papillae (MGUV-39102, Fig. 3Q). Peristome moderately thickened and reflexed.

Dimensions: The single mould found has a diameter of 24.1 mm.

Remarks. – The only specimen found is a mould on which the high degree of convexity of the last whorl preserved and the existence of a wide umbilicus are barely visible. Hovewer, the MAB5 site has provided teleoconch fragments with abundant papillae. The presence of papillae and their particular arrangement and morphology, together with certain characteristics of the peristome, are generally typical of the family Elonidae (see Binder 2002, 2004, 2008, 2017; Harzhauser & Binder 2004). Several fragments studied contain portions of the peristome that show moderate thickening and strong reflection. This is compatible with the existence of an extralabial depression, a character observed by the previously mentioned authors in several species of various genera from the above mentioned family. The papillary pattern observed in our specimens, with a dense and equidistant arrangement of small button-shaped papillae (Fig. 3Q), differs from that of the genera *Papillotopsis*, where the papillae are teardrop-shaped (Binder 2017) and *Tropidomphalus*, where the papillae are oval and lodged within small grooves (Binder 2008). The papillary pattern of the MAB5 fragments is similar to that observed by Harzhauser & Binder (2004) and by Binder (2008) in some species of the genera *Apula*, *Klikia* and *Pseudochloritis*, which suggests placement within the Klikiinae.

Discussion

Faunal composition and ecological requirements

The studied fauna is made up of eight gastropod species, four of which are aquatic and the other four terrestrial. Many of the remains are in a poor state of preservation, being moulds, impressions, fragments or incomplete specimens. Only the specimens of *Pseudamnicola roblesi* sp. nov. and, to a lesser extent, *Gyraulus kleini* are well preserved and could be clearly determined at a specific level together with *Pomatias conicus*. However, the set of preserved features has allowed, albeit with doubts, determinations also at specific level in two other taxa (*Stagnicola* cf. *armaniacensis* and *Ferrissia* cf. *deperdita*) and at genus level in another two (*Palaeoglandina* sp. and *Palaeolotachea* sp.). One taxon, Klikiinae gen. et sp. indet., could only be determined at subfamily level. Although the number of species is small, they belong to seven different families. However, this number summarizes the entire diversity across all the studied samples, while the local diversity per site is lower in most cases (Tab. 1).

The extant representatives of the genera, to which the aquatic pulmonate species *Stagnicola* cf. *armaniacensis*, *Ferrissia* cf. *deperdita* and *Gyraulus kleini* belong live in oligohaline waters, quiet or with weak current, shallow depth and abundant macrophyte vegetation (Adam 1960, Økland 1990, Glöer 2002, Welter-Schultes 2012). *Stagnicola* and *Gyraulus* are also characterised by their ability to withstand periods of desiccation, inhabiting temporary water bodies (Welter-Schultes 2012) and, in the case of *Stagnicola*, flood plains (Fechter & Falkner 1993). *Ferrissia californica* (Rowell, 1863), the single holartic

Table 1. Species located, numbers of specimens and species richness, in the studied sites in the Campisano Ravine. Abbreviations: Frag – fragments; Op – operculum.

	MTR2	BC1	FSA	MAB3–4	MAB5	MAB6–9	CBR0B	CBR0G	CBR1	CBR2	CBR3
Pomatias conicus				5		3	19 Frag 1 Op	13 Frag	31 Frag		
Pseudamnicola roblesi			15						103	46	4
Stagnicola. cf. *armaniacensis*	31	5	7						10		
Ferrissia cf. *deperdita*			41								
Gyraulus kleini	8		71				12	35	41	79	80
Palaeoglandina sp.				2		3					
Palaeotachea sp.	1 Frag	Frag		5	Frag	11	Frag	Frag	Frag	Frag	
Klikiinae gen. et sp. indet.				1	Frag						
Species richness	3	2	4	4	2	3	3	3	5	3	2

species of the genus that habite in Europa (Vinarski & Palatov 2018), has an invasive taxon that often lives among the stems of aquatic vegetation, as well as attached to the undersides of the leaves of the reed belts that grow on the banks of water bodies (Fechter & Falkner 1993, Glöer 2002). However, given the high ecological tolerance of this species, it is found in a variety of habitats (Vecchioni *et al.* 2017). This species also shows little sensitivity to water quality (Glöer 2002), so it can resist eutrophic waters (Van der Velde 1991). The fourth aquatic species identified, *Pseudamnicola roblesi* sp. nov., is an aquatic prosobranch whose extant relatives live in springs, ditches and small permanent watercourses, but also in lakes and rivers (Delicado 2013). Some extant representatives of the family, to which this species belongs (e.g. *Hydrobia* and *Mercuria*), are able to inhabit mesohaline waters (Adam 1960).

Regarding terrestrial species, only *Pomatias conicus* belongs to a genus with extant representatives, which inhabit open forests and thickets on calcareous and humid soils, but being able to withstand dry periods thanks to its calcareous operculum (Martínez-Ortí & Robles 2005, Welter-Schultes 2012). The other three species (*Palaeoglandina* sp., *Palaeotachea* sp. and Klikiinae gen. et sp. indet.) are extinct taxa. As for the genus *Palaeoglandina*, extant Oleacinidae live mostly in warm tropical and subtropical environments (Fechter & Falkner 1993, Welter-Schultes 2012), being the genus *Palaeoglandina* usually associated with relatively humid and warm conditions (Montoya *et al.* 1999). The ecological requirements of the genus *Palaeotachea* are not known, but according to Salvador *et al.* (2016) representatives of the genus may have lived in a rather broad range of well vegetated habitats and climatic conditions, ranging from humid, warm-temperate to subtropical. Concerning Klikiinae, *Apula*, *Klikia* and *Pseudochloritis*, they are extinct genera, and their ecological requirements are uncertain. According to Binder (2004), the presence of papillae on the surface of some genera indicates moist conditions. However, the inferences made for the three genera are ambiguous. Acording to Harzhauser & Binder (2004) and Harzhauser *et al.* (2014a, b), Miocene species of *Apula* prefer humid forest environments as well as some species of *Klikia*, which would have a preference for subtropical forests (Lueger 1981, Binder 2004). However, according to Binder (2008), Höltke & Rasser (2013) and Salvador *et al.* (2016), *Pseudochloritis* species would have a preference for open habitats and warm, dry climatic conditions while, according to Binder (2017), they would prefer forests and warm, humid conditions.

Palaeoenvironmental reconstruction

Despite the small number of species, the composition and state of preservation of the assemblages recorded in each one of the studied sites shows the existence of different depositional environments, making it possible to do various inferences to reconstruct the palaeoenvironment (Tab. 1, Fig. 4). The sites corresponding to the lower (MTR2, BC1) and upper part (CBR0B, CBR0G, CBR1–3) of the Campisano Ravine section present both aquatic and terrestrial species while those located in the middle part of section contain only aquatic (FSA) or terrestrial species (MAB3–4, MAB5 and MAB6–9).

The MTR2 and BC1 sites have yielded abundant *Palaeotachea* sp. fragments with variable degrees of surface alteration. Fragmentation and surface alteration are criteria that provide information about the possible transport and exposure of the remains (López-Sancho *et al.* 1984). The fragments located in these sites, unconnected and with largely worn edges, suggest a considerable transport. The surface alteration, mainly corrosive, is evidence of relatively prolonged exposure prior to burial. The particularly small size of the fragments, the presence of quartz grains and some larger clasts, as well as the location of reptile and small mammal teeth with signs of transport, could be compatible with a more energetic transport in BC1 than in MTR2. The two sites also contain apices and the first whorl fragments of *Stagnicola* cf. *armaniacensis*, being more abundant in MTR2. The broad range of habitats in which *Stagnicola* can be found due to its ability to withstand long periods of desiccation, alongside the fragmentation and surface alteration of *Palaeotachea* shells, would be compatible with both a floodplain and a lake-edge depositional environment subject to temporary desiccation. The absence of detailed sedimentological studies prevents us from selecting one of the two.

The presence of some *Gyraulus kleini* in MTR2, together with the greater abundance of *Stagnicola* cf. *armaniacensis*, suggests a closer proximity to the lake than in the case of BC1, and may even be located at the very shore of the lake. The intercalation of loams with different shades in the deposits could be due to variations in the time of exposure of the sediments (Crespo *et al.* 2019a), consistent with the inferred depositional environments. The presence of *Palaeotachea* sp. in MTR2 and BC1 provides little information given the wide range of habitats it may occupy (Salvador *et al.* 2016). However, its presence is compatible with open spaces, as suggested in BC1 by the presence of the soricid genus *Paenelimnoecus* (Crespo *et al.* 2019b), some of whose species, according to Popov (2003), might prefer open habitats. This interpretation is also supported by the presence of pikas from the genus *Lagopsis* in both sites (Crespo *et al.* 2019a, 2022), a genus that, according to Ge *et al.* (2013), indicates the existence of dry and, consequently, more open environments.

The FSA site has been studied in detail by Álvarez-Parra *et al.* (2021), who qualified it as a Konservat-Lagerstätte and highlighted the possibility of being a meromictic lake

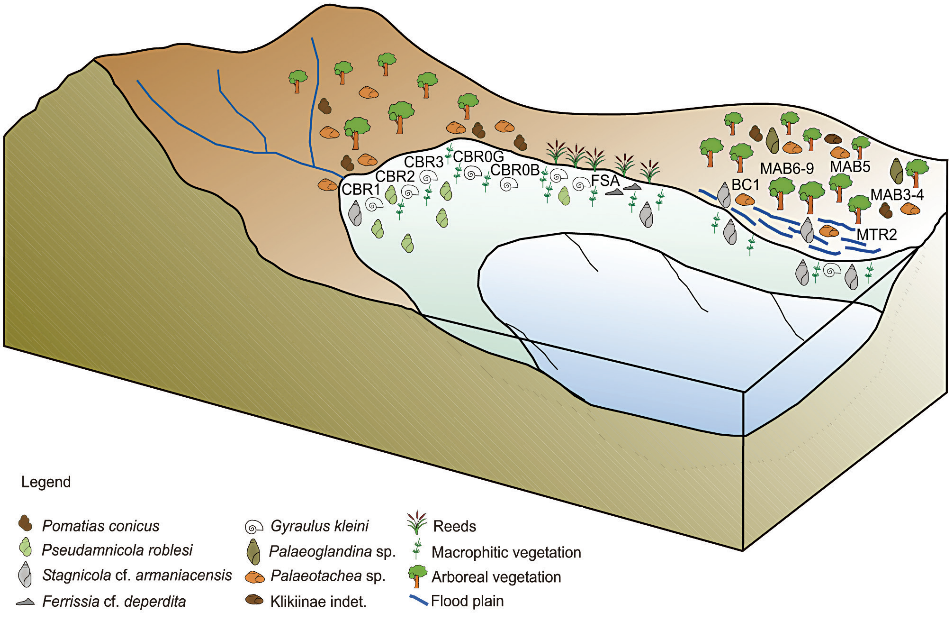

Figure 4. Palaeoenvironmental reconstruction with the location of sites and distribution of molluscs.

with high salinity levels at the bottom that could sustain the existence of microbial mats. This site contains exclusively aquatic taxa whose arrangement shows the absence of preferential orientation, and whose density, with 127 specimens in the samples studied as a whole (Álvarez-Parra *et al.* 2021), is consistent with that observable in life. The lack of preferential orientations indicates the absence of currents in the lake and, together with the density, allows us to assess the degree of hydrodynamism and the possibility of transport which could alter the original composition of the assemblage (Johnson 1960, Ager 1963, Fagerström 1964). Consequently, a still-water depositional environment could be inferred for this site. Furthermore, the abundance of pulmonate species, with a value of 93.3% (Álvarez-Parra *et al.* 2021), is compatible with a shallow aquatic environment with abundant macrophytic vegetation. The presence of *Ferrissia* cf. *deperdita* suggests the possibility of a littoral belt of reeds, although the wide tolerance ecological indicated above this genus prevents it from being confirmed.

The MAB3–4, MAB5 and MAB6–9 sites have exclusively terrestrial taxa in the form of moulds (MAB3–4 and MAB6–9) or fragments (MAB5). The state of preservation of the shell fragments located in MAB5, whitout surface alteration and whit a connection between them as well as sharp edges, suggest the absence of transport, rapid burial and subsequent fossil diagenetic fractures. On the other hand, at the rest of sites, the absence of shell on the specimens and the only presence of moulds is evidence to a whole different diagenetic history that is in need of more detailed studies to be defined. Thus, the paleoenvironmental interpretation is uncertain, and several possibilities can be inferred from the available sedimentological data. According to Crespo *et al.* (2019a), the location of gypsum layers at the base of the MAB section, in particular the multiple layers of black, grey and reddish (ferruginous) loams with gypsum and plant intercalations in MAB5, could be related to low levels of sedimentation and even desiccation. Therefore, on the one hand, these deposits could be related to the transport of the shells to the vegetated edge of a lake. This lacustrine edge would be subject to desiccation as a consequence of variations in its level due to evaporite phenomena. On the other hand, they could also be related to the formation of the, as a consequence of meteoric inputs, of temporary water masses in which the shells of terrestrial molluscs would be trapped. These water bodies could be formed in depressed and vegetated areas located outside the lake inferred in other sites, as suggested by the absence of aquatic taxa. They would also be very shallow and would have a temporary character, being subject to significant variations in level depending on input and evaporation phenomena, and could therefore reach complete desiccation. The concentration of these taxa in the deposits of the central part from the Campisano Ravine section could therefore be explained by a higher level of humidity. This circumstance, also detected by Ríos (2013) and Crespo (2017) would imply a more closed vegetation, which in turn is compatible to the tropical climate inferred by Crespo *et al.* (2020b). Furthermore, according to Crespo *et al.* (2018), the abundance of the dimylid *Plesiodimylus ilercavonicus* in particular in MAB5 indicate very humid conditions and, according to Crespo (2017) and Crespo *et al.* (2019a), the predominant mammal taxa in MAB3 and MAB5 would exhibit forest affinity.

The CBR0B, CBR0G and CBR1–3 sites record both aquatic and terrestrial species. In CBR0B and CBR0G, both aquatic and terrestrial specimens show no surface alteration, which together with the existence of sharp edges and the finding of fragmented connected of *Palaeotachea* sp. would allow to deduce no transport and rapid burial. The existence of compressions during the fossil diagenetic phase would explain the fractures. The presence of black organic-rich shale levels is compatible with abundant vegetation, while the existence of reddish mudstones would be related with temporary desiccations. The abundant presence of *Gyraulus kleini* is consistent with these inferences and, together with its preference for lentic and shallow environments; it suggests a calm, shallow depositional environment. In CBR1, *Pseudamnicola roblesi* sp. nov. dominates over *Stagnicola* cf. *armaniacensis* and *Gyraulus kleini*, which suggests a permanent water body. The site is also notable for the high percentage of sand in the sediment. Given that there is a direct relationship between the grain size of the sediment and the hydrodynamism at the time of deposition (Johnson 1960), an energetic depositional environment is likely. This site also contains fragments of *Palaeotachea* sp. with surface alteration marks and blunt edges, which are compatible with prolonged aerial exposure and transport. Therefore, the depositional palaeoenvironment could correspond to fluvial or alluvial input to the lacustrine system. From CBR1 to CBR3 there is a progressive decrease of *Pseudamnicola roblesi* sp. nov. and an increase of *Gyraulus kleini*, being the most abundant species in CBR2 and CBR3. Also, the percentage of sands and fragments of *Palaeotachea* sp. in CBR2 and CBR3 is minimal. All this seems to indicate a gradual shift of the depositional environment towards less energetic and, probably, also shallower conditions. In contrast, the limestone levels interspersed between these sites could be related to greater depth, which may link to cyclical variations of the lake level, although such inferences would require further sedimentological studies. The absence of *Palaeoglandina* sp. and Klikiinae indet. in the deposits of the higher sections of the sequence (CBR0B, CBR0G, and CBR1–3) suggests a lower humidity and consequently lower tree coverage. The progressively decreasing abundance of *Palaeotachea* sp. and *Pomatias conicus* moving up the section is compatible with the gradual shift from open forests to herbaceous grassland as proposed by Crespo (2017).

The finding of aquatic pulmonates characteristic to lentic, shallow and vegetated environments in all of the sites with aquatic fauna, suggests a lake with quiet waters, shallow depth and the possibility of temporary drying, as well as abundant macrophytic vegetation. However, the presence of aquatic prosobranchs in FSA and CBR1–3 supports a permanent character of the lake. Concerning water chemistry, all the aquatic taxa infer at most oligohaline waters. Álvarez-Parra *et al.* (2021) suggests the possibility of a meromictic lake with a particularly saline bottom. The aquatic taxa found are not controversial with this interpretation, since the extant aquatic pulmonates only inhabit the first few metres of the water column (Dillon 2004) and hydrobiids generally have a greater tolerance to salinity (Adam 1960). The depositional environment inferred for the MTR2 and BC1 sites and the differences in the composition of the CBR0B, CBR0G and and CBR1–3 assemblages could indicate the possibility of variations in the extention and depth of the lake, as well as the possibility of different hydrodynamic situations. The high percentage of sands in the CBR1 site, that reflects a higher hydrodynamism, is here recorded and interpreted as an external water contribution, that could be one of the causes of these variations.

The localised terrestrial taxa are compatible with a surrounding environment with at least moderate vegetation cover and warm climatic conditions.

Palaeobiogeography

The scarcity of previous studies on the mollusc fauna from the early and middle Miocene of the Iberian Peninsula, together with the small number of taxa located in our study, conditions the realization of palaeobiogeographical inferences.

The comparison of the mollusc assemblage recorded in the Campisano Ravine with the assemblages dated to the middle Miocene of the Duero Basin (*e.g.* González-Delgado *et al.* 1986) does not show the existence of any common generic taxa. However, in order to corroborate this statement, a revision of the original material should be carried out.

The comparison of the species found in the Campisano Ravine sites with early and middle Miocene sites of Central Europe (Tab. 2) shows that, *Pomatias conicus*, *Gyraulus kleini* and two of the tentatively identified species (*Stagnicola* cf. *armaniacensis* and *Ferrissia* cf. *deperdita*) have been found in coeval deposits of central Europe (Sandberger 1875; Wenz 1923; Schlickum 1976; Gozhik & Prysjazhnjuk 1978; Piechocki 1997; Harzhauser & Kowalke 2002; Harzhauser & Binder 2004; Kowalke & Reichenbacher 2005; Kókay 2006; Harzhauser *et al.* 2014b; Salvador & Rasser 2014, 2016a, b; Salvador *et al.* 2015, 2016; Neubauer *et al.* 2017; Harzhauser & Neubauer 2018; Höltke *et al.* 2018). *Pseudamnicola roblesi* sp. nov. has only been located in four sites of the Campisano Ravine; so, with the available data, we consider it to be endemic to the Ribesalbes-Alcora Basin. Several species of Helicidae, including those attributed to the genus *Palaeotachea*, as well as Elonidae, including the genera assigned to the subfamily Klikiinae, are commonly cited from the early and middle Miocene of Central Europe (Harzhauser & Neubauer 2021).

Table 2. Taxa located in Campisano Ravine and selected Miocene sites/regions. Abbreviations: FCB – Fore-Carpathian Basin; OSM – Upper Freshwater Molasse.

	Campisano R.	Belchatow-C (Poland)	Lake Rein (Austria)	Bakony Mnts. Layers D-E-F (Hungary)	OSM (Switzerland and Germany)	FCB (Ukraine)	Sansan (France)	Opole (Poland)	Steinheim (Germany)	Vračević (Serbia)	Richardhof (Austria)
	MN4	MN4	MN5	MN5	MN5/6	MN5/7	MN6	MN6	MN7	MN7/8	MN9
Pomatias conicus	■			■	■				■	■	■
Pseudamnicola roblesi	■										
Stagnicola. cf. *armaniacensis*	■		■		■		■				
Ferrissia cf. *deperdita*	■		■	■	■			■	■	■	
Gyraulus kleini	■	■	■	■	■	■			■	■	
Palaeoglandina sp.	■										
Palaeotachea sp.	■										
Klikiinae gen. et sp. indet.	■										
Total	8	1	3	3	4	1	1	1	3	3	1

In summary, the entire fauna shows an affinity with Central European faunas of the early and middle Miocene. However, the scarcity of studies from other sites of the Iberian Peninsula necessary to make comparisons, the small number of species studied in this research and the poor state of preservation, which complicates species identification, call for caution when interpreting biogeographic relationships.

Conclusions

The mollusc fauna found in the fifteen sites studied in the Campisano Ravine consists of eight species, four aquatic and four terrestrial. One of the aquatic species, *Pseudamnicola roblesi*, is new to science and endemic to the area. Four of the identified species are common in some early and middle Miocene sites in Central Europe, indicating potential biogeographic relationships. However, the scarcity of works about the early Miocene malacofauna in the Iberian Peninsula and the low number of species detected herein as well as the doubts about some of the species identifications suggest caution and the need for further studies along with the review of the existing data.

The analysis of the malacological contents of the sites reveals the existence of different depositional environments which, together with the ecological characteristics of each species, allowed inferences about the palaeoenvironment and its evolution. The mollusc assemblage recorded in the Campisano Ravine sites indicates a warm palaeoenvironment in a subtropical to partly tropical climate. The physical environment would be occupied by a lake subject to fluctuations in its extension and depth, being, oligohaline at least in its upper part and containing abundant macrophyte vegetation as well as a shore which could have been occupied by a belt of littoral reeds. The lake would be framed by a space with vegetation coverage that, installed on calcareous soils, would have had composition and structure that would depend on the degree of humidity. This would imply the existence of habitats between herbaceous meadow and closed forest. These habitats, in general, would be more open in the sites located in the lower and upper parts of the section studied and more closed in those in the central part.

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