Ann. Naturhist. Mus. Wien, Serie A	119	115–130	Wien, 15 Feb. 2017

The false limpet *Siphonaria* in the circum-Tethyan Miocene with emphasis on its occurrence in the Paratethys Sea

Mathias Harzhauser[1*], Bernard M. Landau[2] & Anton Breitenberger[3]

(with 3 figures and 1 plate)

Manuscript submitted on December 28th 2015,
the revised manuscript on June 6th 2016.

Abstract

The occurrence of the false limpet genus *Siphonaria* is described for the first time from the Badenian (Langhian) of the Paratethys. Comparison with coetaneous material available from France, Italy and Hungary suggests the presence of at least five morphologically distinct species of this always rare genus in the circum-Tethyan Miocene. Due to its scarcity in the fossil record, the biogeographical and biostratigraphical value of these species is low, but it is a good indicator for rocky intertidal paleo-environments.

Siphonaria vulcanica is described as a new species. *Siphonaria variecostata* Sacco, 1897 and *Helcion subcostaria* d'Orbigny, 1852 are considered subjective junior synonyms of *S. bisiphites* Michelin, 1831. *Patella subpolygona* d'Orbigny, 1852 is considered an unjustified replacement name for *Siphonaria polygona* (Michelotti, 1847). *Siphonaria polygona irregularis* Sacco, 1897 is raised to species rank. *Siphonaria tournoueri* Dollfus & Dautzenberg, 1886 is considered a *nomen nudum*. *Siphonaria tournoueri* Peyrot, 1938 is considered a junior homonym of *S. tournoueri* Vasseur, 1881.

Introduction

The genus *Siphonaria* is currently distributed worldwide in tropical and temperate rocky intertidal habitats (Dayrat *et al.* 2014). Its patchy fossil record dates back to the Cretaceous (Dayrat *et al.* 2011) and a major diversification is observed during Eocene times (Le Renard & Pacaud 1995). After an Oligocene gap, the genus is again well represented during the Miocene (Sacco 1897; Peyrot 1932). Nevertheless, all the fossil

[1] Naturhistorisches Museum Wien, Burgring 7, 1010 Vienna, Austria; e-mail: mathias.harzhauser@nhm-wien.ac.at

[2] Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, Netherlands; Instituto Dom Luiz da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal; and International Health Centres, Av. Infante de Henrique 7, Areias São João, 8200 Albufeira, Portugal; e-mail: bernielandau@sapo.pt

[3] Florastraße 8, 2540 Bad Vöslau, Austria; breitenberger@gmail.com

* Corresponding author

ZooBank LSID: urn:lsid:zoobank.org:pub:79D58234-E6F3-43DC-A29B-6B1435B029C8

species are known only from a few localities and are documented by few specimens. Therefore, the intraspecific variability for most species has been difficult to assess.

In this paper the focus is on Miocene European *Siphonaria* species. From the literature, three species are known from the Early and Middle Miocene of the North-East Atlantic (*Siphonaria bisiphites* Michelin, 1831, *Siphonaria vasconiensis* Michelin, 1831, *Siphonaria tournoueri* Dollfus & Dautzenberg, 1886) and two species are described from the Early Miocene of the Proto-Mediterranean Sea (*Siphonaria polygona* (Michelotti, 1847), *Siphonaria variecostata* Sacco, 1897). No Neogene North Sea occurrences are known to us as and similarly, no *Siphonaria* species have been described from the Paratethys Sea despite its rich Miocene mollusc fauna (Harzhauser & Piller 2007). We can find no Pliocene record of the genus in the abundant North Sea Basin, Atlantic or Mediterranean assemblages. One of us (B.L.) has extensive knowledge of the outstandingly abundant lower Upper Pliocene deposits of Estepona, southern Spain, which probably boasts of over 1000 gastropod species. Rocky shore habitats are represented in Estepona and yet there is no record of *Siphonaria* (B.L. unpublished data). The first post-Miocene European fossil record we can find for the genus is in the upper Pleistocene/Holocene of southern Spain (Lozano-Francisco *et al.* 2002).

The scarcity of fossil *Siphonaria* is most probably related to its agitated rocky-intertidal habitat. Not only is this type of environment consistently underrepresented in the geological record compared to the vast amount of sublittoral and deep marine deposits, but the fragmentation and abrasion by waves also cause a strong preservational bias. The combination of these two factors could explain the comparably poor record of limpets. It is also possible that this genus might simply not have been abundant along the circum-Tethyan shores during Miocene and Pliocene times.

In modern seas, *Siphonaria* is moderately speciose; calculations on its diversity based on shell characters resulted in about 60–70 species worldwide (Hubendick 1946; Gofas & Rosenberg 2015), but molecular data of Dayrat *et al.* (2014) suggest a higher diversity and a distinct provincialism. Unfortunately for palaeontologists, Dayrat's *et al.* (2014) work suggested that conchological characters alone – which are quite variable in *Siphonaria* – are not always reliable in distinguishing species. Despite these problems, molecular data confirmed shell-based identifications for several extant species (Güller *et al.* 2015). Therefore, we are convinced that the available material from the European Miocene can be assigned to at least five species based on their distinct morphologies. Uncertainties, however, remain due to the lack of data on intraspecific variability.

Material and methods

The Paratethyan shells were collected by A.B. at Letkés in Hungary (Fig. 1) in an artificial trench. The shells studied are stored in the collections of the Natural History Museum Vienna (NHMW), the Museo Regionale di Scienze Naturali in Torino (BS), the Collection de géologie of the Université de Bordeaux, the Muséum d'Histoire Naturelle de Bordeaux (MHNBx) and the private collection of Piet Hessel (now part of RGM

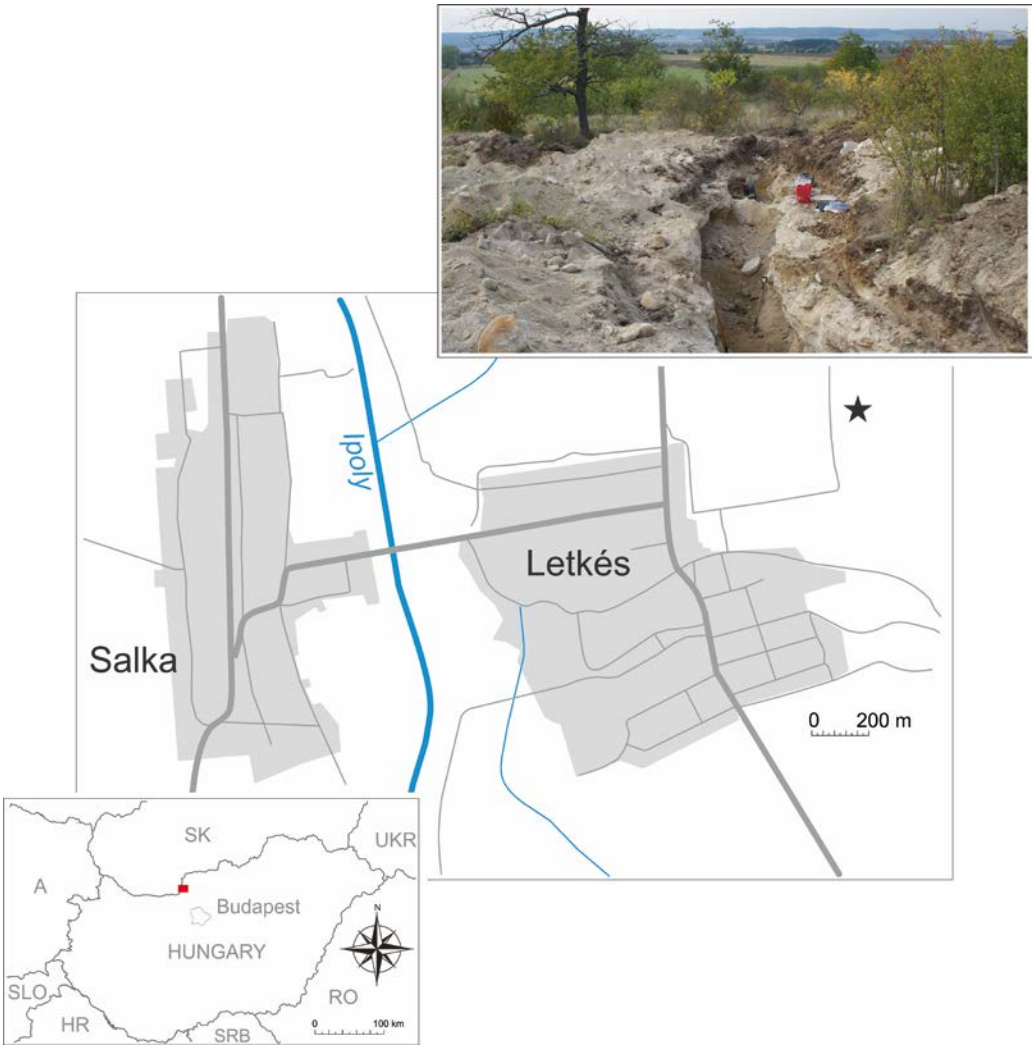


Fig. 1. Geographic position of Letkés in Hungary; the red rectangle in the smaller map indicates the position of the larger map; the asterisk marks the position of the outcrop described by KOVÁCS & VICIÁN (2013); the outcrop picture shows the artificial trench in 2012 and the andesite boulders, which might have served as habitat for the siphonariids (A: Austria, SK: Slovakia, UKR: Ukraine, RO: Romania, SRB: Serbia, HR: Croatia, SLO: Slovenia).

coll. Naturalis Biodiversity Center, Leiden, The Netherlands). The conchological terminology follows HUBENDICK (1946) and DAYRAT *et al*. (2014). We intended to illustrate all type specimens, but several types are lost (*e.g.*, MICHELIN collection, pers. comm. Jean-Michel PACAUD; BENOIST collection, pers. comm Laurent CHARLES; ROVASENDA collection, pers. comm. Daniele ORMEZZANO). Therefore, we re-illustrate the figures given in the respective original papers.

Systematic Paleontology

Class Gastropoda Cuvier, 1795

Subclass Heterobranchia Burmeister, 1837

Superfamily Siphonarioidea Gray, 1827

Family Siphonariidae Gray, 1827

Genus *Siphonaria* G. B. Sowerby I, 1823

Type species: *Siphonaria sipho* G. B. Sowerby I, 1823; by monotypy. Recent, Indo-West Pacific.

Siphonaria bisiphites Michelin, 1831
(Fig. 2a–d)

*1831a *S.*[*iphonaria*] *bisiphites* Michelin: 5, pl. 5, 2 text-figs.
1852 [*Siphonaria*] *bisiphites* Michelin – d'Orbigny: 93.
1896 *S.*[*iphonaria*] *variecostata* Sacco: 96 (nomen nudum).
1897 *Siphonaria*? *variecostata* Sacc. – Sacco: 87, pl. 10, fig. 100.
1932 *Siphonaria bisiphites* Michelin – Peyrot: 215, no. 1418, pl. 12, figs 29, 31, 34, 40, 54.
1984 *Siphonaria*? *variecostata* Sacco, 1897 – Ferrero-Mortara *et al*.: 296, pl. 55, figs 1a–1b.
2001 *Siphonaria bisiphites* Michelin, 1831 – Lozouet *et al*.: 84, pl. 37, figs 10a–10b.

Discussion: *Siphonaria bisiphites* is either a strongly polymorphic species, or possibly represents a species-group. The syntype in Michelin (1831a; herein Fig. 2a) shows a roughly rectangular outline and ~45 primary and secondary radial ribs of similar strength, which are cut by few but deep concentric growth lines; the maximum length is given as 18 mm. Peyrot (1932; herein Fig. 2b) illustrated a distinctly larger specimen with a maximum diameter of 28 mm, an ovoid outline and about 42 radial ribs. Of these, some primary ribs are somewhat bifid and between two primary ribs appears one slightly weaker secondary rib. The muscle scar is deep and delimits a moderately wide, crenulated margin. The specimen described by Lozouet *et al.* (2001) is intermediate in size and has a subquadratic outline agreeing well to Michelin's type. It differs from the other shells in its very broad and bulgy primary ribs and the very regular intercalation of a narrow but prominent secondary rib between each pair of primary ribs. The Aquitanian specimen illustrated herein (Fig. 2c) has also distinct primary ribs but develops 2–3 secondary and tertiary ribs between a pair of primary ribs. This morphotype corresponds fully to the holotype of *Siphonaria variecostata* Sacco, 1897 (BS.104.01.007) from the Burdigalian of the Turin Hills (Fig. 2d). Therefore, we consider *S. variecostata* a subjective junior synonym of *S. bisiphites*.

Lozouet *et al*. (2001) considered the shells described and illustrated by Grateloup (1828, 1836, 1845) as *Patella costaria* (*non* Deshayes, 1824) to be *S. bisiphites*. Therefore, *Helcion subcostaria* d'Orbigny, 1852, which was introduced by d'Orbigny (1852) as a replacement name for Grateloup's *P. costaria*, is a subjective junior synonym of

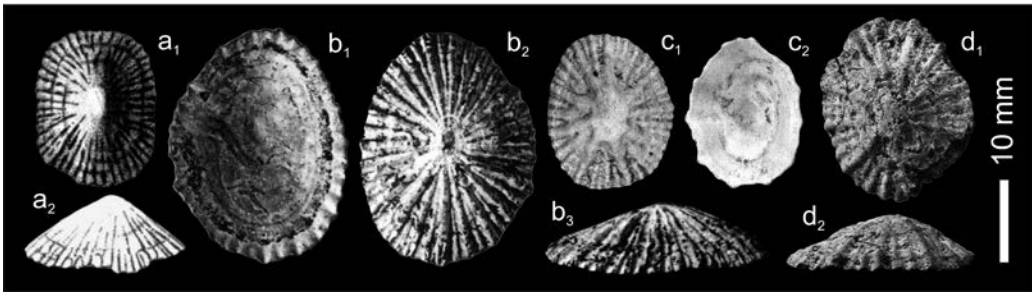


Fig. 2. *Siphonaria bisiphites* MICHELIN, 1831. **a1–a2**: re-illustration of the lost syntypes illustrated in MICHELIN (1831); St-Paul-lès-Dax, France, Burdigalian. **b1–b3**: re-illustration from PEYROT (1932, pl. 12, figs 31, 34, 40), Mérignac, France, Burdigalian. **c1–c2**: specimen from Saint-Martin-d'Oney, Aquitanian; International Fossil Shell Museum, no. 23861. **d1–d2**: holotype of *Siphonaria variecostata* SACCO, 1897 (pl. 10, fig. 100, BS.104.01.007), Turin Hills, Italy, Burdigalian.

Siphonaria bisiphites. With the scant material available, we do not feel it is possible at present to separate the various morphotypes described above, and therefore follow previous authors in considering *S. bisiphites* as a single polymorphic species. The whereabouts of the specimens illustrated by PEYROT (1932, pl. 12, figs 31, 34, 40) is unknown (pers. comm. Laurent CHARLES, Muséum d'Histoire Naturelle de Bordeaux).

Distribution: northeastern Atlantic: Aquitanian (Saucats, Saint-Martin-d'Oney), Burdigalian (St-Paul-lès-Dax, Mérignac) (PEYROT 1932; LOZOUET *et al.* 2001; http://www.fossilshells.nl/); Proto-Mediterranean Sea: Burdigalian (Turin Hills) (as *S. variecostata*).

Siphonaria polygona (MICHELOTTI, 1847)
(Pl. 1, Figs 1–5)

1842 *Patella Saccharina* Linn. LAM. – SISMONDA: 24 (non *Patella saccharina* LINNAEUS, 1758).
*1847 *Patella polygona* SISM. – MICHELOTTI: 133, pl. 5, fig. 9.
1847 [*Patella*] *polygona* E. SISM. – SISMONDA: 25.
1852 [*Patella*] *subpolygona* E. SISM. – D'ORBIGNY: 94.
1896 *Siphonaria polygona* (SISMD.) – SACCO: 96.
1896 [*Siphonaria polygona* (SISMD.)] var. *pluricostulata* SACCO: 96 (nomen nudum).
1896 [*Siphonaria polygona* (SISMD.) var.] *longiuscata* SACCO: 96 (nomen nudum).
1897 *Siphonaria poligona* [sic] (SISMD.) – SACCO: 87, pl. 10, figs 91–95 (non fig. 90 = *Siphonaria irregularis* SACCO, 1897).
1897 *S.*[*iphonaria*] *polygona* var. *pluricostulata* SACC. – SACCO: 87, pl. 10, figs 96–97.
1897 *S.*[*iphonaria*] *polygona* var. *longiuscula* SACC. – SACCO: 87, pl. 10, fig. 98.
1962 *Siphonaria polygona* SISMONDA, 1847 – GLIBERT: 75.
1984 *Siphonaria polygona* (SISMONDA, 1847) – FERRERO-MORTARA *et al.*: 296.
1984 [*Siphonaria polygona*] var. *pluricostulata* SACCO, 1897 – FERRERO-MORTARA *et al.*: 296.
1984 [*Siphonaria polygona*] var. *longiuscula* SACCO, 1897 – FERRERO-MORTARA *et al.*: 296.
2009 *Siphonaria polygona* – ZUNINO & PAVIA: 360.

Material examined: 5 specimens in the collection of the Museo Regionale di Scienze Naturali, Torino (BS.104.01.001, BS.104.01.002, BS.104.01.004, BS.104.01.005, BS.104.01.006).

Description: Small, of about 13–16 mm maximum diameter elongate-ovate to faintly hexagonal (length/width ratio of 1.3–1.5), low (length/height ratio: 4.3), equilateral shells. Pointed, subcentral apex with apical angle of 135°. Shell surface with 17–21 somewhat angular primary and secondary radial ribs; secondary radial ribs may attain same strength as the primary ones and a separation may be difficult. Siphonal ribs not markedly more prominent. Primary ribs distinctly protruding the edge, secondary ribs less protruding. Interspaces between ribs flat, often displaying weak concentric growth lines. Muscle scars deep and distinct, demarcating a broad and undulate margin.

Discussion: The authorship of this species was traditionally attributed to Eugenio Sismonda, who listed it as *Patella saccharina*. This extant Indo-West Pacific species is now treated as *Patelloida saccharina* (Linnaeus, 1758) according to Bouchet (2015), and is clearly unrelated to *Siphonaria*. Michelotti (1847) recognized the mistake, described differences between the Miocene and Recent species and introduced *Patella*

Plate 1 ▶

***Siphonaria polygona* (Michelotti, 1847)**

from the Burdigalian of the Turin Hills (Italy).

Fig. 1: BS.104.01.002, specimen illustrated by Sacco (1897, pl. 10, fig. 91).

Figs 2a–2b: BS.104.01.001, specimen illustrated by Sacco (1897, pl. 10, fig. 92).

Figs 3a–3b: BS.104.01.004, syntype of *S. polygona pluricostulata* Sacco (1897, pl. 10, fig. 96).

Figs 4a–4c: BS.104.01.005, syntype of *S. polygona pluricostulata* Sacco (1897, pl. 10, fig. 97).

Figs 5a–5b: BS.104.01.006, syntype of *S. polygona longiuscula* Sacco (1897, pl. 10, fig. 98).

No exact locality given on labels.

***Siphonaria irregularis* Sacco, 1897**

from the Burdigalian of the Turin Hills (Italy).

Figs 6a–6b: BS.104.01.003, specimen illustrated by Sacco (1897, pl. 10, fig. 90) as *Siphonaria polygona*, no exact locality given on label.

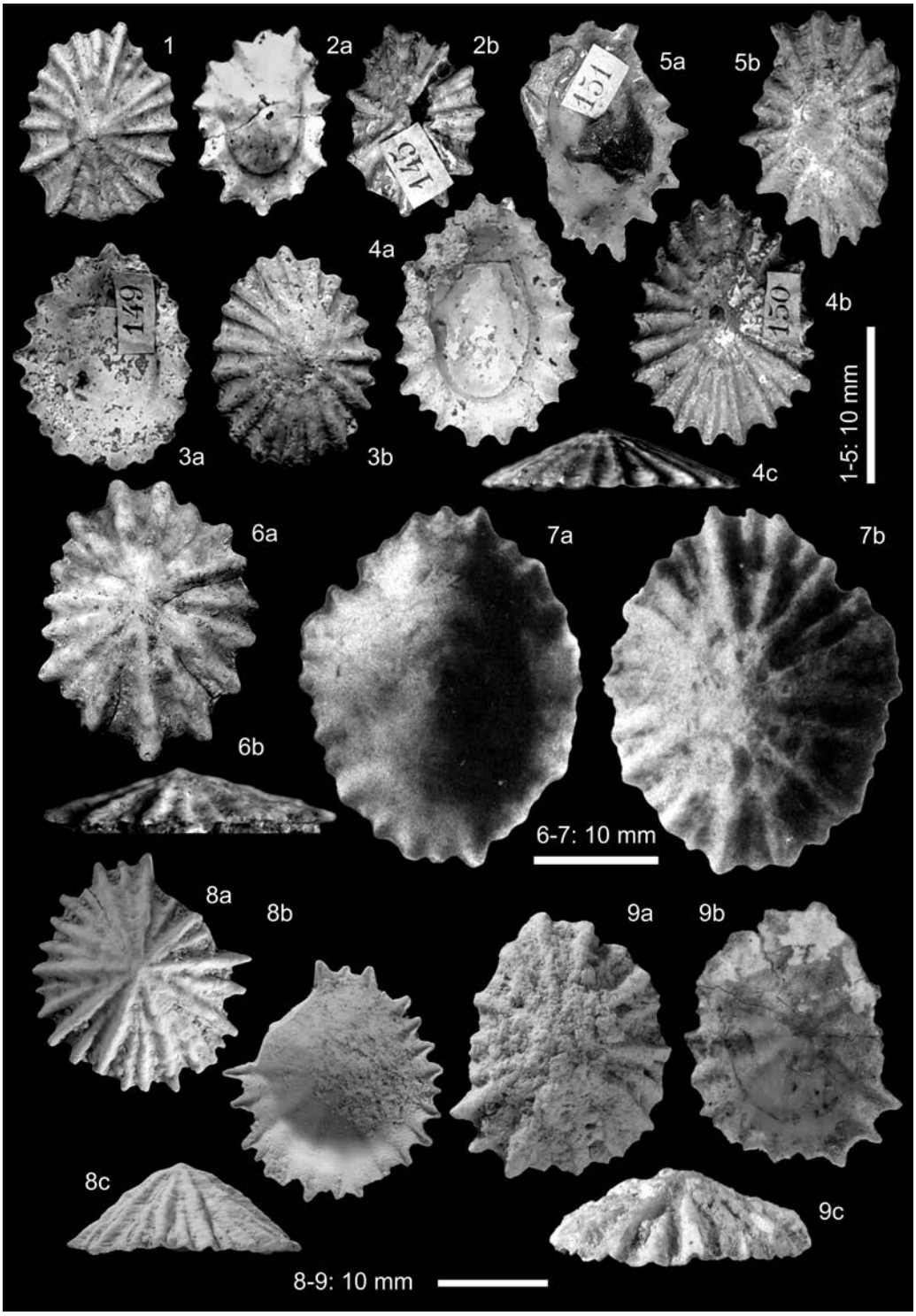
Figs 7a–7b: syntype (or holotype) of *S. polygona irregularis* Sacco (1897, pl. 10, fig. 99) from Sciolze; the specimen is lost (re-illustrated from Sacco, 1897).

***Siphonaria vulcanica* nov. sp.**

from the Badenian (Langhian) of Letkés (Hungary).

Figs 8a–8c: NHMW 2015/0390/0001, holotype.

Figs 9a–9c: NHMW 2015/0390/0002, paratype.


1
2a
2b
5a
5b
4a
4b
3a
3b
4c
1-5: 10 mm
6a
7a
7b
6b
6-7: 10 mm
8a
8b
9a
9b
8c
9c
8-9: 10 mm

polygona for the Miocene species. Nevertheless, probably out of courtesy, he indicated SISMONDA as author. Even D'ORBIGNY (1852), who introduced *subpolygona* as (unjustified) replacement name indicated SISMONDA as author. In any case, the authorship has to be passed to MICHELOTTI (1847) as he made the name available and provided a description. The type illustrated by MICHELOTTI (1847) represents a vaguely pentagonal to hexagonal shell with 12 primary radial ribs and 7 slightly weaker secondary ribs, all of which protrude over the shell margin, giving a deeply crenulated edge. This morphotype corresponds well with the shells (Pl. 1, Figs 1–2) considered by SACCO (1897) to be typical representatives of *S. polygona*. In addition, SACCO (1897) established four new subspecies (variations) of *S. polygona* accompanied by very brief diagnoses. According to these, *S. polygona pluricostulata* differs from the type by more numerous and densely set radial ridges, *S. polygona longiuscula* is elongate and irregularly elliptical and *S. polygona irregularis* is characterized by its robust shell and the secondary ridges close to the shell margin. In *S. polygona longiuscula* the right margin is damaged, resulting in a seemingly irregular elongate shape. Typical *S. polygona* develop around 17 primary ridges and the two specimens of *S. polygona pluricostulata* have only 2 and 4 ridges more. Thus, taking into account the wide intraspecific variability seen in extant *Siphonaria* species (*i. e.*, GÜLLER *et al*., 2015) and considering that all the specimens come from the same localities and geological horizons, there is little reason to separate *pluricostulata* and *longiuscula* as distinct species or subspecies. Only *S. polygona irregularis* differs considerably in its morphology and size and is considered herein to be a distinct species unrelated to *S. polygona* (see under discussion of *S. irregularis*).

Distribution: Proto-Mediterranean Sea: originally mentioned by SISMONDA (1842) vaguely from the Turin Hills. Later, MICHELOTTI (1847) gave Termô-Fôurà as locality, which belongs to the middle to upper Burdigalian Termofourà Formation (ZUNINO & PAVIA, 2009). In addition, SACCO (1897) mentions records from Sciolze, which is most probably also of Burdigalian age.

Siphonaria irregularis SACCO, 1897
(Pl. 1, Figs 6–7)

1896 [*Siphonaria polygona* (SISMD.) var.] *irregularis* SACCO: 96 (nomen nudum).
1897 Siphonaria poligona [sic] (SISMD.) – SACCO: 87, pl. 10, fig. 90 (non *Siphonaria polygona* MICHELOTTI, 1847).
*1897 *S.*[*iphonaria*] *poligona* [sic] var. *irregularis* (ROV.) – SACCO: 87, pl. 10, fig. 99.
1984 [*Siphonaria polygona*] var. *irregularis* SACCO, 1897 – FERRERO-MORTARA *et al.*: 296.

Material examined: 1 specimen in the collection of the Museo Regionale di Scienze Naturali, Torino (BS.104.01.003). The syntype (or holotype) of *Siphonaria polygona irregularis* was part of the ROVASENDA-collection, which was destroyed during World War II.

Description: Large, robust, low shell with subcentral apex; apical angle 150°. Exact size of the lost type specimen is unknown as the illustrations of the exterior and interior

in SACCO (1897) differ slightly in size. The maximum diameter may thus be 31 or 34 mm; maximum diameter of second studied specimen: 23.6 mm; for both specimens the length/width ratio is ~1.2, length/height ratio: 5.5. Exterior with about 17 broad, blunt and somewhat knobby primary ribs and weaker secondary ribs, which become intercalated in later stages of growth; interspaces narrow, concave. Ribs protrude slightly the edge. Muscle scars moderately incised, siphonal groove broad and shallow.

Discussion: Two specimens illustrated by SACCO (1897) as *Siphonaria polygona* differ considerably from the other shells in their much larger size and different sculpture (figs 90 and 99 in SACCO 1897, pl. 10). For one of these shells SACCO (1897) established the varietal name *irregularis*, whereas the other one was treated as typical *S. polygona.* Both shells differ from *S. polygona* by being broader, much larger and solid, with blunt apex, broad and blunt radial ribs and narrow interspaces. In addition, the length/height ratio is much larger in *S. irregularis* and the knobbly ribs are unknown in *S. polygona*. In the available specimen the interior is covered by sediment. Based on these differences, we propose to separate *Siphonaria irregularis* as distinct species.

Distribution: Proto-Mediterranean Sea: Burdigalian of the Turin Hills (Termofourà Formation and Sciolze) (FERRERO-MORTARA *et al.* 1984).

Siphonaria vasconiensis MICHELIN, 1831
(Fig. 3a–e)

?1829 *Patella alta* DE SERRES: 129, pl. 4, fig. 2. (*non Patella miniata* var. *alta* BRAUER, 1878).
*1831b *S.*[*iphonaria*] *Vasconiensis* MICHELIN: 32, pl. 32, 2 text-figs.
1852 [*Siphonaria*] *Vasconiensis* MICHELIN – D'ORBIGNY: 93.
1932 *Siphonaria vasconiensis* MICHELIN – PEYROT: 214, no. 1417, pl. 12, figs 24, 28, 30, 32–33, 41–42.
2001 *Siphonaria vasconiensis* MICHELIN, 1831 – LOZOUET *et al.*: 84, pl. 37, figs 9a–9b.

Material examined: 1 specimen from Letkés in Hungary (NHMW 2015/0390/0003), 1 specimen from Le Houga, Gers, France, Langhian; International Fossil Shell Museum, no. 11578, 1 specimen from St-Paul-lès-Dax in France, illustrated in PEYROT (1932, pl. 12 figs 30, 41, 42) (MHNBx 2014.35.15.45; picture: Laurent CHARLES, Muséum d'Histoire Naturelle de Bordeaux).

Description: Large, solid, high, cap-shaped shell with broad ovoid base (length/width ratio: ~1.2); and convex surface. Maximum diameter ranging around 50 mm; apical angle 100–120°. Apex in near-central position; pointed in well-preserved specimens but usually eroded. Siphonal groove marked by a slight lateral expansion of the margin. Sculpture consisting of numerous more or less wrinkled radial ribs. Secondary and tertiary ribs develop partly from bifurcations or are isolated ribs between the primary ribs. Towards the margins, the ribs become rather uniform in larger specimens. Interspaces smooth and of about the same width as the ribs. Interior with well-developed muscle scars; siphonal groove very shallow and indistinct; margin smooth to weakly undulate.

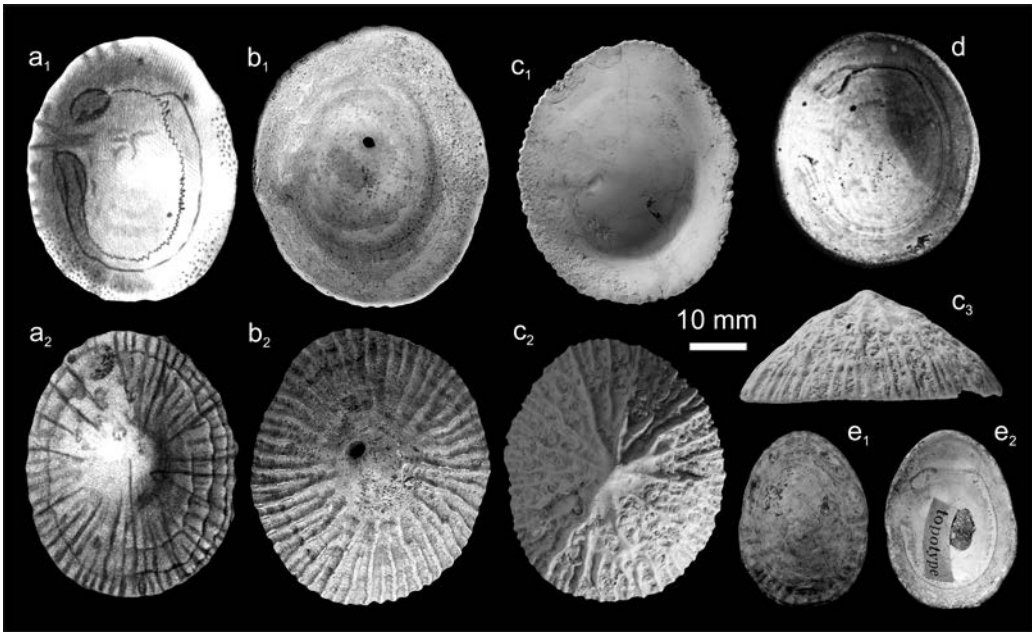


Fig. 3. *Siphonaria vasconiensis* Michelin, 1831. **a1–a2**: re-illustration of the lost syntypes illustrated in Michelin (1831); St-Paul-lès-Dax?, France, Burdigalian. **b1–b2**: specimen from Le Houga, Gers, France, Langhian; International Fossil Shell Museum, no. 11578.**c1–c3**: NHMW 2015/0390/0003, Letkés, Hungary, Badenian (Langhian). **d**: re-illustration from Peyrot (1932, pl. 12, figs 28, 33), Manciet, France, Langhian. **e1–e2**: specimen from Paul-lès-Dax, France, Burdigalian, illustrated in Peyrot (1932, pl. 12 figs 30, 41, 42) (MHNBx 2014.35.15.45; photograph: Laurent Charles, Muséum d'Histoire Naturelle de Bordeaux).

Discussion: *Siphonaria vasconiensis* is the largest *Siphonaria* in the circum-Tethyan Miocene. As is typical for *Siphonaria*, its sculpture is quite variable. Early Miocene shells described by Peyrot (1932) and Lozouet *et al.* (2001) have broad primary and secondary ribs with narrow interspaces. The same morphology is also recorded from the Langhian (Peyrot 1932). The Langhian shells from France and Hungary, described herein, differ in the broader interspaces and the differentiated primary and secondary ribs (Fig. 3c). The drawing of the Burdigalian holotype by Michelin (1831b; herein Fig. 3a) is somewhat idealized but seems to represent an intermediate phenotype. Therefore, considering the vast conchological variability seen in extant *Siphonaria* species, as documented by Dayrat *et al.* (2014) and Güller *et al*. (2015), we consider the observed differences to reflect intraspecific variability. Although this species is large and solid, it had not been recorded so far from the Proto-Mediterranean Sea and the Paratethys. Friedberg (1928) illustrated a large limpet of 45 mm diameter from the Middle Miocene of Poland, which he erroneously identified as *Diodora italica* (Defrance, 1820), but which lacks the typical fissurellid foramen. Outline and sculpture are similar to *Siphonaria vasconiensis*, but the shell is filled with sediment and it is unclear if the prominent concentric growth lines

in the interspaces between the radial ribs are a conchological or a taphonomic feature. As already pointed out by PEYROT (1932) the huge, cap-shaped, French Miocene shell described by DE SERRES (1829) as *Patella alta* might also correspond to *Siphonaria vasconiensis*. This name would have priority over *Siphonaria vasconiensis,* but *Patella alta* is preoccupied by *P. alta* BRAUER, 1878.

The whereabouts of the specimens illustrated by PEYROT (1932, pl. 12, figs 28, 29, 32, 33) is unknown (pers. comm. Laurent CHARLES, Muséum d'Histoire Naturelle de Bordeaux).

Distribution: northeastern Atlantic: Chattian (St-Etienne-d'Orthe), Aquitanian (Saucats), Burdigalian (St-Paul-lès-Dax, Mérignac) and Langhian (Manciet, Le Houga) of the Aquitaine and the Midi-Pyrénées (PEYROT 1932; LOZOUET *et al.* 2001; http://www.fossilshells.nl/). Paratethys: Badenian (Langhian) of Letkés in Hungary. An additional occurrence from the Ottnangian (Burdigalian) of Upper Austria was described as cf. *vasconiensis* by HARZHAUSER *et al.* (2015) but the preservation does not allow a clear identification.

***Siphonaria vulcanica* nov. spe.**

(Pl. 1, Figs 8–10)

Type material: Holotype: Pl. 1, Fig. 8, NHMW 2015/0390/0001, length 22.1 mm, width: 20.3 mm, height: 8.0 mm. Paratype: Pl. 2, Fig. 9, NHMW 2015/0390/0002, length: 24.5 mm, width: 19.3 mm, height: 6.5 mm.

Additional material: 1 fragmentary specimen consisting only of the apical part (collection Anton BREITENBERGER), length 18.2 mm, width: 14.4 mm, height: 5.1 mm.

Stratum typicum: fossil-rich marly sand with coral blocks and andesite boulders of the Sámsonháza Formation (CSEPREGHY-MEZNERICS 1956; CSÁSZÁR 1997). Middle Miocene, early Badenian (Langhian) (KOVÁCS & VICIÁN 2013).

Type locality: Letkés at the western part of the Börzsöny Mts. (Hungary); the locality was detected and shown to A.B. by Zoltán VICIÁN; a description is given by KOVÁCS & VICIÁN 2013.

Name: Referring to the volcanic andesite boulders to which the specimens might have been attached to.

Diagnosis: Medium sized, medium-low (length/height ratio: 2.8–3.7) *Siphonaria* of ovate outline with nodulose, raised radial ribs protruding from edge, terminating in spiny projections.

Description: Medium sized shells with subcircular to slightly elongate base and central apex. Shell low to moderately low. Sculpture comprising 10 strongly raised primary radial ribs with convex tops and nodulose surface. One or rarely two secondary or tertiary ribs are intercalated between each pair of primary ribs raising the number of ribs

to 23 in the holotype and 21 in the paratype. Primary and secondary radial ribs terminate in strongly protruding, internally deeply grooved and slightly recurved spines. Internal radial grooves fade out in the apical region; grooves corresponding to primary ribs are more pronounced. Muscle scars very weak; siphonal groove very shallow, only slightly deeper than the furrows of the other primary ribs; externally coinciding with a primary radial rib.

Discussion: Holotype and paratype differ in the coarser sculpture of the paratype and the lower shell height. Internal features and the number of primary radial ribs, the mode of rib intercalation and the morphology of the spiny projections, however, are identical and therefore we consider both specimens to represent the same species. *Siphonaria vulcanica* is reminiscent of the early Miocene *S. irregularis* in sculpture and size but differs in the more spiny projections, the much higher and narrower ribs, the higher shell and especially in the deep radial grooves in the interior. The early Miocene *S. polygona* is smaller and differs in its elongate outline, much more pronounced muscle scars and the lack of internal grooves.

Superficially, the shells are reminiscent of some members of the fissurellid subfamily Hemitominae Kuroda, Habe & Oyama, 1971. Most Hemitominae differ from *S. vulcanica* in their recurved apex and the deep excurrent groove on the interior (McLean 2011). Only in some species of *Hemitoma* Swainson, 1840, *Montfortulana* Habe, 1961 and *Clypidina* Gray, 1847 is the apex not recurved and the groove may be weak. Representatives of these genera, however, lack strongly protruding radial ribs.

Distribution: Paratethys Sea: only known from the Middle Miocene Badenian (Langhian) of Letkés in Hungary.

Conclusions

The scant material of Miocene *Siphonaria* reveals the presence of at least 5 species in the European Miocene. *Siphonaria bisiphites* and *S. vasconiensis* have been known from the early to middle Miocene of the northeastern Atlantic since the early 19th century. Due to their restricted distribution, these species could have been interpreted as members of an Atlantic bioprovince. Both species, however, seem to have been widely distributed in the circum-Tethyan region. The large *Siphonaria vasconiensis* is now also documented from the middle Miocene of the Paratethys. No direct connection between Paratethys and Atlantic existed at that time (Popov *et al.* 2004). Therefore, its occurrence in the Paratethys indirectly indicates its presence also in the Proto-Mediterranean Sea, although it was not detected there up to now. Similarly, *S. bisiphites* seems to have been present in the Proto-Mediterranean Sea during early Miocene times, but was described there as a separate species (*S. variecostata*). Two additional species occurred during the early Miocene in the Proto-Mediterranean Sea (*S. polygona, S. irregularis*), which had been lumped together so far in the literature. Finally, *S. vulcanica* is a new Paratethyan species, known only from the early Badenian (Langhian) of Hungary at present.

Although a separation of *Siphonaria* species may be difficult based on conchological features alone (DAYRAT *et al.* 2014), the few available specimens of each species described herein suggest a quite reliable separation and no morphologic overlap. A clear evaluation of intraspecific variability, however, would need additional material.

The rocky intertidal habitat of this genus is probably the main reason for the scarcity of this genus in the fossil record. Therefore, the spotty data do not allow any biostratigraphic and biogeographic conclusions. In contrast, its presence in fossil assemblages is a valuable indicator for the closeness of rocky intertidal paleo-environments.

Appendix

"*Siphonaria tournoueri* DOLLFUS & DAUTZENBERG, 1886" [= Patelloidea? indet]

1886 *Siphonaria Tournoueri* DOLLFUS & DAUTZENBERG: 142 (nomen nudum; non VASSEUR, 1881).
1938 *Siphonaria* (?) *Tournoueri* DOLLFUS et DAUTZENBERG (mss.) – PEYROT: 318 (non VASSEUR, 1881).

Discusssion: In their contribution on the Miocene molluscs of the Touraine in France, DOLLFUS & DAUTZENBERG (1886) mentioned *Siphonaria tournoueri* in a list without any description or illustration. Therefore, *Siphonaria tournoueri* DOLLFUS & DAUTZENBERG is a *nomen nudum*. PEYROT (1938) was the first to provide a description, which would have made the name available. *Siphonaria tournoueri*, however, is preoccupied by VASSEUR (1881), who introduced the name for an Eocene species from France. According to PEYROT (1938) the single available specimen lacks the characteristic muscle scars of *Siphonaria* and therefore is more likely to be a patelloid gastropod.

Acknowledgements

We are grateful to Daniele ORMEZZANO (Museo Regionale di Scienze Naturali, Torino, Italy) for providing pictures of the type material of SACCO (1897). Bruno CAHUZAC (Université de Bordeaux) and Laurent CHARLES (Muséum d'Histoire Naturelle de Bordeaux) provided pictures of the type material of the PEYROT collection. HESSEL and Rudi HESSEL (Utrecht), operators of the International Fossil Shell Museum (http://www.fossilshells.nl/index.html), kindly provided pictures of French material. This paper contributes to the FWF project P-23492-B17 "Stratigraphy and paleoecology in the Oligo/Miocene of the Mediterranean". Jean-Michel PACAUD (Muséum National d'Histoire Naturelle, Paris) and Alfréd DULAI (Hungarian Natural History Museum) helped with information on stratigraphy and collections. We are especially grateful to Zoltán VICIÁN (Budapest) who shared his valuable knowledge on the Letkés outcrop and for his support in the field.

The paper profited greatly by the careful reviews of Serge GOFAS (University of Malaga) and an anonymous reviewer.

References

Bouchet, P. (2015): *Patelloida saccharina*. in: MolluscaBase (2015). Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=220948 on 2016-06-06.

Brauer, F. (1878): Bemerkungen über die im kais. Zoologischen Museum aufgefundenen Original-Exemplare zu Ign. v. Born's Testaceis Musei Caesarei Vindobonensis. – Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, 1. Abtheilung, **77**: 1–76.

Burmeister, H. (1837): Handbuch der Naturgeschichte. – Part 2, xii + 369–858 pp., Berlin (Enslin).

Császár, G. (1997): Basic lithostratigraphic units of Hungary, charts and short descriptions. – 114 pp., Budapest (Geological Institute of Hungary).

Csepreghy-Meznerics, I. (1956): Die Molluskenfauna von Szob und Letkés. – Magyar Állami Földtani Intézet Évkönvye (Annales de l'Institut de Géologie Publique de Hungarie), **45**: 361–477.

Cuvier, G. (1795): Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. – Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts, **2**: 433–449.

Dayrat, B., Goulding, T.C. & White, T.R. (2014): Diversity of Indo-West Pacific *Siphonaria* (Mollusca: Gastropoda: Euthyneura). – Zootaxa, **3779**: 246–276.

Dayrat, B., Conrad, M., Balayan, S., White, T.R., Albrecht, C., Golding, R., Gomes, S.R., Harasewych, M.G. & Martins, A.M. (2011): Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): New insights from increased taxon sampling. – Molecular Phylogenetics and Evolution, **59**: 425–437.

Defrance, M.J.L. (1816–1830) in: Cuvier, F. (ed.). Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts. Suivi d'une biographie des plus célèbres naturalistes. Ouvrage destiné aux médecins, aux agriculteurs, aux commerçans, aux artistes, aux manufacturiers, et à tous ceux qui ont intérêt à connoître les productions de la nature, leurs caractères génériques et spécifiques, leur lieu natal, leurs propriétés et leurs usages. – 1–60, 12 unnumbered volumes of plates. Strasbourg (F.G. Levrault) & Paris (Le Normant).

Deshayes, G.P. (1824): Description des Coquilles Fossiles des Environs de Paris. – **2**: 178 pp., Paris (Deshayes).

Dollfus, G.-F. & Dautzenberg, P. (1886): Étude preliminaire de coquilles fossiles des faluns de la Touraine (Suite). – La Feuille des Jeunes Naturalistes, **16/192**: 138–143.

Ferrero Mortara, E.L., Montefameglio, L., Novelli, M., Opesso, G., Pavia, G. & Tampieri, R. (1984): Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco, 2. – Museo Regionale di Scienze Naturali, Cataloghi, **7**: 1–484.

Friedberg, W. (1928): Mięczaki mioceńskie ziem Polskich (Mollusca Miocaenica Poloniae), 1. Ślimaki i łódkonogi, 1. Gastropoda et Scaphopoda. – **5**: 441–631, pls 27–38, Lwow (Muzeum Imienia Dzieduszyckich).

Glibert, M. (1962): Euthyneura et Pulmonata fosiles du Cénozoique Étranger des collections de l'Institut Royal des Sciences Naturelles de Belgique. – Institut Royal des Sciences Naturelles de Belgique, Mémoires, **70**: 1–140.

GOFAS, S. & ROSENBERG, G. (2015): *Siphonaria* G. B. SOWERBY I, 1823. In: MolluscaBase (2015). Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=138489 on 2015-08-21.

GRATELOUP, J.P.S. de (1828): Tableau des coquilles fossiles qu'on rencontre dans les terrains calcaire tertiaires (faluns) des environs de Dax, dans le Département des Landes. – Bulletins d'Histoire Naturelle de la Société Linnéenne de Bordeaux, **2**: 72–109.

GRATELOUP, J.P.S. de (1836): Introduction à la conchyliologie fossile des terrains tertiaires du Bassin de l'Adour. – Actes de la Société Linnéenne de Bordeaux, **8**: 247–299.

GRATELOUP, J.P.S. de (1845–1847): Conchyliologie fossile des terrains tertiaires du Bassin de l'Adour (environs de Dax), 1. Univalves. Atlas. – 48 pls, Bordeaux (Th. Lafargue).

GRAY, J.E. (1827): Plate Mollusca [= plate 3], plate Mollusca III [= plate 4], plate Mollusca IV [= plate 6]. – In: SMEDLEY, E. & ROSE, H.J. (eds.): Encyclopaedia Metropolitana, **7**: Plates to Zoology (Samuel Taylor Coleridge).

GRAY, J.E. (1847): A list of the genera of Recent Mollusca, their synonyma and types. – Proceedings of the Zoological Society of London, **1847**: 129–219.

GÜLLER,M., ZELAYA, D.G. & ITUARTE, C. (2015, online): How many *Siphonaria* species (Gastropoda: Euthyneura) live in southern South America? – Journal of Molluscan Studies, doi: 10.1093/mollus/eyv036.

HABE, T. (1961): Coloured illustrations of the shells of Japan, volume 2. – 182+42 pp., 66 pls, Osaka (Hoikusha).

HARZHAUSER, M. & PILLER, W.E. (2007): Benchmark data of a changing sea. Palaeogeography, Palaeobiogeography and events in the Central Paratethys during the Miocene. –Palaeogeography, Palaeoclimatology, Palaeoecology, **253**: 8–31.

HARZHAUSER, M., LANDAU, B.M., MANDIC, O., KROH, A., KUTTELWASCHER, K., GRUNERT, P., SCHNEIDER, S. & DANNINGER, W. (2015): Gastropods of an Ottnangian (Early Miocene) rocky shore in the North Alpine Foreland Basin (Allerding, Austria). – Jahrbuch der Geologischen Bundesanstalt, **154**: 83–113.

HUBENDICK, B. (1946): Systematic monograph of the Patelliforma. – Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien, **23**: 1–93.

KOVÁCS, Z. & VICIÁN, Z. (2013): Badenian (Middle Miocene) Conoidean (Neogastropoda) fauna from Letkés (N Hungary). – Fragmenta Palaeontologica Hungarica, **30**: 53–100.

KURODA, T., HABE, T. & OYAMA, K. (1971): The sea shells of Sagami Bay. – 489 pp., 1219 pls, Tokyao (Maruzen).

LE RENARD, J. & PACAUD, J.-M. (1995): Révision des Mollusques paléogènes du Bassin de Paris. 2 – Liste des références primaires des espèces. – Cossmanniana, **3**: 65–132.

LINNAEUS, C. (1758): Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 1. Editio decima, reformata. – 824 pp., Holmiae (Laurentii Salvii).

LOZANO-FRANCISCO, M.C., VERA-PELÁEZ, J.L., SIMÓN VALLEJO, M.D. & CORTÉS SÁNCHEZ, M. (2004): Nuevos datos sobre el registro malacológico del Pleistoceno Superior-Holoceno de la Cueva de Nerja (Málaga, España). – Revista Española de Paleontología**,** **19**: 215–228.

LOZOUET, P., LESPORT, J.F. & RENARD, P. (2001): Révision des Gastropoda (Mollusca) du stratotype de l'Aquitanien (Miocène inf.): site de Saucats 'Lariey', Gironde, France. – Cossmanniana, hors série **3**: 189 pp., 37 pls.

MCLEAN, J.H. (2011): Reinstatement of the fissurellid subfamily Hemitominae, with the description of new genera, and proposed evolutionary lineage, based on morphological characters of shell and radula (Gastropoda: Vetigastropoda). – Malacologia, **54**: 407–427.

MICHELIN, H. (1831a): Siphonaire. *Siphonaria* SOWERBY, S. bisiphite. *S. bisiphites*. MICHELIN. – Magasin de Zoologie, **1**: 5.

MICHELIN (1831b): Siphonaire. *Siphonaria* SOWERBY, S. de Gascogne. *S. vasconiensis* MICHELIN. – Magasin de Zoologie, **1**: 32.

MICHELOTTI, G. (1847): Description des fossiles des terrains miocènes de l'Italie septentrionale. Ouvrage publié par la société Hollandaise des Sciences, et accompagné d'un atlas de 17 planches. – 408 pp., Leiden (A. Arns & Compie).

ORBIGNY, A. D' (1852): Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés, faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique, **3**: 1–196, index 1–189, Paris (Victor Masson).

PEYROT, A. (1932): Conchologie néogénique de l'Aquitaine. – Actes de la Société Linnéenne de Bordeaux, **84**: 5–288.

PEYROT, A. (1938): Les mollusques testacés univalves des dépots Helvétiens du Bassin Ligérien. Catalogue critique, descriptif et illustré. – Actes de la Société Linnéenne de Bordeaux, **89**: 5–361.

POPOV, S.V., RÖGL, F., ROZANOV, A.Y., STEININGER, F.F., SHCHERBA, I.G. & KOVÁČ, M. (2004): Lithological-Paleogeographic maps of Paratethys. 10 Maps Late Eocene to Pliocene. – Courier Forschungsinstitut Senckenberg, **250**: 1–46.

SACCO, F. (1896): I molluschi dei terreni terziarii del Piemonte e della Liguria. Parti XIX, XX, XXI e XXII (fine die Gasteropodi e Scafopodi). – Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Universita di Torino, **11**: 79–98.

SACCO, F. (1897): I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 22: Gasteropoda (fine) (Pleurotomariidae, Scissurellidae, Haliotidae, Fissurellidae, Tecturidae, Patellidae, Oocorythidae, Cyclophoridae, Cyclostomidae, Aciculidae, Truncatellidae, Actaeonidae, Tornatinidae, Scaphandridae, Bullidae, Cylicnidae, Philinidae, Umbrellidae). – Pulmonata (Testacellidae, Limacidae, Vitrinidae, Helicidae, Pupidae, Stenogyridae, Succineidae, Auriculidae, Limnaeidae, Physidae; Siphonariidae). Amphineura (Chitonidae). – Scaphopoda (Dentaliidae). – 128 pp., Torino (Carlo Clausen).

SERRES, M. DE (1829): Géognosie des terrains tertiaires, ou tableau des principaux animaux invertébrés des terrains marins tertiaires du Midi de la France. – 276 pp., Montpellier (Pomathio-Durville).

SISMONDA, A.E. (1842): Synopsis methodica animalium invertebratorum pedemontii fossilium. – 142 pp., Augustae Taurinorum (Typis Regiis).

SISMONDA, E. (1847): Synopsis methodica animalium invertebratorum pedemontii fossilium (exceptis speciebus ineditis). – viii + 62 pp., Augustae Taurinorum (Typis Regiis).

SOWERBY, G.B., I. (1822–1834): The genera of recent and fossil shells, for the use of students in conchology and geology: plates of genera; also corresponding letter-press, descriptive of the characters by which each genus is distinguished. Particularly the land, fresh water & marine nature of each genus, as well as the strata in which fossil species occur. – Vol. 1, 274 pp. Vol. 2 (Atlas), 264 pls, London (G.B. Sowerby).

SWAINSON, W. (1840): A treatise on malacology, or shells and shell-fish. – 2+viii+419 pp., London (Longman).

VASSEUR, G. (1881): Recherches géologiques sur les terrains tertiaires de la France occidentale. 1ere partie: Bretagne. – 432 pp., Paris (Masson).

ZUNINO, M. & PAVIA, G. (2009): Lower to Middle Miocene mollusc assemblages from the Torino hills (NW Italy): synthesis of new data and chronostratigraphical arrangement. – Rivista Italiana di Paleontologia e Stratigrafia, **115**: 349–370.