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Chemosymbiotic bivalves from Miocene methane-seep carbonates in Italy

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Abstract.—Eleven species of chemosymbiotic bivalves are reported from middle to late Miocene methane seep deposits ('Calcari a *Lucina*') in the Italian Apennines, including seven new species and one new genus. The new species are *Bathymodiolus* (s.l.) *moroniae* and *B.* (s.l.) *miomediterraneus* among the Bathymodiolinae and *Archivesica aharoni*, *A. apenninica*, *A. strigarum*, and '*Pliocardia*' *italica* among the Vesicomyidae; specimens from the middle Miocene of Deruta are reported as *Archivesica* aff. *aharoni*. *Samiolus iohannesbaptistae* new genus new species is introduced for an unusual mytilid with a commarginally ribbed surface, which might be the first non-bathymodiolin mytilid obligate to the seep environment. The two large lucinid species from which these deposits derived their informal name 'Calcari a *Lucina*' are identified as *Meganodontia hoernea* (Des Moulins, 1868) and *Lucinoma perusina* (Sacco, 1901). With *Chanellaxinus* sp., we report the first thyasirid from a Neogene deep-water seep deposit in Italy and the first fossil occurrence of this genus.

Introduction

Limestone deposits yielding large lucinid bivalves have been known for centuries from the Miocene deposits in Italy, and were termed 'Calcari a *Lucina*' (Manzoni, 1876; Coppi, 1877; Scarabelli, 1880; Sacco, 1901; Di Stefano, 1903). Due to their isolated occurrence in deep-water sediments and the large bivalves preserved in them, they were considered to have been transported from shallow water (Ricci Lucchi and Veggiani, 1967). This view changed after the first discovery of faunal communities at methane seeps in the deep Gulf of Mexico with similarly large bivalves (Paull et al., 1984) and the recognition that methane seep carbonates can be identified based on their distinctive, light carbon isotope signature (Hovland et al., 1987). The 'Calcari a *Lucina*' deposits throughout Italy are now considered as ancient deep-water methane seep deposits (Clari et al., 1988; Conti et al., 1993; Terzi, 1993; Aharon and Sen Gupta, 1994; Berti et al., 1994; Ricci Lucchi and Vai, 1994; Taviani, 1994; Terzi et al., 1994; Peckmann et al., 1999; Clari et al., 2004b; Conti et al., 2004, 2010). Despite this wealth of geologic literature on these deposits, modern studies on the macrofauna are relatively rare (Moroni, 1966; Taviani, 1994, 2011, 2014; Taviani et al., 2011). The purpose of the present contribution is to provide a revision of the major taxa of chemosymbiotic bivalves of the 'Calcari a *Lucina*' deposits, with exclusion of solemyids.

Materials and methods

Specimens were coated with ammonium chloride for photography. The material is from twelve seep deposits of middle to late Miocene age (Fig. 1) associated with deep-water hemipelagic marls or turbidites, mostly ascribed to the Marnoso-arenacea Formation. Their geological and stratigraphic context is described in various publications (Vai et al., 1997; Conti and Fontana, 1999; Clari et al., 2004b; Taviani, 2011). A short description of the localities is provided in the Appendix.

Repositories and institutional abbreviations.—MGGC: Museo Geologico Giovanni Capellini, University of Bologna; MSF: Museo Civico di Scienze Naturali, Faenza; MZB: Museo dell'Evoluzione (formerly Zoologia), University of Bologna; MRSN: Museo Regionale di Scienze Naturali, Torino (managing the Bellardi and Sacco collection, property of the Turin University).

Systematic paleontology

Class Bivalvia Linnaeus, 1758
Subclass Pteriomorphia Beurlen, 1944
Order Mytilida Férussac, 1822
Family Mytilidae Rafinesque, 1815
Genus *Bathymodiolus* Kenk and Wilson, 1985

Type species.—*Bathymodiolus thermophilus* Kenk and Wilson, 1985, Recent, Galapagos Rift Zone, by original designation.

Remarks.—Molecular phylogenetic studies have shown that species currently classified as *Bathymodiolus* belong to at least two clades within the bathymodiolins (Gustafson et al., 1998; Jones et al., 2006; Lorion et al., 2010, 2013; Thubaut et al., 2013), of which those related to *B. childressi* may be placed in a separate genus. This species group is often referred to as the '*childressi* clade' and it is recommended to use "*Bathymodiolus*" only in quotation marks for these species until the taxonomic uncertainties

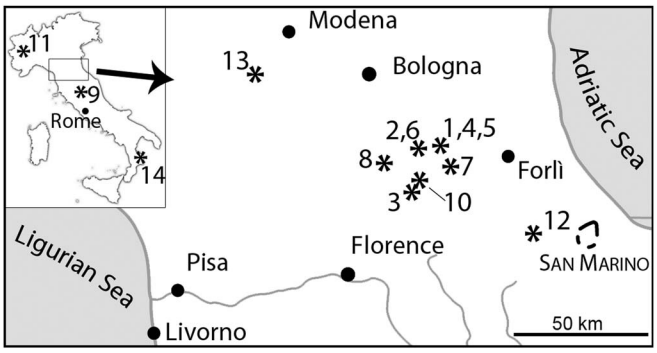

Figure 1. Maps showing the fossil localities discussed in the text. Left panel, general map of Italy showing all localities: 1 = Abisso "Mornig", 2 = Ca' Carnè, 3 = Ca' Cavalmagra, 4 = Monticino-Limisano – Castelnuovo junction, 5 = Ca' Fornace, 6 = Ca' Pianté, 7 = Case Rovereti, 8 = Castelvecchio, 9 = Deruta, 10 = Le Colline, 11 = Marmorito, 12 = Montepetra, 13 = Sasso delle Streghe, 14 = Verzino.

are settled (Gustafson et al., 1998). Morphologically, the two clades can be distinguished based on muscle-scar pattern (Gustafson et al., 1998), which, unfortunately, is not preserved in any of the fossils reported here from northern Italy. Therefore, we refer to them as *Bathymodiolus* (sensu lato).

Bathymodiolus (s.l.) *moroniae* new species
Figure 2

1966 *Modiolus* (*Modiolus*) *exbrocchii exbrocchii* Sacco; Moroni, p. 78, pl. 5, fig. 2, pl. 6, fig. 4.
1996 *Bathymodiolus exbrocchii* Sacco; Taviani, fig. 2a, 4c.
2001 Modiolinid Taviani, fig. 20.7a.
2011 "*Bathymodiolus*" cf. *exbrocchii* (Sacco, 1898); Taviani, fig. 3c.

Type specimens.—Holotype: MGGC 21907, single right valve from Case Rovereti. Paratypes: seven specimens from Case Rovereti: MZB 27218, 27268, 27270, 27272, 27273; MGGC 21921, 21922; one from Monticino-Limisano – Castelnuovo junction: MSF 1100; one from Ca' Piantè (MSF 2135, on same large block as MSF 1360); one from Abisso "Mornig" (MSF 2119).

Diagnosis.—Medium- to large-sized "*Bathymodiolus*" with blunt, elevated umbo at anterior 10% of total shell length; dorsal and ventral margins nearly straight, posterodorsal corner at posterior third of shell; maximum inflation just anterior to anterior third of shell.

Occurrence.—Late Miocene seep carbonates in Italy.

Description.—Moderately inflated modioliform shell, maximum inflation at ~27% of total shell length; blunt, elevated umbo at anterior 10% of total shell length, anterior margin narrow, convex; ventral margin straight, slightly concave in large specimens; dorsal margin straight to very slightly curved; posterodorsal corner at posterior third of shell; surface smooth except for growth increments; hinge area in juvenile specimens with row of taxodont teeth below the ligament attachment line, smooth in adults; pallial line distant from shell margin, numerous mantle muscle scars toward interior; shell composed of a calcitic fibrous prismatic outer layer and a nacreous inner layer.

Etymology.—To honor Maria Antonietta Moroni, for her seminal work on the 'Calcari a *Lucina*' fauna.

Materials.—Forty-four valves (including MZB 27064, 27271, 27278, 27281) from Case Rovereti; three specimens from Verzino (MGGC 21923, 21924, 21925); one from Deruta (MGGC 21926); seven articulated shells from Deruta (MRSN, under cf. *Bathymodiolus exbrocchii*, PU 40607); one articulated specimen from Verzino MGGC 21927; three articulated shells (MSF 1360) plus one valve from Ca' Piantè; and specimens from Montepetra; four valves from block from Monticino-Limisano – Castelnuovo junction, Brisighella (MSF 1106-1109); five valves from Abisso "Mornig" (MSF 1086, 1090, 1094, 1097, 2120); see Table 1 for measurements.

Remarks.—The assignment of this species to *Bathymodiolus* (sensu lato) is based on its general shape, the change from a hinge with denticles in young specimen to an edentulous hinge in adults, its shell microstructure (cf., Génio et al., 2012), and its mass occurrence at seep deposits. The early juvenile shell shape and adductor and retractor muscle scars, which have been used to identify other fossil bathymodiolins (Kiel, 2006; Kiel and Goedert, 2007; Saether et al., 2010; Amano and Jenkins, 2011; Kiel and Amano, 2013) are not preserved in *Bathymodiolus* (s.l.) *moroniae* n. sp.

Nelli (1903) and Moroni (1966) had identified this species as *Modiolus* (*Modiolus*) *exbrocchii exbrocchii* Sacco, 1898, which was named by Sacco (1898) based on an illustration of *Modiola brocchii* Mayer in Hörnes, 1870 from the Vienna Basin (Hörnes, 1870, p. 345, pl. 45, fig. 13a, b). However, this species differs from *B*. (s.l.) *moroniae* by being more elongate and by having a distinct and sharp ridge running from the umbo to the posteroventral margin, whereas *B*. (s.l.) *moroniae* is smoothly convex. Furthermore, specimens of *B*. *moroniae* with the size of *M*. *exbrocchii* as figured by Hörnes (11 cm) are more compact and less elongate that *M*. *exbrocchii*.

Most similar in general shell shape are specimens of *B*. *brevior* von Cosel, Métivier, and Hashimoto, 1994 living at hydrothermal vents in the Indian Ocean (this population was formerly called *B*. *marisindicus* Hashimoto, 2001, but later synonymized with *B*. *brevior*, based on molecular data), and *B*. *puteoserpensis* von Cosel, Métivier, and Hashimoto, 1994 from the Mid-Atlantic Ridge (von Cosel et al., 1994; Hashimoto, 2001). Another similar species is *B*. *brooksi* from the Gulf of Mexico (Gustafson et al., 1998). Interestingly, these three morphologically most similar species all belong to *Bathymodiolus* sensu strictu and not to the *childressi* clade.

Unlike bathymodiolins at most other fossil seep deposits, *Bathymodiolus* (s.l.) *moroniae* n. sp. occurs mostly as disarticulated valves, especially in adult stages.

Bathymodiolus (s.l.) *miomediterraneus* new species
Figure 3

Type specimens.—Holotype: MGGC 21908; paratypes: MSF 1351 (two articulated shells), MSF 1352 (two articulated shells,

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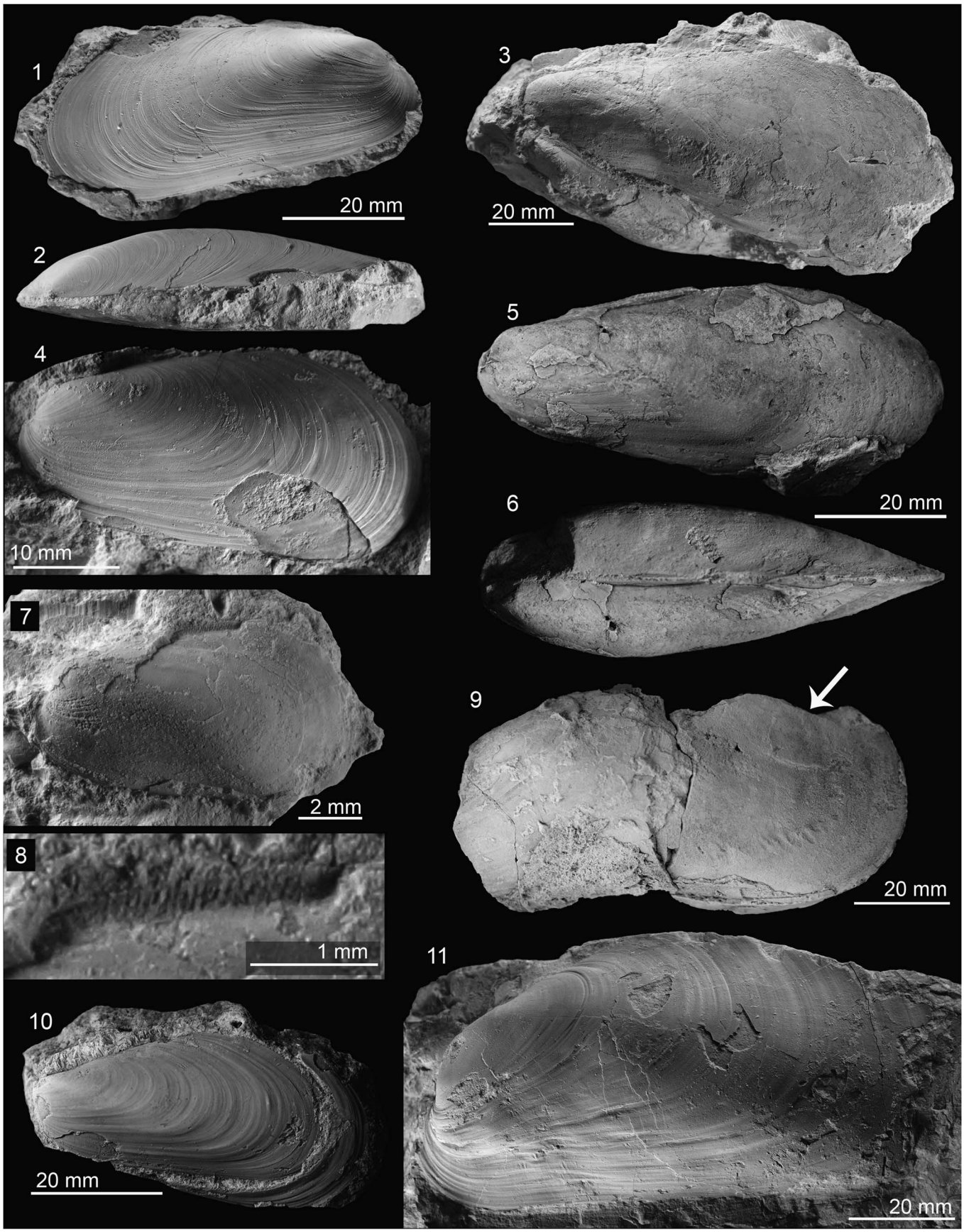

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Table 1. Measurements of *Bathymodiolus* (s.l.) *moroniae* new species; H = height, L = length, W = width of two valves, except when indicated otherwise.

Locality	Specimen	L (mm)	H (mm)	W (mm)
Case Rovereti	MZB 21907, holotype	61	27.8	9.3 (single)
Case Rovereti	MZB 27270, paratype	41.7	21.4	8.5 (single)
Case Rovereti	MZB 27218, paratype	52.0		
Case Rovereti	MZB 27268, paratype	72 (incomplete)	33.0	13 (single)
Case Rovereti	MZB 27273, paratype	110 (incomplete)	49	17 (single)
Case Rovereti	MZB 27273, specimen on same block	64.0	29	
Case Rovereti	MZB 27272	39.0	20	12
Case Rovereti	MGGC 21927	27.6	14.3	9.5
Verzino	MGGC 21923	74 (incomplete)	37	9.5 (single)
Verzino	MGGC 21924	61 (incomplete)	25	18 (single)
Verzino	MGGC 21925	87 (incomplete)	47	
Case Rovereti	MGGC 21920	95	42	15.5 (single)
Case Rovereti	MGGC 21921	41.2 (incomplete)	20	10.4
Case Rovereti	MGGC 21922	11	5.4	2 (single)
Bivio Castelnuovo	MSF 1100	101.5 (incomplete)	49.5	17.5
Ca' Piantè	MSF 1360, paratype	133	52	16
Ca' Piantè	MSF 1360, specimen on same block	93 (incomplete)	40	12
Abisso "Mornig"	MSF 1086			
Abisso "Mornig"	MSF 2119			
Abisso "Mornig"	MSF 2120	85		
Abisso "Mornig"	MSF 1090	60		
Abisso "Mornig"	MSF 1097	85		
Abisso "Mornig"	MSF 1094	82 (incomplete)		

one figured), MSF 1353 (right valve), MSF 1190 (left valve); all types from Le Colline.

Diagnosis.—Small- to medium-sized "*Bathymodiolus*" with subterminal umbo, broad anterior margin, and arched dorsal margin; maximum inflation just anterior to middle of shell; blunt ridge running from umbo to posteroventral corner.

Occurrence.—Middle Miocene (early Serravallian) seep carbonates at Le Colline in northern Italy.

Description.—Well inflated, moderately sized, arched modioliform shell with low, subterminal umbo; maximum inflation just anterior of center; anterior margin broad and well rounded, posterodorsal margin broadly arched in large specimens, smaller specimens with distinct posterodorsal corner, ventral margin slightly concave in small specimens, strongly concave in large ones; posterior margin gently rounded; blunt ridge running from umbo to posteroventral corner; surface smooth except for growth increments.

Etymology.—Referring to the Miocene Mediterranean Basin.

Materials.—Three specimens from Le Colline (MSF 2136); see Table 2 for measurements.

Remarks.—Similar in shape is '*Modiola*' *pistacina* Sacco, 1904 from the Burdigalian of Piedmont (Sacco, 1904, pl. 29, fig. 6a, b; Merlino, 2007, pl. 6, figs. 8, 9); the type specimen is small (~13 mm long) and has the umbo in a more posterior position and a broader anterior margin than *B. miomediterraneus* n. sp. '*Modiola*' *pistacina* may be related to small bathymodiolins such as "*Idas*" and should be further investigated in the context of whale- and wood-fall communities in the Italian Neogene. The middle Miocene '*Modiola*' *exbrocchii* (e.g., the specimen illustrated as *Modiola brocchii* by Hörnes, 1870) and its variation *M. exbrocchii* var. *tauroparva* Sacco, 1898, a small species of ~20 mm length (Sacco, 1898, pl. 11, figs. 28, 29; Merlino, 2007, pl. 6, fig. 7), have a more elevated umbo and a more distinctive ridge running from the umbo to the posterior-ventral margin than *B. miomediterraneus*. The new species differs from *Bathymodiolus* (s.l.) *moroniæ* n. sp. by having the umbo in a more anterior (subterminal) position. The most similar Recent species are *Bathymodiolus mauritanicus* von Cosel, 2002, which occurs off West Africa and in the Gulf of Cadiz (von Cosel, 2002; Génio et al., 2008) and appears to have a broader posterior margin than *B.* (s.l.) *miomediterraneus* n. sp., and the Japanese *Bathymodiolus hirtus* Okutani, Fujikura, and Sasaki, 2004, which has a more elevated umbo as adult than *B.* (s.l.) *miomediterraneus* n. sp. and is broader (less slender) as juvenile (Okutani et al., 2004). A fossil species with a similar subterminal umbo is the presumably Oligocene *Bathymodiolus* (s.l.) *palmarensis* from Colombia (Kiel et al., 2010), but it differs from *B.* (s.l.) *miomediterraneus* n. sp. by being more elongate and by having almost straight anterior and posterior margins. *Bathymodiolus* (s.l.) *miomediterraneus* n. sp. is typically found with articulated valves, in contrast to *Bathymodiolus* (s.l.) *moroniae* n. sp. and *Samiolus iohannesbaptistae* n. gen. n. sp.

Genus *Samiolus* new genus

Type species.—*Samiolus iohannesbaptistae* new genus new species, from late Miocene seep deposits in northern Italy.

Figure 2. *Bathymodiolus* (s.l.) *moroniae* new species from Miocene seep deposits in Italy: (**1, 2**) holotype (MGGC 21907) from Case Rovereti, isolated right valve; (**3**) paratype (MZB 27273) from Case Rovereti, internal mold of large specimen, left valve; (**4**) paratype (MZB 27270) from Case Rovereti, left valve with preserved shell; (**5, 6**) paratype (MRSN PU 40607.01) from Deruta, internal mold of articulated specimen; (**7, 8**) paratype (MGGC 21922) from Case Rovereti, left valve of juvenile specimen showing fine taxodont dentition on posterior side of shell; (**9**) paratype (MSF 2119) from Abisso "Mornig," left valve, anterior side with shell remains, posterior side internal mold showing pallial line and adductor muscle scar; (**10**) paratype (MRSN PU 40607.02) from Deruta, left valve with preserved shell; (**11**) paratype (MSF 1100) from the Monticino-Limisano – Castelnuovo junction, large right valve with preserved shell.

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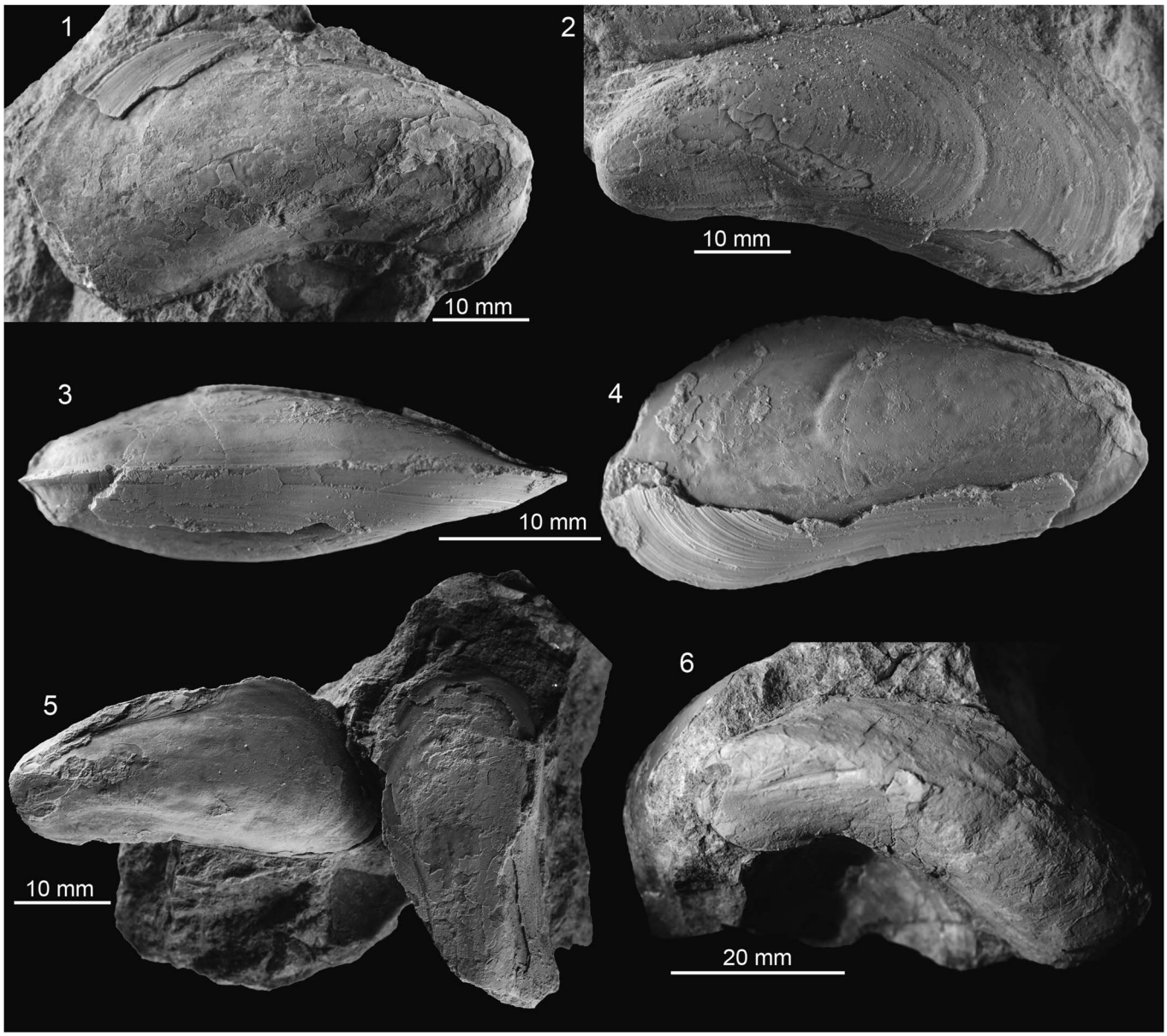

Figure 3. *Bathymodiolus* (s.l.) *miomediterraneus* new species from the middle Miocene seep deposit at Le Colline, northern Italy: (**1**) paratype (MSF 1353) with strongly concave ventral margin, right valve; (**2**) holotype (MGGC 21908) showing broadly arched dorsal margin, left valve; (**3, 4**) paratype (MSF 1352), small specimen showing right valve and in ventral view, respectively; (**5**) block with two paratypes (MSF 1351), view of left valves; (**6**) strongly arched, gerontic specimen (MSF 1190).

Table 2. Measurements of *Bathymodiolus* (s.l.) *miomediterraneus* new species, all specimens from Le Colline, northern Italy; H = height, L = length, W = width of two valves, except when indicated otherwise.

Specimen	L (mm)	H (mm)	W (mm)
holotype, MGGC 21908, MSF 1246	55.5	25.1	10 (single)
MSF 1190	54.0	24.5	8.2 (single)
MSF 1351	51.0	22.0	9.6 (single)
MSF 1352	34.0	15.0	11.0
MSF 1353	33.5 (incomplete)	17.6	
MSF unnumbered	36.3	18.0	12.0
MSF unnumbered	57.7	27.6	7.5 (single)
MSF unnumbered	37.8	16.4	13.7

Diagnosis.—Small- to medium-sized modioliform shell; strong, almost angular ridge from umbo to posteroventral corner; posterior part of shell sculptured by roughly commarginal wrinkles, unlike any other mytilid.

Etymology.—The name combines the name *Sami*, crediting the paleontologist Marco Sami, who was responsible for collecting a substantial number of valuable macrofossils from 'Calcari a *Lucina*', including this new taxon, with the mytilid genus *Modiolus*, which has a similar shell shape.

Remarks.—*Samiolus* n. gen. contains presently only the type species. A similar strong and sharp ridge can be seen in *Gibbomodiola taurarcuata* Sacco, 1898 from the Italian Miocene (Sacco, 1898, pl. 11, figs. 34a, 35b; Merlino, 2007, pl. 6, fig. 10), but this species lacks wrinkles (own observations on Sacco's type material housed in the Turin Museum). Another species with a similar ridge is *Modiola dombraviensis* Kittl, 1887 from middle Miocene 'blue deep-water clays' in eastern Czech Republic and southern Poland (Kittl, 1887, p. 272, pl. 9, figs. 7–11).

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But *Modiola dombraviensis* has a nearly smooth surface with only fine growth increments and lacks the wrinkled sculpture of *Samiolus iohannesbaptistae* n. sp. (own observation of material housed in the Natural History Museum Vienna). This wrinkled surface sculpture distinguishes *Samiolus iohannesbaptistae* n. gen. n. sp. also from all fossil and extant bathymodiolins (Squires and Goedert, 1991; von Cosel and Olu, 1998; Gustafson et al., 1998; von Cosel, 2002; Sasaki et al., 2005; Desbruyères et al., 2006; von Cosel and Janssen, 2008; Lorion et al., 2010; Amano and Jenkins, 2011).

Samiolus iohannesbaptistae new species
Figure 4

Type specimens.—Holotype MGGC 21910 from Ca' Carnè; paratypes: three specimens from Ca' Carnè: MSF 1073, MSF 1120 (left valve), MZB 60090; one specimen from Ca' Piantè: MSF 1355.

Diagnosis.—Same as generic diagnosis.

Occurrence.—Late Miocene (late Tortonian) seep carbonates in northern Italy.

Description.—Modioliform, small- to moderately sized shell, umbo subterminal; posterodorsal margin slightly arched,

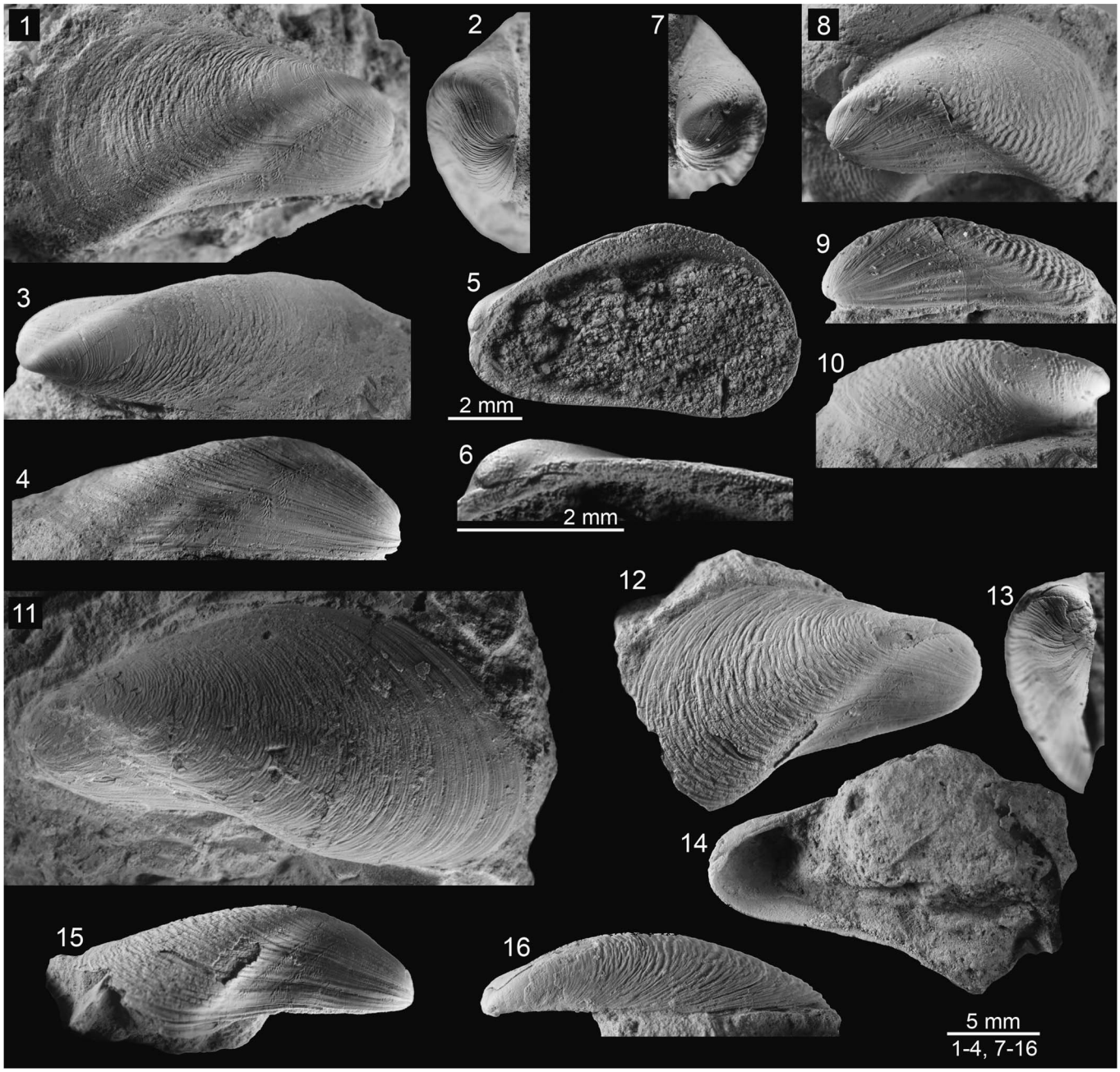

Figure 4. *Samiolus iohannesbaptistae* new genus new species from late Miocene seep deposits in northern Italy: (**1–4**) paratype (MSF 1073) from Ca' Carnè, four views on right valve; (**5, 6**) interior of small specimen (MGGC 23010) from Ca' Carnè, showing hinge dentition of right valve; (**7–10**) paratype (MSF 1120) from Ca' Carnè, right valve; (**11**) large specimen (MSF 1355) from Ca' Piantè, left valve; (**12–16**) holotype (MGGC 21910) from Ca' Carnè, five views of right valve.

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posterodorsal corner at ~60% total shell length, ventral margin convex; strong ridge starting posterior of umbo, running to posteroventral corner, anterodorsal margin of ridge almost angular, followed by broad groove; shell surface anterior of ridge smooth except for growth lines, posterior side shows ribbing or wrinkles, resulting from irregular, roughly commarginal thickenings. Juvenile specimen with fine taxodont hinge teeth along entire posterodorsal margin and on oval hinge plate below beak; hinge area in adult smooth. Largest specimen 33 mm long, 17 mm high, single valve 7 mm wide; a juvenile specimen with taxodont hinge teeth measures 8.3 mm in length.

Etymology.—To honor Gian Battista Vai in recognition of his leading role in the modern study of 'Calcari a *Lucina*.'

Materials.—Eight specimens from Ca' Carnè; six from Ca' Piantè; three valves from Montepetra (MZB 60095), and one valve from Case Rovereti (MSF 1356); see Table 3 for measurements.

Remarks.—We have found mostly disarticulated specimens of this species. One specimen has been figured by Sami and Taviani (2015, fig. 7).

Subclass Heterodonta Neumayr, 1884
Family Thyasiridae Dall, 1900
Genus *Channelaxinus* Valentich-Scott and Coan in Coan and Valentich-Scott, 2012

Type species.—*Channelaxinus oliveri* Valentich-Scott and Coan in Coan and Valentich-Scott (2012), (by original designation); Recent, Bahía Santiago, Colima, México.

Channelaxinus sp.
Figure 5

Description.—Shells subrectangular, thin-shelled, reaching 20 mm in length and 16 in height, only slightly inflated, sculptured by irregular growth lines and indistinct, blunt ridge running from umbo to postero-ventral corner; beak prosogyrate, projecting slightly above dorsal margin; anterior margin straight to slightly concave, ventral margin gently convex, postero-ventral corner well rounded, posterior margin gently convex below sulcus, postero-dorsal margin slightly convex, with deep sinus at end of posterior sulcus; posterior sulcus deep, bordered by sharp ridge, area between sulcus and postero-dorsal margin narrow, with narrow submarginal sulcus; anterior adductor muscle scar thin, elongate, weakly impressed, separated from pallial line, length just over half of shell length; interior radiating striae distinct.

Table 3. Measurements of *Samiolus* (s.l.) *iohannesbaptistae* new genus and species; H = height, L = length, W = width of two valves, except when indicated otherwise.

Locality	Specimen	L (mm)	H (mm)	W (mm)
Ca' Carnè	MGGC 21910, holotype	19.0	1.1	5.7 (single)
Ca' Carnè	MSF 1119	12.6	7.5	3 (single)
Ca' Carnè	MSF 1120, paratype	14.6	9.0	3.5 (single)
Ca' Carnè	MSF 1073, paratype	20.2	10.0	4.6 (single)
Ca' Carnè	MGGC unnumbered	20.2 (incomplete)	10.2	4 (single)
Ca' Carnè	MGGC unnumbered	18.0	8.8	4 (single)
Ca' Carnè	MGGC unnumbered	8.5	4.7	1.8 (single)
Ca' Piantè	MSF 1071	16.7	13.5	4.5 (single)
Ca' Piantè	MSF 1072	33.2	16.3	7.7 (single)
Ca' Piantè	MSF 1355, paratype	30.0	15.0	8 (single)
Case Rovereti	MSF 1356	25.0	13.5	6 (single)

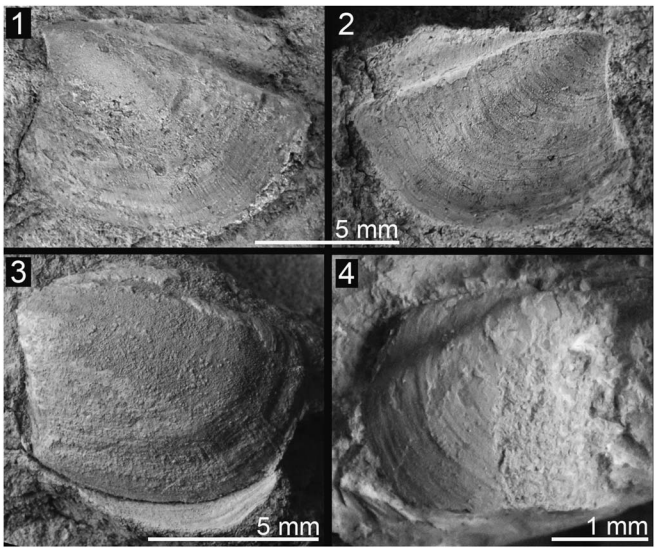

Figure 5. *Channelaxinus* sp. from the middle Miocene (Langhian) of Ca' Cavalmagra, northern Italy: (**1, 2**) left valve (MSF 2113), internal mold and counterpart with small amount of shell preserved; (**3**) left valve (MSF 1287), internal mold with few shell remains; (**4**) right valve (MSF 2112) of small specimen.

Materials.—Three specimens from Ca' Cavalmagra (MSF 1287, 2112, 2113).

Occurrence.—Only known so far from the late Langhian of Ca' Cavalmagra.

Remarks.—A superficially similar thyasirid from the Miocene of the Turin Hills is *Thyasira michelottii* (Hörnes, 1875), but it clearly differs from *Channelaxinus* sp. reported here by having a much shorter anterior adductor muscle scar (Zuschin et al., 2001). The extant type species *Channelaxinus oliveri* differs from *Channelaxinus* sp. mainly by having a narrower angle between the anterior and dorsal margins and a blunter (less pointed) umbo (Coan and Valentich-Scott, 2012; Oliver and Frey, 2014). This is the first fossil record of *Channelaxinus*.

Family Lucinidae Fleming, 1828
Genus *Meganodontia* Bouchet and von Cosel, 2004

Type species.—*Meganodontia acetabulum* Bouchet and von Cosel, 2004 (by original designation); Recent, in 256–472 m depth off northern Taiwan.

Meganodontia hoernea (Des Moulins, 1868)
Figures 6, 7

1868 *Lucina hoernea* Des Moulins, p. 368.
1901 *Lucina globulosa* var. *hörnea* Sacco, p. 67, pl. 15, figs. 31–33, pl. 16, fig. 1.
1901 *Lucina globulosa* var. *alta* Sacco, p. 68, pl. 15, fig. 4.

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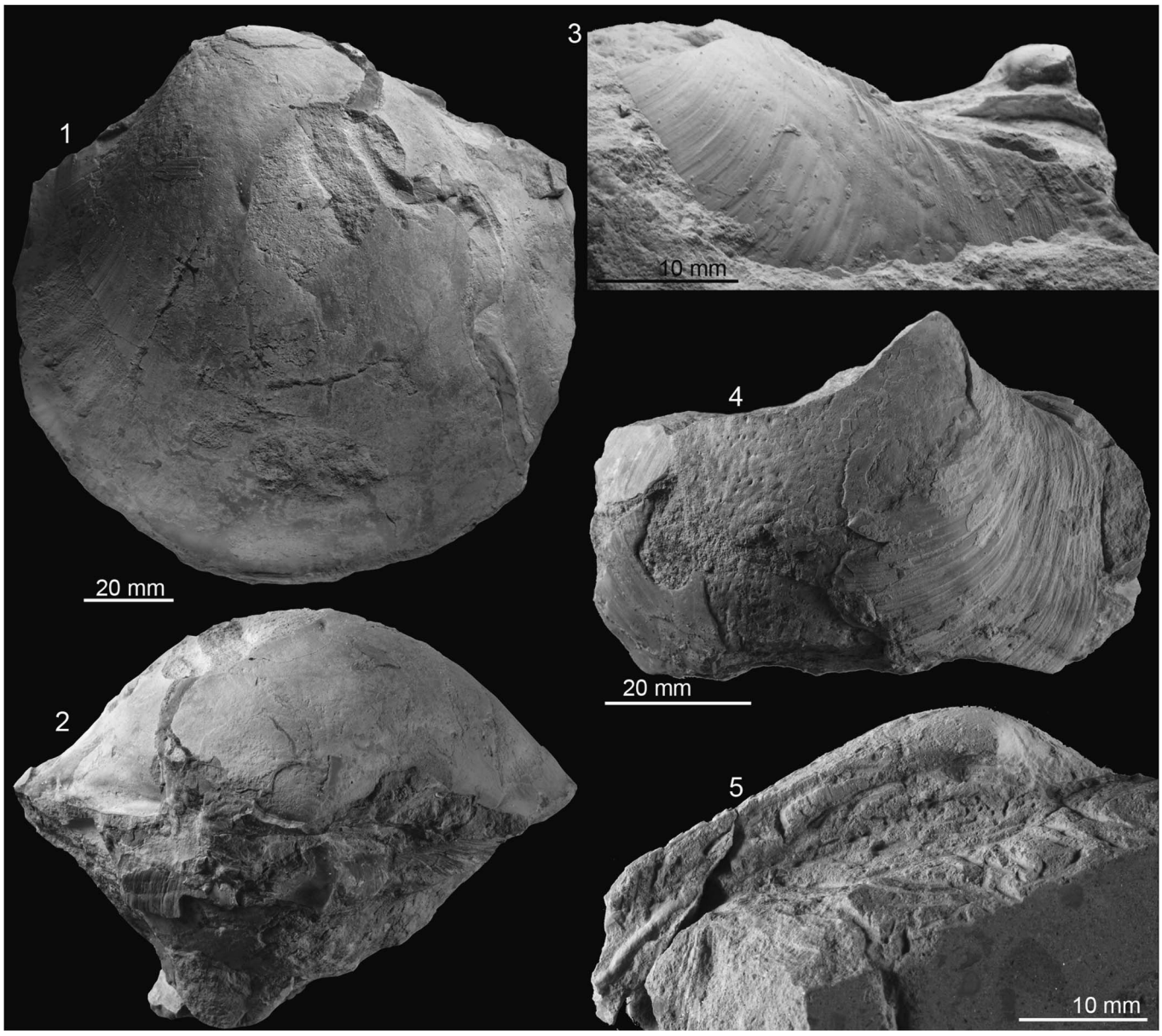

Figure 6. *Meganodontia hoernea* (Des Moulins, 1868) from the late Miocene seep deposit at Ca' Piantè in northern Italy: (**1**) internal mold of left valve (MGGC 23003) showing the elongate anterior adductor muscle scar; (**2**) dorsal view of same specimen as Figure 6.1; (3) left valve in foreground showing posterodorsal shell margin, right valve in background showing edentulous hinge (MGGC 23004); (**4**) outer shell of right valve seen in the background of Figure 6.3; (5) hinge and ligament nymph in left valve (MGGC 23005).

1901 *Lucina globulosa* var. *perinaequilatera* Sacco, p. 68, pl. 15, fig. 5.
1966 *Lucina hoernea*; Moroni, p. 80, pl. 3, fig. 3.
2001 *Lucina* Taviani, fig. 20.1.
2011 "*Lucina*" sp. Taviani, fig. 3a.

Description.—Very large, globular shells, height/length-ratio 0.9; umbones elevated, prosogyrate; external sculpture of fine, irregular, commarginal growth lines, posterodorsal sulcus shallow but distinct; lunule lanceolate, bordered by sharp, smooth ridge. Hinge plate narrow to moderately broad, edentulous, ligament nymph narrow. Anterior adductor muscle scar elongate, detached from pallial line for ~80% of its length, angle of deviation ~30°, width about half the distance to pallial line, curved in the opposite direction as shell margin, reaching below midline to ~44% of total shell height; somewhat constricted posteriorly just below the point of detachment. Interior of shell with numerous pustules, often in rows radiating form umbo; pallial blood vessel scar visible.

Materials.—Eight specimens from Ca' Piantè (MSF 1357; 2100–2104, 2110); 45 articulated shells from Deruta (as *Lucina globulosa hoernea* Desmoulins, Bellardi and Sacco collection in MRSN, PU 40597–40601); one articulated shell from Bersano (as *Lucina globulosa* [Deshayes] var *hoernea*, Bellardi and Sacco collection in MRSN, BS 154.01.001); one articulated shell from Albugnano (as *Lucina globulosa* [Deshayes] var *hoernea* Desmoulins, Bellardi and Sacco collection in MRSN,

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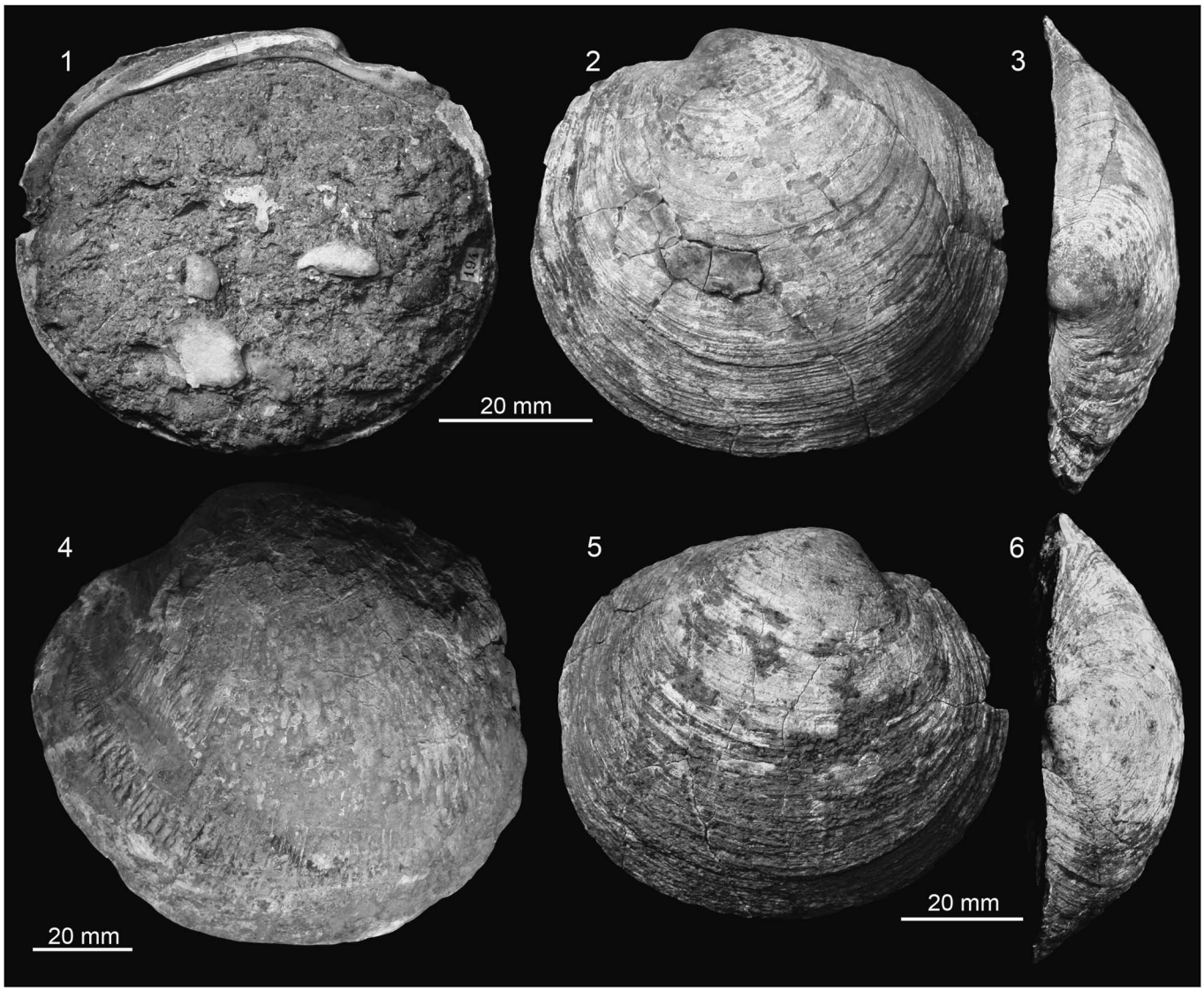

Figure 7. *Meganodontia hoernea* (Des Moulins, 1868), specimens from Sacco's collection from the Turin Hills: (**1–3**) left valve (MRSN BS 154.01.002) from Albugnano, with well-preserved shell material, showing hinge area and external sculpture; (**4**) view of left valve of internal mold (MRSN PU 40603.01) from an unknown locality, showing the elongate anterior adductor muscle scar and the internal pustules; (**5, 6**) right valve (MRSN BS 154.01.001) from Albugnano, showing external sculpture.

BS.154.01.002); two articulated shells from Pino Torinese (as *Lucina globulosa* [Deshayes] var *hoernea* Desmoulins, Bellardi and Sacco collection in MRSN, BS.154.01.003 and BS.154.01.004); one articulated shell from Pera del Gal, Turin Hills (as *Lucina globulosa* [Deshayes] *taurofuchsi* Sacco, 1901, Bellardi and Sacco collection in MRSN, BS.154.01.007); one articulated shell from Pino Torinese (as *Lucina globulosa* [Deshayes] *alta* Sacco, 1901, Bellardi and Sacco collection in MRSN, BS.154.01.008); one articulated shell from Pino Torinese (as *Lucina globulosa* [Deshayes] *perinaequilatera* Sacco, 1901, Bellardi and Sacco collection in MRSN BS.154.01.009); more than 20 articulated shells (molds) from Sasso delle Streghe (Modena), a dozen articulated shells from other localities of the Modena and Forlì Apennines; a dozen articulated shells from the Turin Hills (Sacco's collection in MRSN); see Table 4 for measurements.

Occurrence.—Middle to late Miocene seep carbonates in Italy.

Table 4. Measurements of *Meganodontia hoernea* (Des Moulins, 1868), all specimens from Ca' Piantè, northern Italy; H = height, L = length, W = width of two valves, except when indicated otherwise.

Locality	Specimen	L (mm)	H (mm)	W (mm)
Ca' Piantè	MSF 1357	124.5	123.5	83.0
Ca' Piantè	MGGC 23004	93	65 (incomplete)	29
Ca' Piantè	MSF 2100	180	180	100
Ca' Piantè	MSF 2101	170	160	90
Ca' Piantè	MSF 2102	120	135	85
Ca' Piantè	MSF 2103	150	140	90
Ca' Piantè	MSF 2104	110	110	65
Ca' Piantè	MSF 2110	130	140	83

Remarks.—Bouchet and von Cosel (2004) considered "*Lucina*" *hoernea* not to belong to *Meganodontia* because it has more globose and prominent umbones than *M. acetabulum* and because internal features of "*Lucina*" *hoernea* were not known to them. Here, we show that "*Lucina*" *hoernea* has an edentulous and narrow hinge plate, as well as an elongate, blade-shaped anterior adductor muscle scar just like

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Meganodontia acetabulum. Therefore we consider "*Lucina*" *hoernea* as belonging to *Meganodontia*, but as distinct from *M. acetabulum*. In addition to the differences mentioned above, *Meganodontia hoernea* has a less distinctive posterior adductor muscle scar than *Meganodontia acetabulum*. Moroni (1966) provided an extensive synonymy for *Meganodontia hoernea*. In the *Meganodontia* species from the early Miocene of Cuba (Kiel and Hansen, 2015), the anterior adductor muscle scar deviates from the pallial line at a broader angle, as in *M. hoernea*. Examination of Sacco's type material showed that his "variations" *L. globulosa* var. *alta* Sacco, 1901 and *L. globulosa* var. *perinaequilatera* Sacco, 1901 represent deformed specimens of *Meganodontia hoernea* and should therefore be considered as synonyms.

Taylor et al. (2011) tentatively assigned *Meganodontia* to their new subfamily Pegophyseminae, whose species are united by some unusual morphological characters, including thin, globular, smooth shells, a narrow edentulous hinge with an internal and laterally extended ligament in most species (Taylor et al., 2011). *Meganodontia hoernea* is a common and widespread species in the Miocene of Italy, associated with 'Calcari a *Lucina*' limestones and reducing deep-sea marly sediments.

Genus *Lucinoma* Dall, 1901

Type species.—*Lucina filosa* Stimpson, 1851 (by original designation); Recent, northwest Atlantic.

Lucinoma perusina (Sacco, 1901)
Figures 8, 9

1901 *Dentilucina perusina* Sacco, p. 83, pl. 19, figs. 12–14.
1901 *Dentilucina perusina* var. *pseudorotunda* Sacco, pl. 21, fig. 15.
1966 *Phacoides* (*Lucinoma*) *perusinus* (Sacco); Moroni, p. 82, pl. 5, figs. 1, 3, pl. 6, figs. 1, 2.
1996 Lucinidae Taviani, fig. 4b.

Description.—Medium- to large-sized *Lucinoma*, outline of shell oval in small specimens, becoming more round in large ones; umbones central, prosogyrate, elevated; surface sculptured by fine, irregular growth increments or commarginal ribs, posterior sulcus only weakly developed; lunule elongate, heart-shaped, moderately excavated, bordered by distinct angulation; escutcheon lanceolate, wide; anterior adductor muscle scar thin, elongate, reaching well below midline of shell, detached from pallial line for more than three-quarters of its length, deviates from pallial line by ~10°; posterior adductor muscle scar oval, dorsally pointed; hinge plate broad, two strong, radiating cardinal teeth in each valve, one anterior lateral tooth in each valve, posterior lateral teeth not seen.

Materials.—Ten specimens from Ca' Piantè and six specimens from Santa Sofia; six shells from Montepetra, all articulated; one specimen on block with articulated *Archivesica* sp. (MSF 2111); four articulated shells (MSF 2114–2117) and a cluster (MSF 2118) from erratic blocks in Sintria Creek, near Ca' Fornace; 26 articulated shells from Deruta (as *Dentilucina* cf *perusina* Deshayes, Bellardi and Sacco collection in the Turin Museum, PU 40604); ten articulated shells from Deruta (as *Lucina globulosa* Deshayes, Bellardi and Sacco collection in the Turin Museum, PU 40602); one articulated shell from Deruta (Bellardi and Sacco collection in the Turin Museum, as *Dentilucina perusina* Sacco *pseudorotunda* Sacco, 1901, BS.154.03.034) ; see Table 5 for measurements and specimen numbers.

Occurrence.—Middle to late Miocene seep carbonates, from northern Italy to Sicily.

Remarks.—There is no formal description of *Dentilucina perusina* in Sacco (1901); he used this name in the discussion of *Dentilucina barrandei* (Mayer, 1871), and illustrated three specimens as *D. perusina*, including one as *Dentilucina perusina* var. *pseudorotunda* Sacco, 1901; all specimens are from Deruta. The figured specimens of *D. perusina* sensu strictu are not present at MRSN and are presumably lost; here, we illustrate the specimen previously illustrated as *Dentilucina perusina* var. *pseudorotunda* Sacco (1901, pl. 21, fig. 15) and designate it as lectotype for *Dentilucina perusina*. Sacco's illustrated specimens of *D. perusina* sensu strictu are more oval than the rather round *D. p. pseudorotunda*; however, virtually all of the 37 specimens of Bellardi and Sacco collection from Deruta (housed in MRSN) are of the round shape of *D. p. pseudorotunda*. Hence, we consider this as the typical shape of *D. perusina*. Moroni (1966) provided an extensive synonymy for this species.

Externally similar is the Miocene "*Dentilucina" barrandei* from the Turin Hills, but its cardinal teeth are smaller than in *L. perusina* and they are nearly parallel, in contrast to the radiating teeth in *D. perusina*. Among the extant species, *Lucinoma kazani* Salas and Woodside, 2002 living at seeps in the Mediterranean Sea, has a similar shell but less inflated, a similarly short and well-defined lunule, and similar fine commarginal ribs, whereas the North Atlantic-Mediterranean *L. borealis* has a broader and more elongate lunule, and its ribs are more lamellar than in *L. perusina* and *L. kazani* (Salas and Woodside, 2002). None of the *Lucinoma* species known from Japan are particularly similar to *L. perusina* (Okutani, 2000).

Family Vesicomyidae Dall and Simpson, 1901
Genus *Archivesica* Dall, 1908

Type species.—*Callocardia gigas* Dall, 1895 (by original designation); Recent, Gulf of California.

Remarks.—There is currently little consensus which species belong to the genus *Archivesica.* While the concept of Amano and Kiel (2007), which includes middle Eocene to Recent species is probably too broad (cf., Amano and Kiel, 2012), the view of Krylova and Sahling (2010) to include only two extant species in addition to the type, may be a little too narrow. In a recent molecular phylogenetic analysis (Audzijonyte et al., 2012), a monophyletic clade called the '*gigas* group' emerged and included 14 named and five unnamed species, including the type species of *Archivesica.* Because the species described below are morphologically most similar to several members of this clade—*Archivesica soyoae* (Okutani, 1957) *A. kilmeri* (Bernard, 1974), *A. okutanii*

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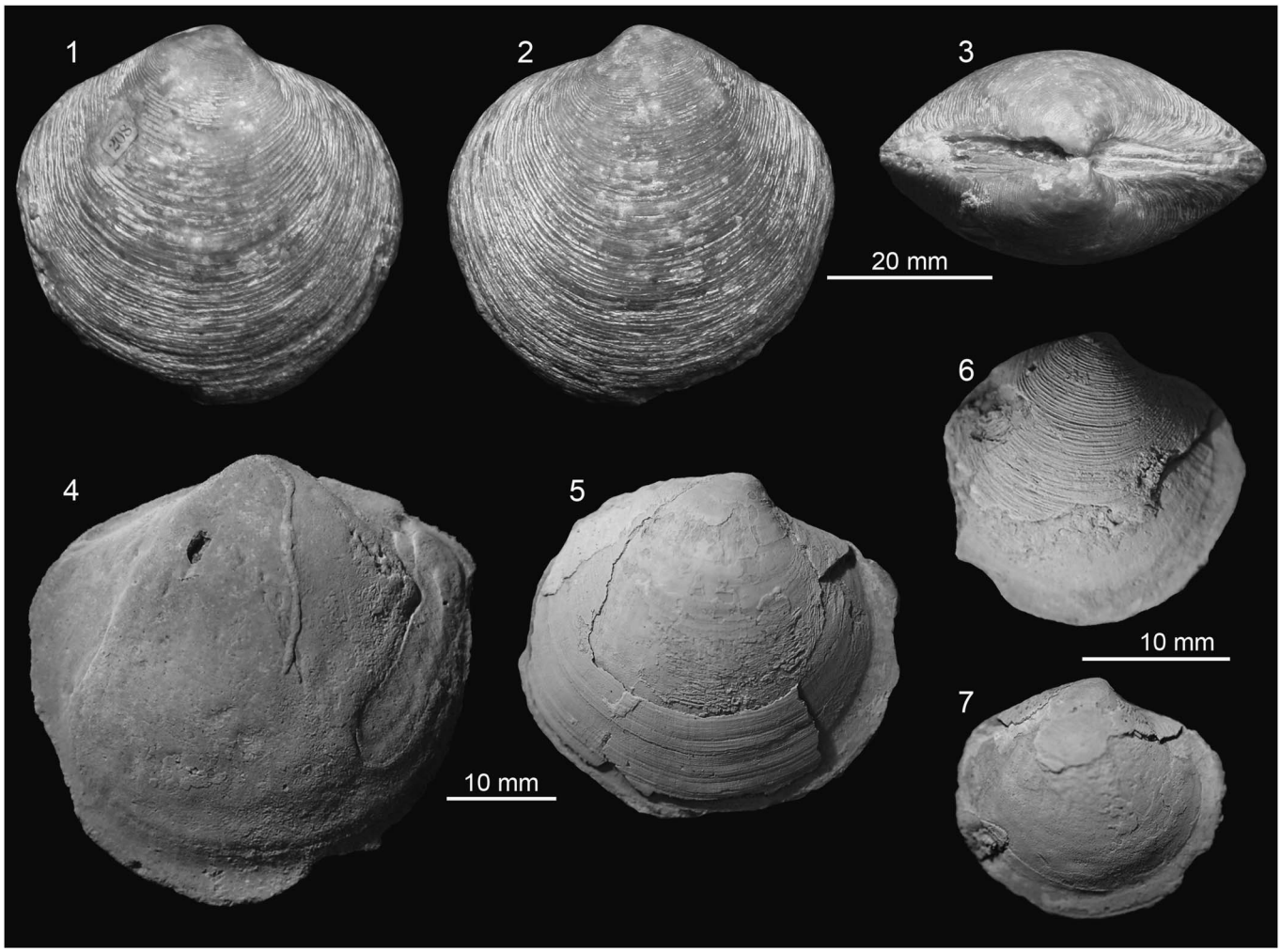

Figure 8. *Lucinoma perusina* (Sacco, 1901) from the late Miocene type locality at Deruta, northern Italy: (**1–3**) lectotype (MRSN BS.154.03.034), originally illustrated as "*Dentilucina perusina* var. *pseudorotunda*" (Sacco, 1901, pl. 19, fig. 15); (4) large internal mold (MRSN PU 40604.01) showing muscle scars and pallial line in right valve; (**5**) right valve of medium-sized specimen (MRSN PU 40604.02) with defoliated outer shell layer, giving it a smooth appearance; (**6**) right valve of small specimen (MRSN PU 40606.01) showing surface sculpture; (**7**) right valve of small specimen (MRSN PU 40606.02).

(Kojima and Ohta, 1997), and *A. kawamurai* (Kuroda, 1943)—we assign them to *Archivesica*. Other authors (Krylova and Janssen, 2006; Krylova and Sahling, 2010) have separated these species into the genera *Archivesica*, *Phreagena*, and *Akebiconcha*, but they have not consistently emerged as monophyletic groups in molecular phylogenetic studies (Audzijonyte et al., 2012; Valdés et al., 2013).

The first claim of the occurrence of large deep-water vesicomyids in the Mediterranean Miocene was based on the discovery in 1992 (Taviani et al., 1992; Taviani, 1996) of a bed containing '*Calyptogena*' (=*Archivesica*) associated with turbidites in the Romagna Apennines (for details see Berti et al., 1994; Taviani, 2014). However, large vesicomyids such as those reported here are not rare in some well-studied outcrops and their occurrence could not have escaped the attention of former investigators. They most likely were identified as *Lutraria* or veneroideans, or, as in the case of the Bellardi and Sacco collection at MRSN from Deruta, as cf. "Tellinidae?". In this respect, *Taurotapes craverii* (Michelotti, 1847) from the lower Miocene of the Turin area (Sacco, 1904) deserves special attention. Elongated bivalves were reported under this name from a putative Miocene hydrocarbon seep at Roccapalumba (Nicosia, 1956), which most likely represent *Archivesica*-like vesicomyids (unpublished observation, M. Taviani, 2016).

Archivesica aharoni new species
Figures 10, 11

1994 *Calyptogena* n. sp. Taviani, fig. 3e.
1996 ?*Calyptogena* sp. Taviani, figs. 3a, b.
2001 *Calyptogena* sp. Taviani, fig. 20.9b.
2011 *Calyptogena* n. sp. Taviani, fig. 3e.

Type specimens.—Holotype MGGC 21909 from Ca' Piantè. Paratypes: three specimens from Ca' Piantè (MSF 1048, 1051, 1053); one from Marmorito (MGGC 21928); two from Case Rovereti (MZB 23846, 28075); three from Verzino (MZB 28076, 28077, 23009); see Table 6 for measurements.

Diagnosis.—Large *Archivesica* with pointed posterior margin, often with posterior ridge and sulcus below; anterior adductor muscle scar large and round, right valve with three radiating, equally sized teeth.

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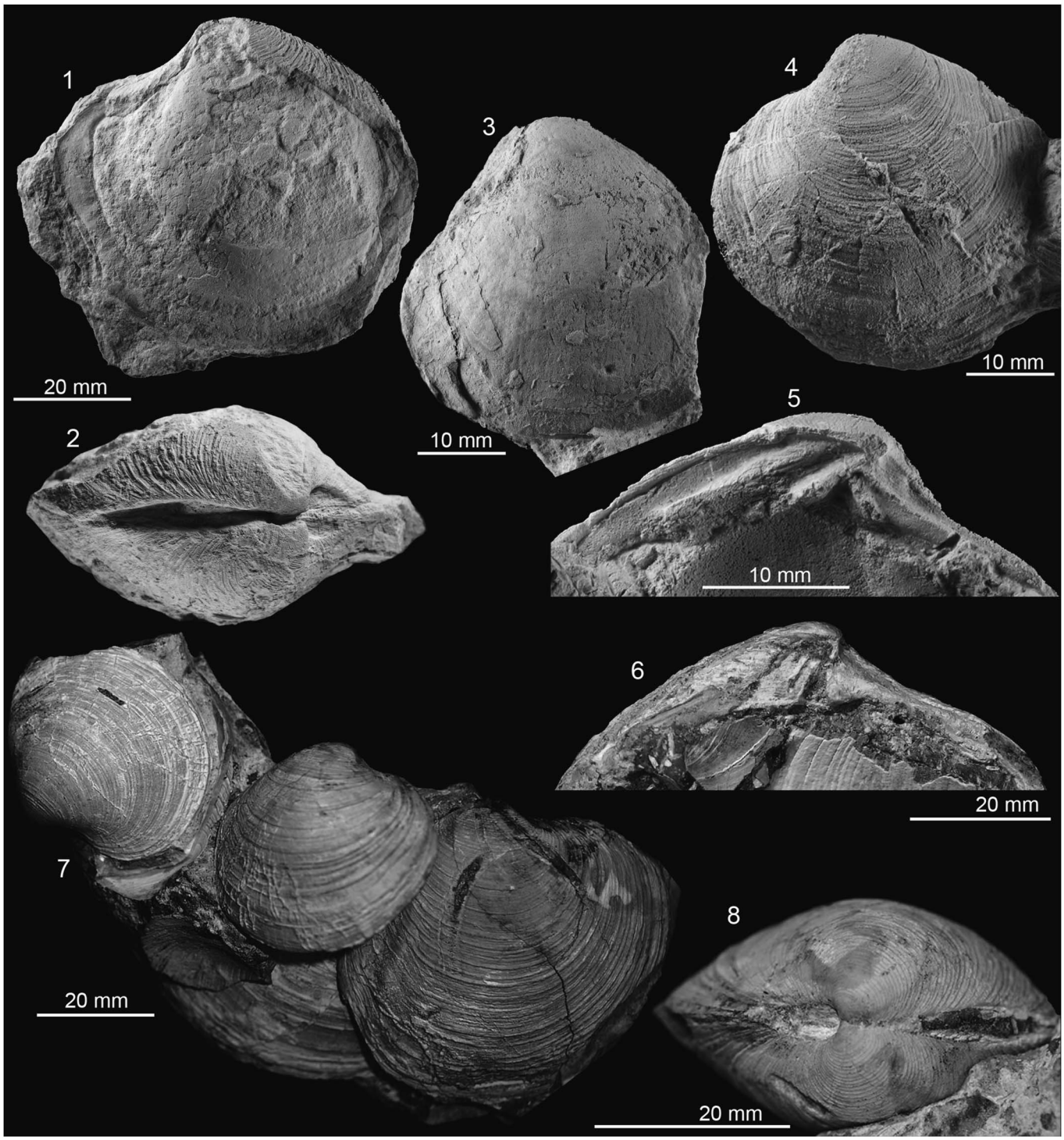

Figure 9. *Lucinoma perusina* (Sacco, 1901) from late Miocene seep deposits in northern Italy: (**1**) partial internal mold of a left valve (MGGC 23006) showing anterior adductor muscle scar, from Ca' Piantè; (**2**) dorsal view of same specimen as in Figure 9.1, showing lunule; (**3**) internal mold of left valve (MGGC 23007) showing anterior adductor muscle scar, from Ca' Piantè; (**4**) left valve (MGGC 23008) showing external sculpture, from Ca' Piantè; (**5**) hinge of same specimen as in Figure 9.4; (6) hinge of a large specimen (MSF 2116) from Ca' Fornace; (**7**) block from Ca' Fornace with several specimens (MSF 2118) showing their external surfaces; (**8**) dorsal view showing umbones, lunule and escutcheon, middle specimen from Figure 9.7.

Occurrence.—Late Miocene seep carbonates in Italy.

Description.—Moderately large (up to 115 mm long), elongate-veneriform shell with umbo anterior at ~28% total shell length; anterior side strongly convex, slightly pointed; ventral side evenly curved; posterodorsal margin only slightly convex, transition to posterior margin at clear angulation; posterior margin pointed at its ventral side. Beak elevated, blunt, slightly prosogyrate; external sculpture of rough growth lines only; no lunula or lunular incision, escutcheon narrow with sharp edges, length about two-thirds of posteroventral margin. Anterior adductor muscle scar distinct and round, pallial line starting at

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Table 5. Measurements of *Lucinoma perusina* (Sacco, 1901); H = height, L = length, W = width of two valves, except when indicated otherwise.

Locality	Specimen	L (mm)	H (mm)	W (mm)
Casa Piantè	MGGC 23006	52.5	50.4	31.3
Casa Piantè	MGGC 23007	43	43	11.4 (single)
Casa Piantè	MGGC unnumbered	35.5	35	20
Casa Piantè	MGGC unnumbered	55.5	59	20.5 (single)
Case Rovereti	MGGC unnumbered	44.5	45.6	10.8 (single)
Case Rovereti	MGGC unnumbered	54	40 (incomplete)	15.4 (single)
Ca' Piantè	MGGC unnumbered	42	45	single
Ca' Fornace	MSF 2118 (block with several specimens)	71	70	43

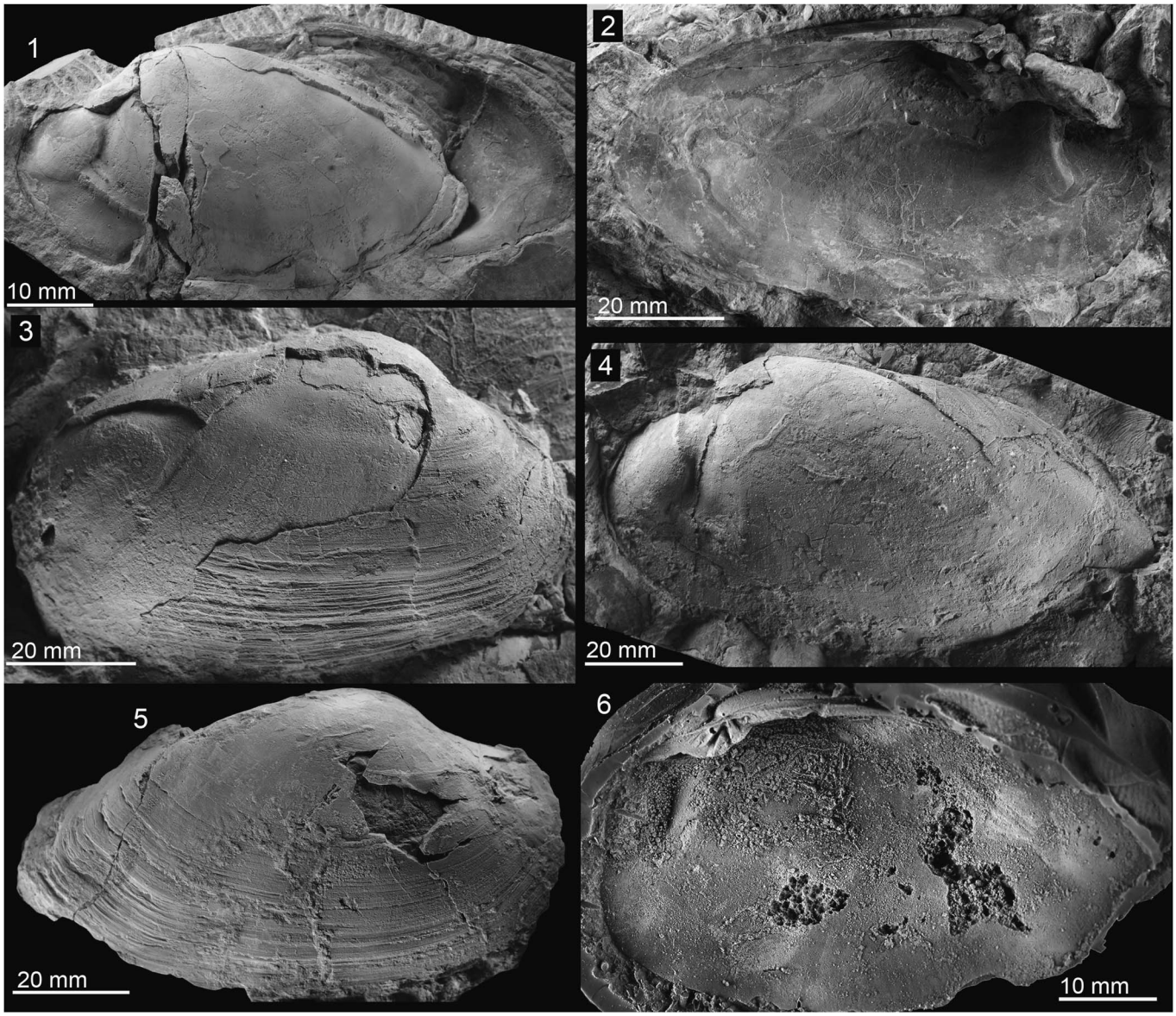

Figure 10. *Archivesica aharoni* new species from Miocene seep deposit in Italy: (**1**) holotype (MGGC 21909), semi-articulated specimen, internal mold of left valve showing anterior adductor muscle scar, and interior of right valve, from Ca' Pianté; (**2**) paratype (MSF 1048), internal view of left valve, from Ca' Pianté; (**3**) paratype (MSF 1051), right valve with partially preserved shell, from Ca' Pianté; (**4**) paratype (MZB 23846), internal mold of left valve, from Ca' Rovereti; (**5**) paratype (MSF 1046), exterior of left valve, from Ca' Rovereti; (**6**) paratype (MGGC 21928), rubber cast of right valve showing hinge and the lacking pallial sinus, from Marmorito.

its posteroventral corner, distinct only in anterior half of shell. Hinge plate high but short; RV with three equally strong cardinal teeth that radiate anteroventrally, a distinctive inverted-V-shaped groove between hinge teeth and nymph plate forms the subumbonal pit; cardinal 1 straight, oblique to anterodorsal margin, cardinals 3a and 3b not connected, 3a subparallel to anterodorsal margin, 3b almost at right angle to it; nymph plate narrow. LV with three teeth, cardinal 2a parallel to anterodorsal

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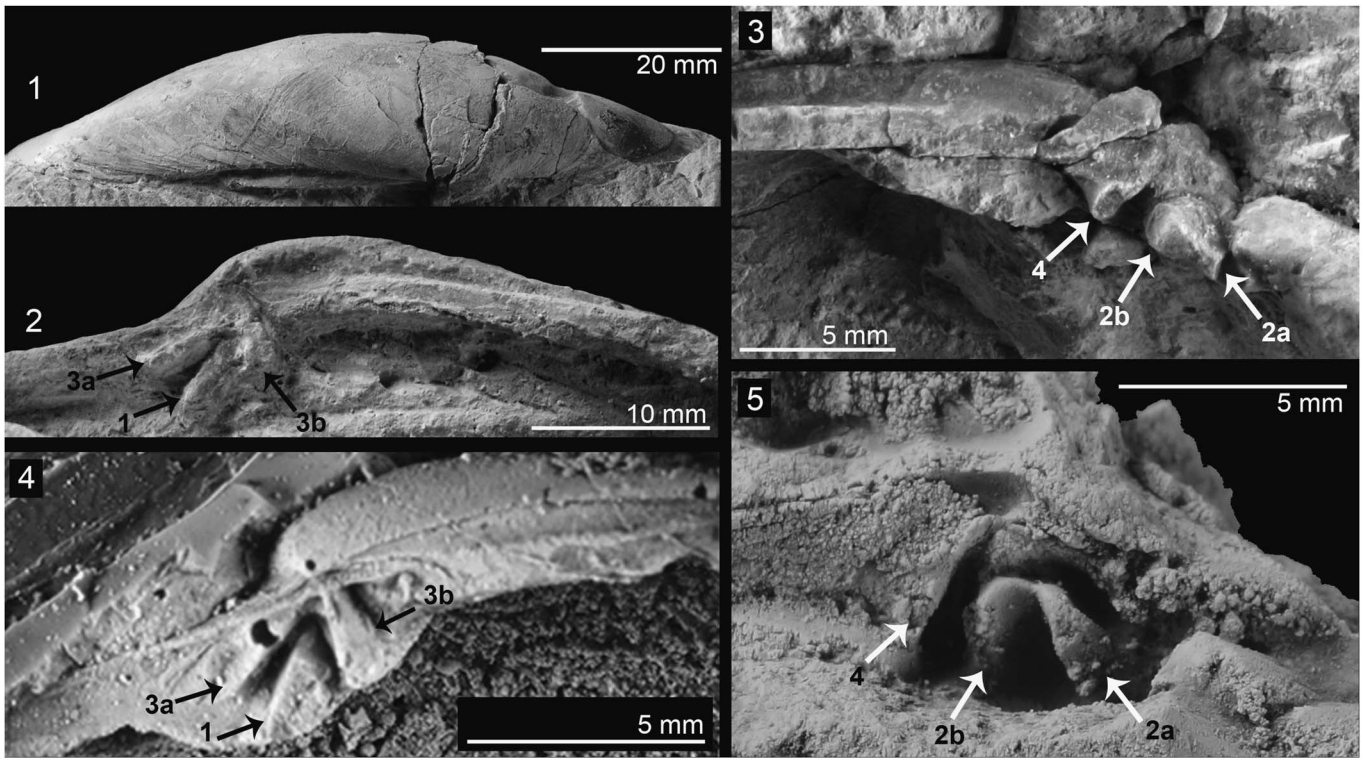

Figure 11. *Archivesica aharoni* new species from Miocene seep deposit in Italy: (**1, 2**) holotype (MGGC 21909) from Ca' Pianté, dorsal view, and close-up of hinge of right valve, respectively; (**3**) paratype (MSF 1048) from Ca' Pianté, close-up of hinge of left valve; (**4**) paratype (MGGC 21928) close-up of hinge of right valve; (**5**) paratype (MGGC 23009) from Verzino, close-up of hinge of left valve.

Table 6. Measurements of *Archivesica aharoni* new species; H = height, L = length, W = width of two valves.

Locality	Specimen	L (mm)	H (mm)	W (mm)
Ca' Piantè	MGGC 21909, holotype	99.0	54.0	16.0
Ca' Piantè	MSF 1048	85.0	46.0	
Ca' Piantè	MSF 1055	65 (incomplete)	55.0	15.0
Ca' Piantè	MSF 1053	81.0	51.0	36
Ca' Piantè	MSF 1046	96.0	53.0	21 (single)
Ca' Piantè	MSF1051	88.0	51.0	14.0
Case Rovereti	MZB 23846, paratype	115.0	63.0	11 (single)
Case Rovereti	MZB 28075	85.0	51.0	33
Verzino	MZB 28077	95.0	54.0	39.5
Verzino	MZB 28076	90.0	53.0	19 (single)
Verzino	MGGC 23009, paratype	64 (incomplete)	38.0	21.0

margin, wedge-shaped, tapering anteriorly, 2b short, perpendicular to 2a, 4 short, wedge-shaped, nearly perpendicular to ventral shell margin.

Etymology.—For Paul Aharon, Tuscaloosa, Alabama, in recognition of his relevant work on Gulf of Mexico recent cold seeps and 'Calcari a *Lucina*' fossil counterparts.

Materials.—Two specimens from Ca' Piantè (MSF 1055, 1358) and four shells from Verzino (MGGC 23002).

Remarks.—The two most similar species are the extant Japanese *Archivesica soyoae* and *A. kawamurai*. The former differs from *A. aharoni* n. sp. mainly by having a broader nymph plate and the teeth in the left valve are more elongate (Sasaki et al., 2005). In addition to the left valve teeth of *Archivesica kawamurai* being more elongate than in *A. aharoni* n. sp., the teeth of the right valve are more slender (Sasaki et al., 2005; Amano and Kiel, 2010). The geographically close *Phreagena* sp. from a ca. 25,000 years old vent field on the Mid-Atlantic Ridge (Lartaud et al., 2010) differs from *A. aharoni* n. sp. by having the anterior onset of the pallial line in a more anterior position, cardinal tooth 3b in the right valve points posteriorly rather than ventrally as in *A. aharoni* n. sp., and its escutcheon is much broader. The late Miocene *A. shikamai* Amano and Kiel, 2010 from Japan differs by generally having straighter and more parallel dorsal and ventral margins.

Archivesica aff. *aharoni* Kiel and Taviani, herein
Figure 12

Description.—Shells up to 94 mm long, elongate-veneriform shell with umbo anterior at ~26–35% total shell length; anterior margin either pointed or truncate; ventral margin evenly curved; posterodorsal margin almost straight to slightly convex, transition to posterior margin with clear angulation in specimens with truncate posterior margin, or more rounded in specimens with pointed posterior margin. Beak elevated, blunt, slightly prosogyrate; external sculpture of rough growth lines only; no lunula or lunular incision. Anterior adductor muscle scar distinct and round, pallial line starting at its posteroventral corner, pallial sinus small, shallow; posterior adductor muscle scar large, round, with anteriorly pointed hook at dorsal margin. Hinge plate high but short; RV with three equally strong cardinal teeth that radiate anteroventrally; LV with three teeth, cardinal 2a wedge-shaped, tapering anteriorly, parallel to anterodorsal margin, 2b and 4 short.

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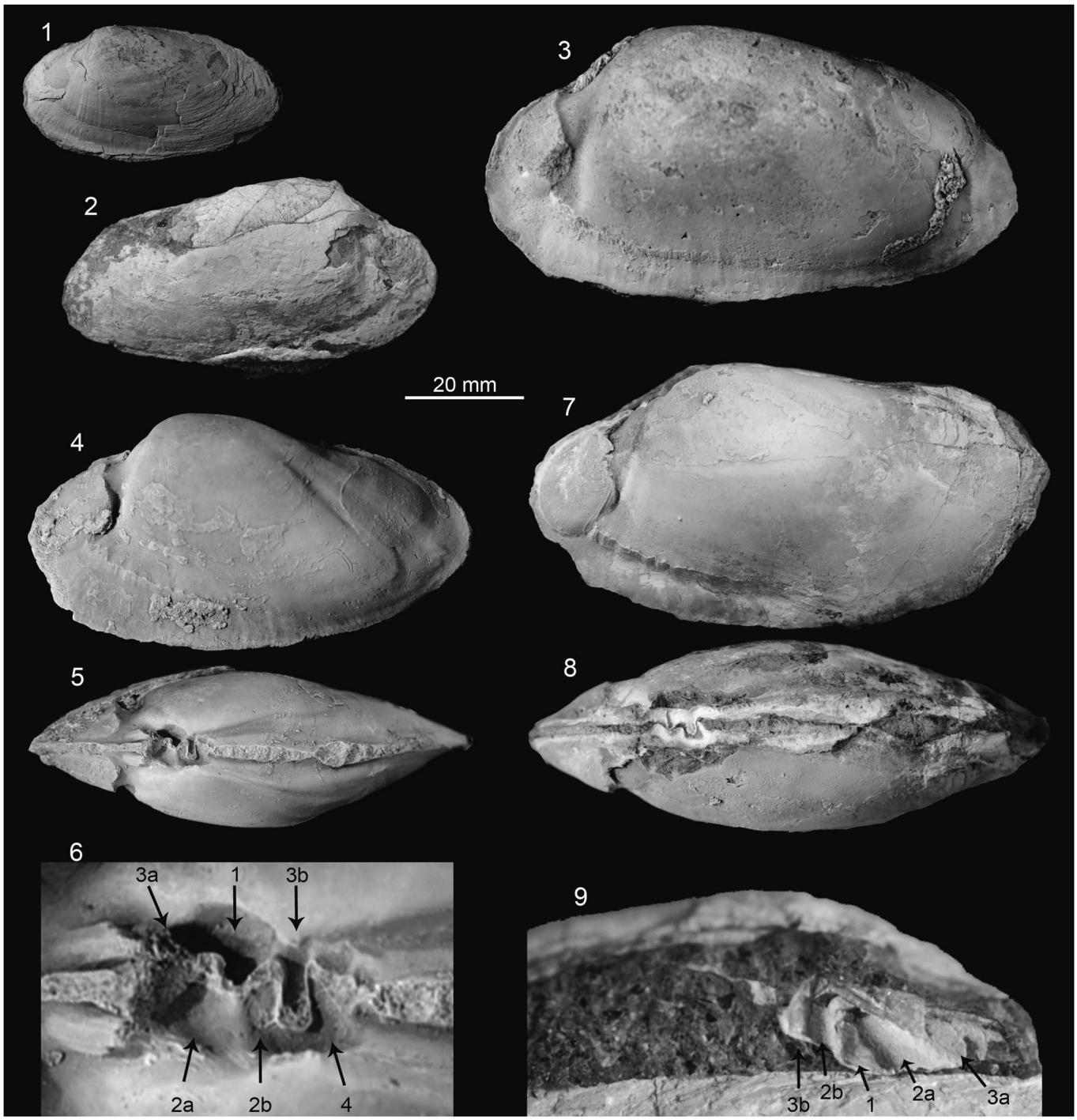

Figure 12. *Archivesica* aff. *aharoni* new species from the middle Miocene seep deposit at Deruta in northern Italy: (**1**) left valve of small specimen (MRSN PU 40611.02) showing shell outline; (**2**) right valve of medium-sized specimen (MRSN PU 40609.01) showing shell outline; (**3**) large specimen (MRSN PU 40608-01) showing muscle attachment scars and pallial line; (**4–6**) moderately sized specimen (MRSN PU 40608.02), (**4**) view of left valve showing pointed posterior end, muscle attachment scars and pallial line, (**5**) dorsal view showing hinge area, (**6**) close-up of hinge area; (**7, 8**) large specimen (MRSN PU 40608.03), (**7**) view of left valve showing anterior muscle attachment scars and pallial line, (**8**) dorsal view showing hinge area; (**9**) (MRSN PU 40609.01) detached hinge region showing fractured teeth of the right valve and molds of the teeth of the left valve.

Materials.—Four lots of articulated bivalves, mostly molds, but some with preserved portions of the shell, labeled as "cf. Tellinidae (?)" in the Bellardi and Sacco collection at MRSN (N40608: 20 specimens, largest specimen $L \times H \times W = 100 \times 54 \times 35$ mm; PU 40609: 25 specimens, largest specimen $82 \times 38 \times 20$ mm; N40610: 30 specimens, largest specimen $79 \times 40 \times 24$ mm; PU 40611: 16 specimens., largest specimen $45 \times 22 \times 6$ mm); four additional specimens (MGGC 21930, 21931; MZB 60096, 60097).

Occurrence.—Middle Miocene (Serravallian) seep carbonate at Deruta in northern Italy.

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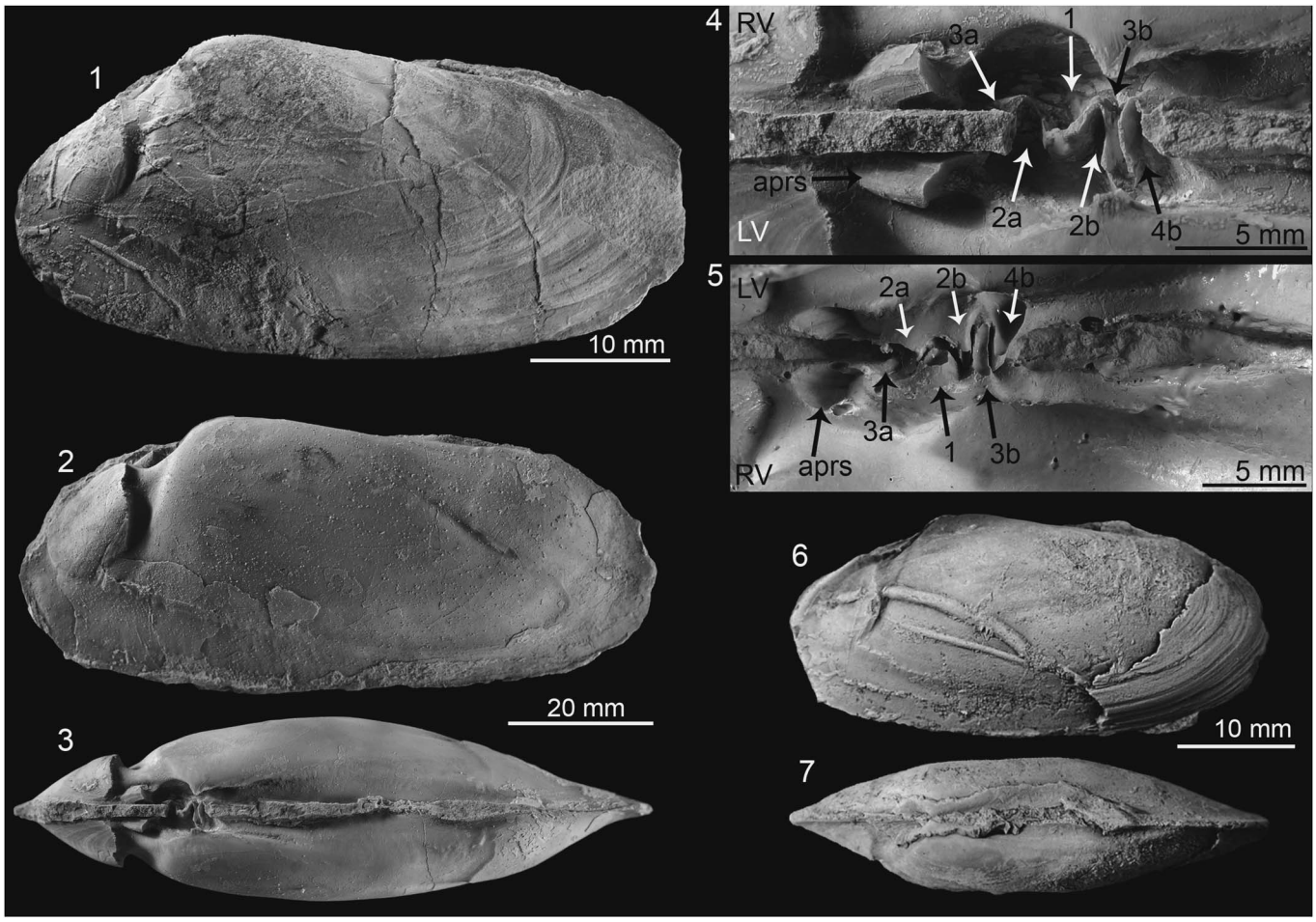

Figure 13. *Archivesica strigarum* new species from the middle to late Miocene seep deposits in northern Italy: (**1**) paratype (MGGC 21929) from Sasso delle Streghe, left valve showing the round anterior adductor muscle scar; (**2–5**) holotype (MZB 28095) from Sasso delle Streghe, internal mold; (**2**) left valve, (**3**) dorsal view, (**4**) close-up of hinge area, (**5**) silicon rubber cast of hinge area; (**6, 7**) paratype (MRSN PU 40611.01), small specimen from Deruta. Abbreviations: aprs, anterior pedal retractor scar; LV, left valve; RV, right valve.

Remarks.—These specimens share all features of *A. aharoni*, but are slightly smaller and consistently lack the posterior ridge and groove that can be seen in many specimens of *A. aharoni* from the type locality. Furthermore, the posterior part of the pallial line and the posterior adductor muscle scar can be more clearly seen than in specimens of *A. aharoni* from the type locality, but this might be a taphonomic artifact.

Archivesica strigarum new species
Figure 13

2001 *Calyptogena* sp. Taviani, fig. 20.8a.

Type specimens.—Holotype: MZB 28095, internal mold from Sasso delle Streghe (87 × 38 × 24.5 mm). Paratypes: MGGC 21929, specimen with partially preserved external features from Sasso delle Streghe; MRSN PU 40611, small specimen from Deruta (41 × 19 × 11.5 mm).

Diagnosis.—Elongate *Archivesica*, beak situated anteriorly at ~26% of total shell length; onset of pallial line at posteroventral margin of anterior adductor muscle scar; no pallial sinus.

Occurrence.—Middle Miocene seep carbonates in northern Italy.

Description.—Elongate veneriform shell (max. dimensions L = 95 mm, H = 45 mm, W = 30 mm) with beak situated in anterior third of shell; anterior margin well rounded, posterodorsal margin only slightly tapering, posterior margin broadly rounded, ventral margin gently rounded, shell surface smooth except for growth lines. Anterior adductor muscle scar broadly oval, bordered posteriorly by distinct ridge; pedal retractor scar oval, distinct from adductor muscle scar; onset of pallial line at posteroventral margin of anterior adductor muscle scar, obliquely cutting across anteroventral shell margin; pallial sinus small, shallow, pointed. RV hinge with thick cardinal 1; cardinal 3a thick, elongate; cardinal 3b thin and very long; LV hinge with cardinal 2a thick, elongate; cardinal 2b thin and close to almost equally shaped cardinal 4b.

Etymology.—For the type locality at Sasso delle Streghe (the witches' rock; *Striga* Latin for witch).

Materials.—Slab with five decalcified shells from Sasso delle Streghe (MGGC 23000); one incomplete articulated mold (MSF 1357); one specimen from Deruta (MRSN PU 40610).

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Remarks.—Extant species with similar hinge dentition and pallial line include *Archivesica gigas*, *A. kawamurai*, *A. kilmeri*, and *A. okutanii* (Dall, 1895; Kuroda, 1943; Bernard, 1974; Kojima and Ohta, 1997). Among the characters used to distinguish *Phreagena* from *Archivesica* was the anterior pedal retractor scar, which is deeply impressed in *Phreagena*, but shallow in *Archivesica* (Krylova and Janssen, 2006); in *A. strigarum* it is deeply impressed. *Archivesica strigrarum* n. sp. is more elongate than *Archivesica aharoni* n. sp. and has a more oval (rather than round) anterior adductor muscle scar. It lacks the arched posterodorsal margin and posterodorsal ridge of *A. apenninica* n. sp. and its anterior adductor muscle scar is oval in contrast to the more quadrate scar of *A. apenninica* n. sp. Compared to the elongate specimens of *A. apenninica* n. sp., it has a longer anterior portion. It is also more elongate than most other species of *Archivesica*, except the early Miocene *A. sakoi* Amano et al., 2014 from southern Japan.

Archivesica apenninica new species
Figure 14

Type specimens.—Holotype: MGGC 23001. Paratypes: MSF 2121, 2123, 2125, 2126; all types from Castelvecchio.

Diagnosis.—Large for the genus; dorsal margin broadly arched, ridge running from umbo to posterior margin; anterior adductor muscle scar oval with groove running toward umbo; no pallial sinus; three radiating and almost equally strong cardinal teeth in each valve.

Occurrence.—Only known from the middle Miocene (early Serravallian) seep carbonate at Castelvecchio in northern Italy.

Description.—Elongate-veneriform shell, up to 125 mm long, umbo broad, elevated, slightly prosogyrate, anterior at ~28–33% total shell length. Anterior shell margin strongly convex; ventral margin gently and evenly curved; posterodorsal margin broadly arched, transition to posterior margin indistinct, angulate only in very elongate specimens; posterior margin strongly convex and somewhat pointed. External sculpture of rough growth lines; distinct ridge or angulation from umbo to posterior margin; no

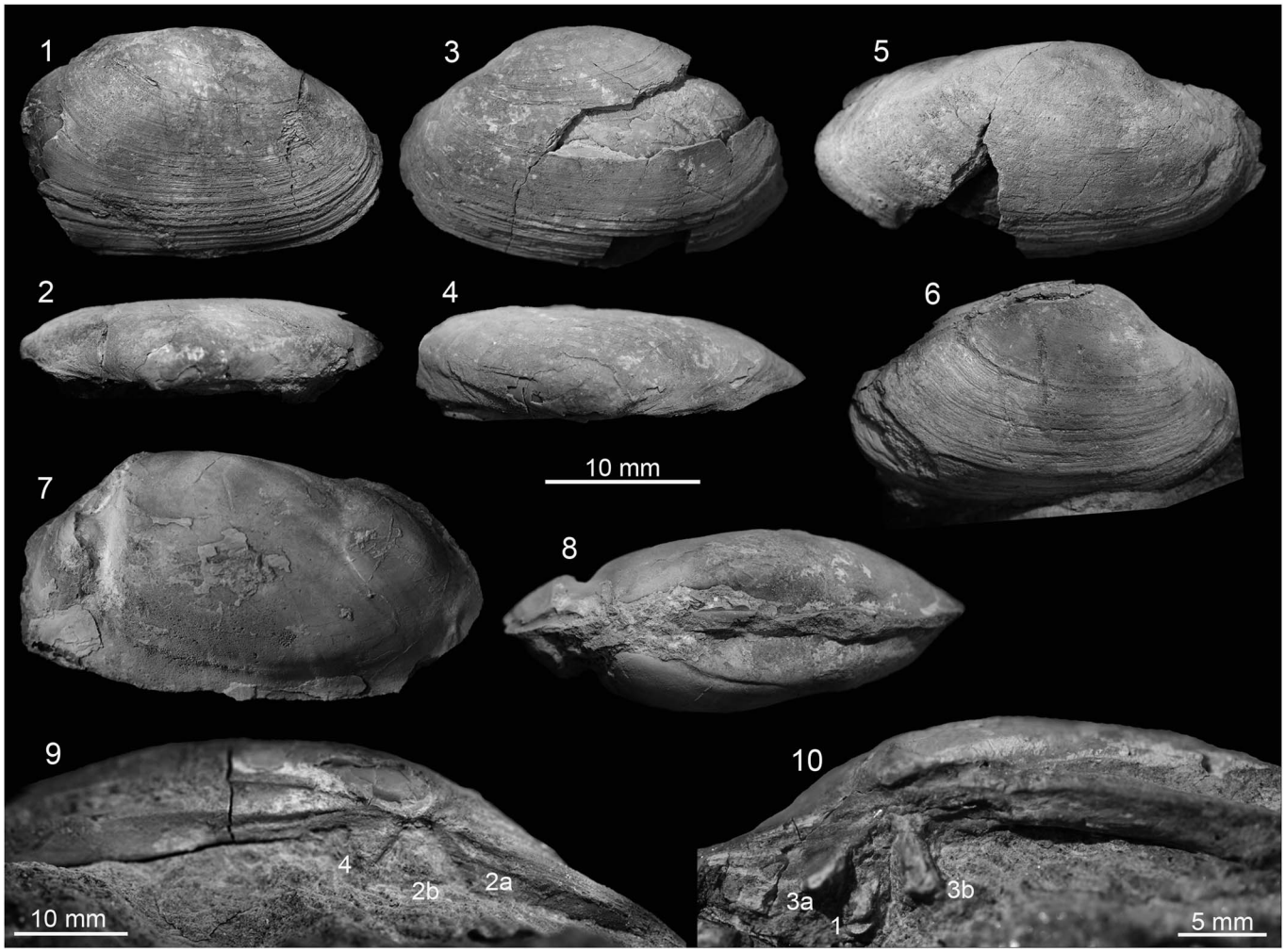

Figure 14. *Archivesica apenninica* new species, from the middle Miocene seep deposit at Castelvecchio in northern Italy: (**1, 2, 10**) holotype MGGC 23001, right valve with damaged posterior margin; view of outer shell surface, dorsal view, and close-up of hinge dentition, respectively; (**3, 4, 9**) paratype MSF 2125, left valve; view of outer shell surface, dorsal view, and close-up of hinge dentition, respectively; (**5**) paratype MSF 2123, right valve of very elongate specimen; (**6**) paratype MSF 2121, right valve with damaged posterodorsal margin; (**7, 8**) paratype MSF 2126, internal mold showing muscle attachment scars and pallial line; view of left valve and dorsal view, respectively.

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lunula or lunular incision, escutcheon narrow with sharp edges, length at least half of posteroventral margin. Anterior adductor muscle scar distinct, oval, somewhat pointed anteroventrally, most deeply impressed on posterior side, with groove extending toward umbo; anterior pedal retractor scar small, oval, distinct from adductor muscle scar; pallial line starting at posteroventral corner of anterior adductor scar, running oblique toward ventral shell margin in anterior half of shell, parallel to it afterward, sharply bent upward below center of posterior adductor scar, pallial sinus small, shallow. Hinge plate high but short; RV with three equally strong cardinal teeth that radiate toward ventral margin, cardinals 3a and 3b not connected, subumbonal pit present, nymph plate narrow; LV with three widely radiating teeth, cardinal 2a weak, 2b short, wedge-shaped, not connected to 2a, 4 short, nearly perpendicular to 2a.

Etymology.—For the Apennine Mountains, Italy.

Materials.—All specimens from Castelvecchio; MSF 2121–2132 and several fragmentary specimens at MSF; see Table 7 for measurements.

Remarks.—*Archivesica apenninica* n. sp. is variable in elongation, but the characteristic broadly arched posterodorsal margin, as well as the nearly equally strong hinge teeth are seen in all available specimens. A similar broadly arched posterodorsal margin is present in the Recent Japanese species *A. solidissima* (Okutani, Hashimoto, and Fujikura, 1992), *A. soyoae* (Okutani, 1957), and *A. okutanii* (Kojima and Ohta, 1997), but these species differ from *A. apenninica* either by having a concave ventral margin or by having more anteriorly pointing cardinal teeth (Sasaki et al., 2005). The pallial sinus is more pronounced in extant species than in *A. apenninica*.

Table 7. Measurements of *Archivesica apenninca* new species, all specimens from Castelvecchio; H = height, L = length, W = width of two valves, except when indicated otherwise.

Specimen	L (mm)	H (mm)	W (mm)
MGGC 23001 (holotype)	96	64	19 (RV)
MSF 2123 (paratype)	123	61	20 (RV)
MSF 2127	122	69	17 (LV)
MSF 2122	122 (incompl.)	70	17 (LV)
MSF 2126 (paratype)	120	62.5	45 (articulated)
MSF 2124	110	64	24 (LV)
MSF 2125 (paratype)	109	67	26 (LV)
MSF 2121 (paratype)	108	63	21 (RV)
MSF 2129	104	70	50 (articulated)
MSF 2131	103 (incompl.)	71	51 (articulated)
MSF 2128	85 (incompl.)	57	19 (RV)

Genus *Pliocardia* Woodring, 1925

Type species.—*Anomalocardia bowdeniana* Dall, 1903, late Pliocene Bowden Formation, Jamaica, by monotypy.

Remarks.—*Pliocardia* is currently a dustbin taxon used for small to moderately sized, oval and thick-shelled species with an *Archivesica*-like hinge dentition. Molecular phylogenetic studies indicate two separate groups among species with the general shape of *Pliocardia*: one includes the species *Vesicomya stearnsii*, *Calyptogena ponderosa*, *C. cordata*, and '*Pliocardia*' *krylovata*, the other includes *Vesicomya kuroshimana*, *V. crenulomarginata*, and specimens called "cf. *venusta*" (Kojima et al., 2004; Martin and Goffredi, 2011; Audzijonyte et al., 2012). Several additional extant species for which no molecular data are available are also included in this genus (Krylova and Sahling, 2010), as well as several fossil taxa (Amano and Kiel, 2007, 2012). As it is still unclear to which of those groups (if at all) the type species of *Pliocardia* belongs. The identity of this genus remains unclear and it is only used in quotation marks for the species reported below.

"*Pliocardia*" *italica* new species
Figure 15

Type specimens.—Holotype: MGGC 21909 (cast: MSF 1277). Paratype: MSF 1275; all types from the middle Miocene of Ca' Cavalmagra.

Diagnosis.—Large, inflated *Pliocardia* with strong, protruding, prosogyrate beak, small anterior portion and broadly expanded posterior portion.

Occurrence.—Known only from Ca' Cavalmagra.

Description.—Well-inflated specimens with large, protruding beak in anterior third of shell; anterior part of shell short, somewhat pointed, posterior part broadly expanded; anterior adductor muscle scar in ventral half of shell, broadly oval, onset

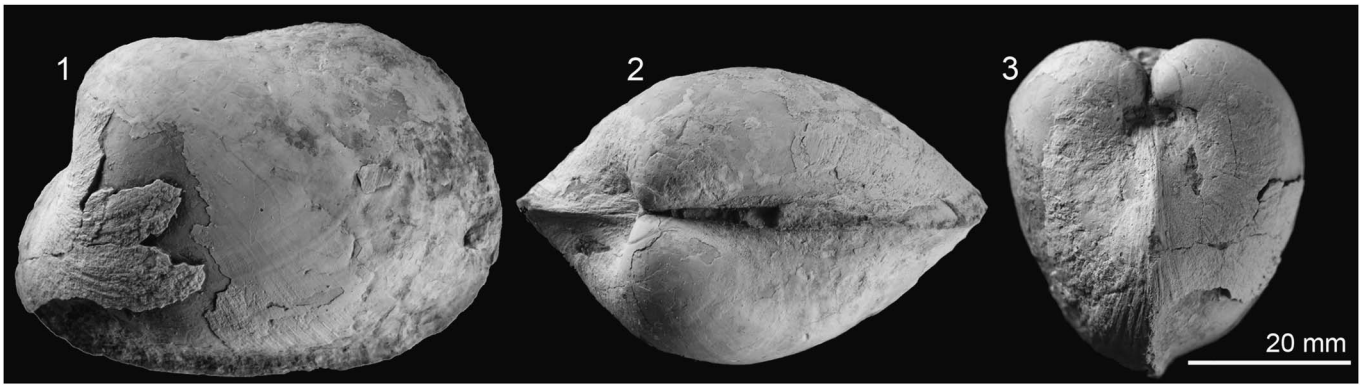

Figure 15. "*Pliocardia*" *italica* new species from the middle Miocene seep deposits at Ca' Cavalmagra in northern Italy, holotype (MGGC 21909); (**1**) exterior of left valve; (**2**) ventral side; (**3**) anterior side.

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of pallial line at its posteroventral corner, pallial sinus small and shallow, posterior adductor muscle scar indistinct, very close to posterior shell margin; interior of posterior part of shell with distinct radial grooves.

Etymology.—Refers to the geographic area that is the source of all studied material.

Materials.—One articulated specimen (MSF 1276) and nine isolated valves (MSF 1273, 1274, 1279, 2105–2109; MZB 60218); see Table 8 for measurements.

Remarks.—Most similar to "*Pliocardia*" *italica* n. sp. are two extant species from the central Indo-Pacific Ocean: "*Pliocardia*" *solidissima* (Prashad, 1932) and "*Pliocardia*" *ticaonica* (Dall, 1908). Both have a similarly large and prosogyrate umbo and broad posterior margin, but differ from the Italian Miocene "*Pliocardia*" *italica* n. sp. by having a more convex posterodorsal margin; in addition, *P. ticaonica* is shorter than "*Pliocardia*" *italica* n. sp. Among the taxa from the Caribbean Sea and the Gulf of Mexico, "*Pliocardia*" *caribbea* (Boss, 1967) has a broader anterior margin and has the anterior adductor muscle scar in a more dorsal position; "*Pliocardia*" *cordata* (Boss, 1968) is shorter and has a smaller and more pointed beak; and "*Pliocardia*" *ponderosa* (Boss, 1968) seems to have a steeper sloping posterodorsal margin.

Discussion

The present study is intended to provide a taxonomic baseline for future biogeographic and evolutionary studies. At first glance, the bivalve fauna of the 'Calcari a *Lucina*' seep deposits show a wide range of biogeographic links to places as distant as the Recent western Pacific (*Bathymodiolus*, *Archivesica*, and *Meganodontia*), the Recent Indian Ocean ("*Pliocardia*"), as well as the Miocene Caribbean seep faunas (*Meganodontia*). We identified 11 chemosymbiotic bivalve species from the middle to late Miocene 'Calcari a *Lucina*' methane-seep deposits in northern Italy, among them three mytilids, one thyasirid, two lucinids, and four or five vesicomyids.

Apart from *Bathymodiolus* (s.l.) *moroniae* n. sp. and *B.* (s.l.) *miomediterraneus* n. sp. (two species that resemble extant bathymodiolins) the taxonomic affinity of the new genus and species *Samiolus iohannesbaptistae* is unclear. This taxon might represent a rare case of a genus that occurs exclusively at deep-water methane seeps, but does not belong to the bathymodiolins. An interesting taphonomic aspect of the mytilids is the common occurrence of *B.* (s.l.) *moroniae* n. sp. and *Samiolus iohannesbaptistae* n. gen. n. sp. as disarticulated shells, which is in contrast to the articulated mode of occurrence of the vast majority of other fossil seep-associated bathymodiolins (Squires and Goedert, 1991; Amano et al., 2010; Kiel et al., 2010; Saether et al., 2010; Amano and Jenkins, 2011; Kiel and Amano, 2013). Articulated shells, including juveniles and giant specimens up to 133 mm in length, indeed occur at Ca' Piantè, as well as in Deruta, but this is rather an exception than the rule. At the well-sampled sites at Montepetra and Case Rovereti, where disarticulated mussel shells are common, the co-occurring vesicomyids and lucinids were found as articulated or semi-articulated shells. This excludes the possibility that the mussel shells disarticulated due to transport, but suggests in-situ disarticulation, either by the force of the ligament, or perhaps due to large scavengers.

In addition to the seep-inhabiting bathymodiolins reported here, a bathymodiolin named *Adipicola apenninica* Danise, Bertolaso, and Dominici, 2016 was recently described from a whale bone from the middle Miocene (Langhian) Pantano Formation in the vicinity of the town of Carpineti (Reggio Emilia province, northern Italy). *Adipicola apenninica* was reported as being very abundant, where the associated thyasirids and lucinids were rare (Danise et al., 2016).

Most Cretaceous to extant lucinids at methane seeps belong to either the Codakiinae or the Myrteinae (Taylor et al., 2011; Kiel, 2013). Thus, if the inclusion of *Meganodontia* in Pegophyseminae (cf., Taylor et al., 2011, 2014) is correct, it would be the third lucinid subfamily to have a considerable fossil history at methane seeps (Taylor et al., 2014; Kiel and Hansen, 2015).

The taxonomy of the Vesicomyidae is still in flux, partially due to the frequent convergence among their few shell characters (Krylova and Sahling, 2010). Amano and Kiel (2010) recently questioned Paleogene records of *Archivesica*, and Amano et al. (2014) identified the early Miocene Japanese *A. sakoi* Amano et al., 2014 as earliest member of *Archivesica* sensu strictu. The middle Miocene *Archivesica strigarum* n. sp. introduced here is thus among the earliest *Archivesica* species and is, just as *A. sakoi*, very elongate compared to extant *Archivesica* species.

Table 8. Material of "*Pliocardia*" *italica* new species, all specimens from Ca' Cavalmagra; H = height, L = length, W = width of two valves.

Specimen	L (mm)	H (mm)	W (mm)
MGGC 21909 (holotype)	59.6	42.1	37
MSF 1275 (paratype)	56.6	39.4	31
MSF 1276		50	30
MSF 1274 (LV)	55		
MSF 2105 (RV)			
MSF 2106 (LV)			
MSF 2107 (RV)	60		
MSF 2108 (LV)	60		
MSF 2109 (RV)		50	35

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Appendix

Details of localities (see Figure 1) of Miocene methane-seep bivalves reported in this paper. Regarding the localities from Piedmont mentioned here in the context of the Sacco collection at MRSN (Albugnano, Bersano, Pera del Gal , Pino Torinese, etc.), the reader must refer to the catalog edited by Merlino (2007). The material illustrated by Moroni (1966) was reported to have been stored in the Museo Geologico Giovanni Capellini, University of Bologna, with the S. Sofia collection (catalog numbers 121–140); however, the collection is not present in this museum and is possibly kept in the University of Palermo, but not traceable at present (G. Ruggieri, personal communication, 1996).

1. Abisso "Mornig".—Micritic limestone blocks near the entrance of "Mornig" cave, SE of Castelnuovo, not far from Brisighella (Ravenna province), Romagna Apennine, northern Italy; coordinates: 44°13'40"N, 11°44'72"E; Tossignano marls, late Miocene (late Tortonian).

2. Ca' Carnè.—Marly to micritic limestone deposits just S-SE of Ca' Carnè ("Vena del Gesso Romagnola" Regional Park visit center), near Brisighella (Ravenna province), Romagna Apennine, northern Italy; coordinates: 44°13'40"N, 11°44'72"E; Tossignano marls, late Miocene (late Tortonian).

3. Ca' Cavalmagra.—Limestone (calcarenitic) deposit SSE of Palazzuolo (Firenze province), Tuscan Romagna Appenine, northern Italy; coordinates: 44°05'78"N, 11°33'62"E; Marnoso-arenacea Formation, middle Miocene (upper Langhian).

4. Monticino-Limisano – Castelnuovo junction.—Few scattered limestone blocks near the junction between Castelnuovo street and Calbane street, not far from Brisighella (Ravenna province), Romagna Appenine, northern Italy; coordinates 44°14'03.07"N; 11°44'18.72"E; late Miocene (late Tortonian).

5. Ca' Fornace.—Erratic limestone blocks in the Sintria Creek downstream of the bridge near Ca' Fornace, near Brisighella (Ravenna province), Romagna Apennine, northern Italy; coordinates: 44°14'14"N, 11°44'40"E; late Miocene (late Tortonian).

6. Ca' Pianté.—Scattered marly to micritic limestone blocks SW of Ca' Pianté, not far from Ca' Carnè and near Brisighella (Ravenna province), Romagna Appenine, northern Italy; late Miocene (late Tortonian); additional information can be found in Conti and Fontana (1998).

7. Case Rovereti.—Large isolated limestone block just NW of the small village of Raggio, near Santa Sofia (Forlì province), Romagna Appenine, Italy; coordinates: 43°55'38"N, 11°56'43"E; located on San Paolo Marls but not necessarily belonging to such stratigraphic unit, late Miocene (middle Tortonian–early Messinian). This deposit has previously been described in more detail (Moroni, 1966; Taviani, 1994; Terzi et al., 1994; Clari et al., 2004a).

8. Castelvecchio.—Limestone (calcarenitic) deposit just W of small village of Castelvecchio, Piancaldoli, near Firenzuola (Firenze province), Tuscan Romagna Apennine, northern Italy; coordinates: 44°11'53"N, 11°24'18"E; Marnoso-arenacea Formation, middle Miocene (early Serravallian).

9. Deruta.—Small blocks at Fosso Castelleone 2 km SE of Deruta (Perugia province), central Italy; coordinates 42°58'15.47"N; 12°26'35.48"E. Upper Miocene (Serravallian). This area was described by Clari et al. (2004b).

10. Le Colline.—Scattered marly to micritic limestone blocks outcrop NE of Salecchio, near Palazzuolo (Firenze province), Tuscan Romagna Appenine, northern Italy; coordinates: 44°06'17"N, 11°34'53"E; Marnoso-arenacea Formation, middle Miocene (early Serravallian); further information on this outcrop is provided by Conti and Fontana (1998).

11. Marmorito.—Limestone deposits near the village of Marmorito in the Monferrato hills, east of Torino in the Piedmont Basin in northern Italy; coordinates: 45°03'24"N, 08°01'11"E; late Miocene

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(Tortonian). This well-known deposit was described in more detail elsewhere (Clari et al., 1988; Martire et al., 2010).

12. Montepetra.—Large limestone deposit on the southeastern margin of the village of Montepetra (Forlì-Cesena province), northern Italy; coordinates: 43°55'50.67"N, 12°11'38.22"E. (late Tortonian). This deposit is well described in the literature (Taviani, 1994; Conti and Fontana, 1998; Clari et al., 2004b; Conti et al., 2010).

13. Sasso delle Streghe.—A 30 m high marly limestone peak near the village of Rocca Santa Maria (Modena province), northern Italy; coordinates: 44°28'40.02"N, 10°47'40.11"E; Termina Formation, Miocene (late Serravallian–Tortonian) (Taviani, 1994; Conti and Fontana, 1998; Taviani, 2001; Clari et al., 2004b; Conti et al., 2010). Also known in the past as 'Sasso delle Cappe' (Clams' rock).

14. Verzino.—Small isolated outcrops in the Crotone basin along the steep right slope of the Vitravo river, between the villages of Verzino and Pallagorio at the localities of Maradera-Occhito (Crotone province), southern Italy; coordinates 39°31'90"N 16°87'32"E to 39°30'97"N 16°87'92"E (late Miocene: Tortonian to Messinian?). More information is reported by Gualtieri (1998).

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