



First record of the genus *Adipicola* (Mollusca: Bivalvia: Mytilidae) and description of a new species from the Argentine SW Atlantic Ocean

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Abstract

This work describes a new species of a whale fall mytilid, *Adipicola leticiae* n. sp., which was found on the skull of a sei whale, *Balaenoptera borealis*, collected by a trawling vessel off the Gulf of San Jorge, Argentina. The species represents the first record of a deep water mytilid living on organic remains from the Argentine Sea. The new species is characterized by its combination of an elongated and fragile shell of up to 20 mm in length, lack of periostracal hair, lack of hinge teeth and crenulations, and its straight ventral margin. *Adipicola leticiae* is morphologically compared to other Bathymodiolinae. Current problems of delimiting *Adipicola* from *Idas* and *Terua* are outlined.

Key words: deep water mytilid, Argentina, whale fall

Introduction

Sunken dead whales have incidentally been found by deep sea trawling. These sporadic samples are often colonized by several groups of invertebrates. Molluscan assemblages are the best documented, however, basically because they remain attached to the bones when they are recovered in trawls (Smith & Baco 2003). Whale-fall communities share certain species with sunken-wood and vent-and-seep communities (Smith *et al.* 1989; Smith & Baco 2003). Distel *et al.* (2000) found a close relationship between *Bathymodiolus* Kenk & Wilson, 1985, and *Tamu* Gustafson, Turner, Lutz & Vrijenhoek, 1998, which are associated to vents and seeps, and with *Idas* Jeffreys, 1876, *Adipicola* Dautzenberg, 1927, and *Benthomodiolus* Dell, 1987, which are usually associated with organic-fall substrates. However, while Oliver (2015) has provided a revision of all species of *Benthomodiolus* (Mytilinae), bathymodioline genera still remain poorly resolved.

Species that have been attributed to *Adipicola* live attached by byssus to sunken-wood and whale-fall substrates (Dall *et al.* 1938; Dell 1987, 1995; Prashad 1932; Thiele & Jaeckel 1931). It has been recorded at various localities in the Indo Pacific, North Pacific, around South Africa and in European waters (Dall *et al.* 1938; Dell 1987, 1995; Habe 1958; Marshall 1900; Pailleret *et al.* 2007; Prashad 1932; Thiele & Jaeckel 1931; Verco 1908; Woodward 1854). The oldest *Adipicola* species are from the middle Miocene (Amano 1984; Amano & Little 2005; Danise *et al.* 2016); other bathymodiolines associated with organic falls are already known from the upper Eocene (Amano *et al.* 2007; Kiel & Goedert 2006).

In this work, we suggest a new species belonging to *Adipicola* based on a morphological comparison with all other species that were or are still placed in *Adipicola* (Table 1). The validity of the genus *Adipicola* is discussed in the systematic part.

Material and methods

The species herein described is based on twelve specimens collected by the trawling vessel “Cabo Buena Esperanza” during July, 2010, which were attached to the skull of a sei whale, *Balaenoptera borealis* Lesson. All specimens of the type series are deposited in the Invertebrate Collection of IBIOMAR, CCT-Centro Nacional Patagónico, Puerto Madryn (CNP-Inv) under the catalogue numbers CNP-Inv 2229-2233. The repository and type locality of all compared species are listed in Table 1. The present work has been registered in ZooBank (<http://www.zoobank.org>).

All specimens of the present material were removed from the skull by hand. Most of the shells were still articulated. However, their examination occurred several months after their collection inhibiting genetic studies.

The measurements reported in Table 2 were carried out with a digital caliper. Length was measured as longest anterior to posterior extension, height as largest diameter vertical to length; H/L is the height/length ratio expressed in per cent; B/L is the distance from the anterior end of the shell to the beak expressed in per cent. Both of these parameters are adopted from Dell (1987) to facilitate comparisons. Comparisons with the seven Recent and two Miocene species were carried out after examination of high quality photographs of type material and direct examination of the types from the NHMUK. The suprageneric classification follows Carter *et al.* (2011).

The following institutional abbreviations are used:

JUE	Department of Geoscience, Joetsu University of Education, Joetsu City, Japan.
MSNF	Museo di Storia Naturale, Firenze, Italy.
NHMUK	Natural History Museum, London, Great Britain.
NMNZ	Te Papa Tongawa National Museum of New Zealand, Wellington, New Zealand.
NSMT	Mo, National Museum of Nature and Science, Tokyo, Japan.
SAMA	The South Australian Museum, Adelaide; Australia.
USNM	United States National Museum, Washington, USA.
ZMA	Naturalis Biodiversity Center (Zoölogisch Museum Amsterdam), Leiden, The Netherlands.
ZMB	Museum für Naturkunde, Berlin, Germany.

Systematics

Order Mytilida Férussac, 1822

Family Mytilidae Rafinesque, 1815

Genus *Adipicola* Dautzenberg, 1927

[= *Myrina* Adams & Adams, 1857 (non Fabricius, 1807)].

Type species (by monotypy). *Modiolarca pelagica* Forbes in Woodward, 1854.

Diagnosis. Shell medium size, shell length up to 40 mm, equivalve, subequilateral, fragile, antero-posteriorly elongate; external surface smooth with irregular growth lines covered by a yellowish to brownish periostracum, periostracal hair absent; valves without gape; umbo subcentral to anterior; internally white to nacreous; hinge plate without teeth or crenulations in adults.

Posterior byssal retractors not divided; pedal retractors integrated with the posterior byssal retractors; demibranchs thick, outer and inner demibranchs equal in size. [Soft anatomical features after Coan *et al.* (2000); Gustafson *et al.* (1998); Ockelmann & Dinesen (2011).]

Species included. Species are listed in Table 1.

Distribution. NE Atlantic from Iceland to Portugal, Mediterranean Sea, Marmara Sea; SW and SE Atlantic (Argentine Sea and West Coast of South Africa), Indo-Pacific (West Coast of Sumatra); Pacific Ocean from off Hawaii and Japan to off New Zealand.

Remarks. The genus *Adipicola* was proposed by Dautzenberg (1927) as a substitute name for *Myrina* Adams

& Adams, 1857, which was preoccupied by *Myrina* Fabricius, 1807. Iredale (1939) suggested to replace *Myrina* by *Miridas*, but its type species *Myrina coppingeri* Smith, 1885, is currently placed in *Idas* (Dell 1987). *Miridas* and *Adipicola* are not synonyms, therefore.

Warén (1991) regarded *Adipicola* to be synonymous with *Idas* stating that the main difference, the retention of "crenulated areas along the hinge line" in adult *Idas* but not in *Adipicola*, is only of infrageneric value. However, Coan *et al.* (2000), Gustafson *et al.* (1998) and Ockelmann & Dinesen (2011) found anatomical differences in pedal retractor muscle association, demibranch length and type of gills which would support the validity of two genera. Also, molecular data suggest that *Adipicola* and *Idas* are not monophyletic (Duperron & Gros 2016; Fujita *et al.* 2009; Génio *et al.* 2012; Kyuno *et al.* 2009; Lorion *et al.* 2009, 2010, 2012, 2013; Rodrigues *et al.* 2013; Thubaut *et al.* 2013a & b). These contrasting points of view are well reflected by the two classification approaches of Huber (2010, 2015).

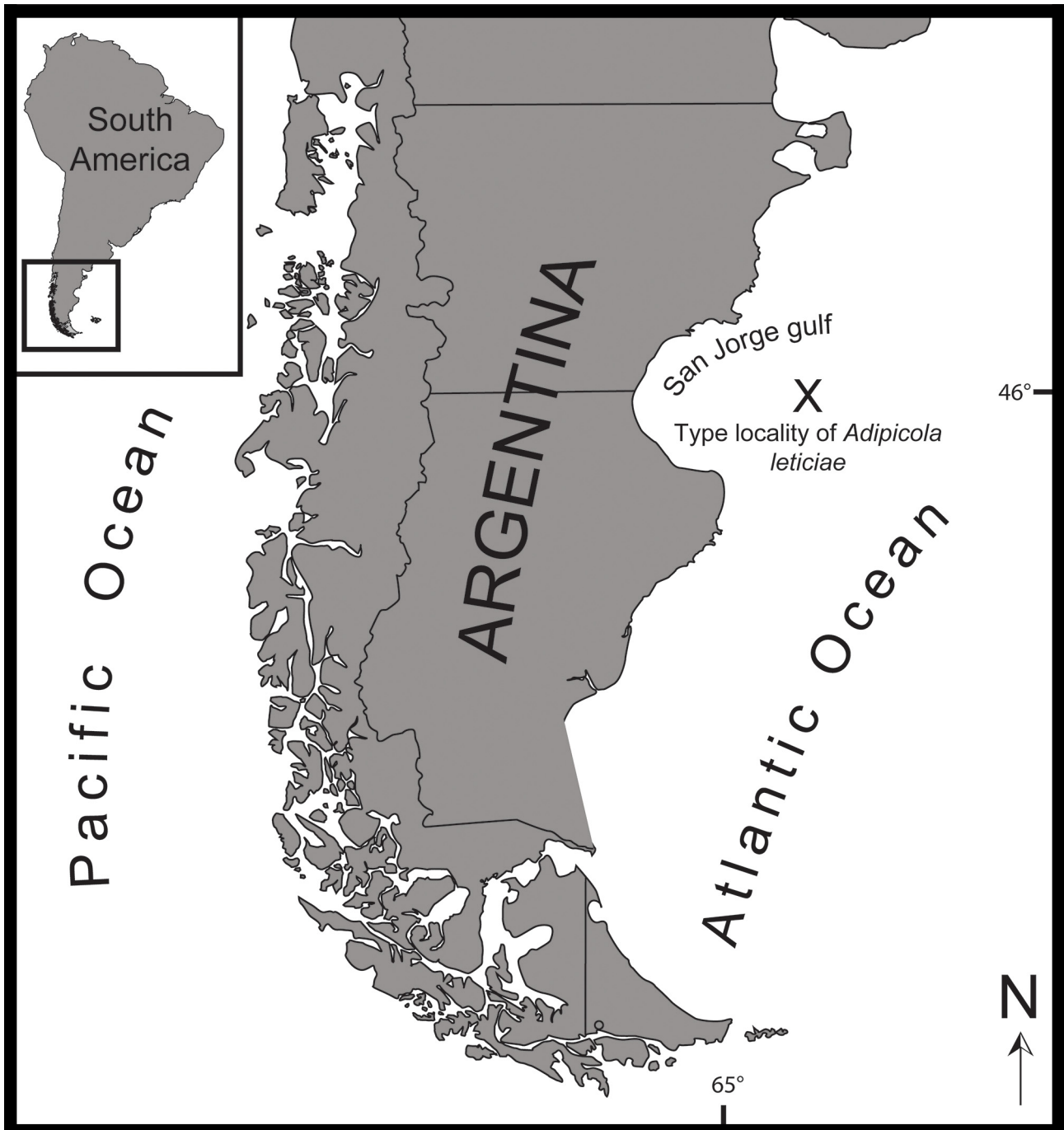


FIGURE 1. Map showing the type locality (X) of *Adipicola leticiae* new species.

TABLE 1. List of recent and fossil species that were or are placed in *Adipicola* Dautzenberg, 1927. “*Adipicola*” species probably represent a new genus the proposed name of which is unavailable, however (Thubaut *et al.* 2013b).

Species	Type Locality	Type Material
<i>Adipicola leticiae</i> n. sp.	46° 10' S; 61° 50' W, off San Jorge gulf, Argentina, from a depth of 104.	Holotype CNP-Inv 2229 and twelve paratypes: CNP-Inv 2230, one articulated specimen, CNP-Inv 2231, one articulated specimen, CNP-Inv 2232 one articulated specimen and CNP-Inv 2233, nine articulated specimens, all attached to the skull of a sei whale <i>Balaenoptera borealis</i>
<i>Adipicola osseocola</i> Dell, 1987	42° 51.0' S, 176° 54.5' W, NE of Chatham Islands, 880 m, New Zealand.	Holotype NMNZ M. 75026 and three paratypes M. 75027.
<i>Adipicola pelagica</i> (Forbes in Woodward, 1854)	Off the Cape of Good Hope, South Africa	Two syntypes NHMUK 1849.12.10.67–68.
<i>Adipicola projecta</i> (Verco, 1908)	Off Beachport, South Australia, 200 fathoms	Holotype, SAMA D13042, one right valve.
“ <i>Adipicola</i> ” <i>longissima</i> Thiele & Jaeckel, 1931	Off coast of Sumatra (1° 48.9'N, 96° 53' E) in 1143 m	Syntypes ZMB 77803, four specimens.
“ <i>Adipicola</i> ” <i>simpsoni</i> Marshall, 1900	North edge of the Great Fisher Bank, about 150 miles N.E. of Aberdeen, 40–50 fathoms	Three syntypes NHMUK 1900.10.16.19–21
<i>Gigantidas crypta</i> (Dall, Bartsch & Rehder, 1938)	Off Oahu, Hawaii, Albatross R/V St. 3810 at 386 m depth.	Holotype USNM 333333.
<i>Idas dubius</i> (Prashad, 1932)	St. 297, 10° 39'S, 123°40'E; depth 520 m, east of Roti Island, Indonesia.	Holotype ZMA.MOLL.135265 and paratype is ZMA.MOLL.135270
<i>Idas iwaotakii</i> (Habe, 1958)	Off Chikuzen-Okinoshima, Fukuoka prefecture, Japan 85 m, collected with a gillnet for lobster fishing	Holotype and two paratypes from type locality NSMT-Mo 39878. Two additional paratypes from Tanabe bay.
<i>Terua arcuatilis</i> Dell, 1995	Northeast of Chatham islands, 42° 56.2' S, 175° 32.6' W, 880–882 m depth, New Zealand.	Holotype NMNZ M. 089788, several hundred paratypes M. 89789, 400 additional paratypes M. 100386, 900 m on whale skull.
<i>Terua pacifica</i> (Dall, Bartsch & Rehder, 1938)	Albatross St. 3909, off Oahu, Hawaii 563–589 m	Holotype USNM 173020, a complete specimen
<i>Adipicola apenninica</i> Danise, Bertolaso & Dominici, 2016)	Paniano Formation, Middle Miocene. Casella di Romagnono, 3.3 km E of Carpinetti, Emilia region, Italy 44°27.46'N, 10°33.59'E.	Holotype, MSNF no. IGF 102221; Paratypes, MSNF nos. IGF 102220, 102222–3.
<i>Adipicola chikubetsuensis</i> (Amano, 1984)	Chikubetsu Formation Lower middle Miocene, 5.5 km upstream of Setakinal River, Shosanbetsu, northwestern Hokkaido, Japan.	Holotype, JUE no. 15002; Paratypes, JUE nos. 15003–1, 15003–2, 15003–3, 15003–4.

It adds to the problem that the type species of *Idas*, *I. argenteus* Jeffreys, 1876, is not representative of the genus because of its adaptations to carnivory and absence of symbiotic bacteria (Ockelmann & Dinesen 2011; Rodrigues *et al.* 2014) whereas the type of *Adipicola*, *A. pelagica*, is a very rare species which has not been found again for a number of years. Hence, a revision including morphological and molecular investigations is currently not possible. This said, we can only state that our new species is morphologically closer to *Adipicola* than to *Idas*.

Analogous to the above problem, the validity of the genus *Terua* is still unresolved. Dell (1987) synonymized *Terua* with *Adipicola* after morphological comparisons of their type species and Duperron & Gros (2016) suggested a closer genetic relationship between *A. pacifica* and *Terua* **n. sp.** from Guadeloupe, in the Caribbean Sea, which raises the question of the relationship between *Adipicola leticiae* **n. sp.** and *Terua*. In this speculative context, we prefer to maintain the genus *Adipicola*.

***Adipicola leticiae* new species**

Figs 2A–J, 3A–K, 4A–D

Type material. Holotype CNP-Inv 2229 and twelve paratypes: CNP-Inv 2230, one articulated specimen, CNP-Inv 2231, one articulated specimen, CNP-Inv 2232, one articulated specimen and CNP-Inv 2233, nine articulated specimens, all attached to the skull of a sei whale *Balaenoptera borealis*.

Type locality. 46° 10' S; 61° 50' W, off San Jorge Gulf, Argentina, from a depth of 104 m (Fig. 1). The collection date was July 21, 2010.

Etymology. This species is dedicated to Leticia Mercante, the first author's wife, for her invaluable support during many years.

Diagnosis. The new species is characterized by the combination of the following characters: adult shell of medium size, up to 20 mm in length, elongate, fragile, ventral margin straight, distance from umbos to anterior shell margin about 30% of shell length; larval shell with prodissoconch 1 of about 175 µm and prodissoconch 2 with a size between 425 to 580 µm in length.

Description. Shell, fragile, subequilateral, equivalve, subrectangular, with anterior end rounded, dorsal-anterior margin anteriorly inclined, lunule not defined; dorsal-posterior margin straight, posterior end rounded, ventral margin straight; umbones prosogyrate, not in touch, placed at 30% of shell length measured from the anterior margin. Periostracum dark-reddish brown. Ligament extending along the dorsal-posterior margin for about 65% of posterior length. External surface smooth with irregular growth wrinkles, periostracal hair absent. Internally white, porcelaneous, pallial line complete, without sinus; hinge plate without teeth or crenulations below umbo or behind ligament; posterior adductor scar circular, anterior scar oval, slightly smaller; pedal retractors fused with the posterior byssal retractors just above the posterior scar; anterior retractor scars not observed; prodissoconch 1 about 175 µm, prodissoconch 2 size between 425 to 580 µm in length. No direct anatomical observations could be made on the dried remains.

Morphological comparisons. The conchological features are compared with other Bathymodiolinae species that were or still are placed in *Adipicola*. Among these, *A. osseocola* Dell, 1987, has a more sharply pointed anterior shell margin and its ventral margin is softly arched rather than straight (Figs 5A–B).

Adipicola pelagica (Forbes in Woodward, 1854) has a slightly arched ventral margin and a less forward-placed umbo (see B/L ratio) than *A. leticiae* **n. sp.**; it also attains a larger size of up to 36 mm in the holotype (Figs 5C–F).

The taxonomic position of *A. projecta* (Verco, 1908) is contentious. Originally described as *Modiola* Lamarck, 1801, Lamprell & Healy (1998) included it in *Idas*, Dell (1987) placed it in *Adipicola*, and Huber (2010) suggested a new genus for this species. Type material was not found in the cabinets of SAMA. The original description and illustration by Verco (1908, p. 195, pl.13, figs. 12–13) suggest an *Adipicola* species distinguishable from our new species by a less elongate shell. Although the ventral border is nearly straight and almost parallel with the dorsal margin, both the shell length and ligament groove are shorter than in *A. leticiae* **n. sp.**

“*Adipicola*” *longissima* Thiele & Jaeckel, 1931, is a regionally rather restricted species (Pante *et al.* 2012) that is predominantly attached to *Nypa fruticans* nuts, in localities where palm trees grow (Philippines, Indonesia and Solomon Islands mainly). Genetically, it clusters with “*Adipicola*” *simpsoni* Marshall, 1900. Therefore, Thubaut *et al.* (2013b) proposed a new generic name, “*Nypamodiolus*” for the two species. Unfortunately, the introduction of the genus name does not fulfil the requirements of the ICZN code (especially Art. 13) and is unavailable, therefore.

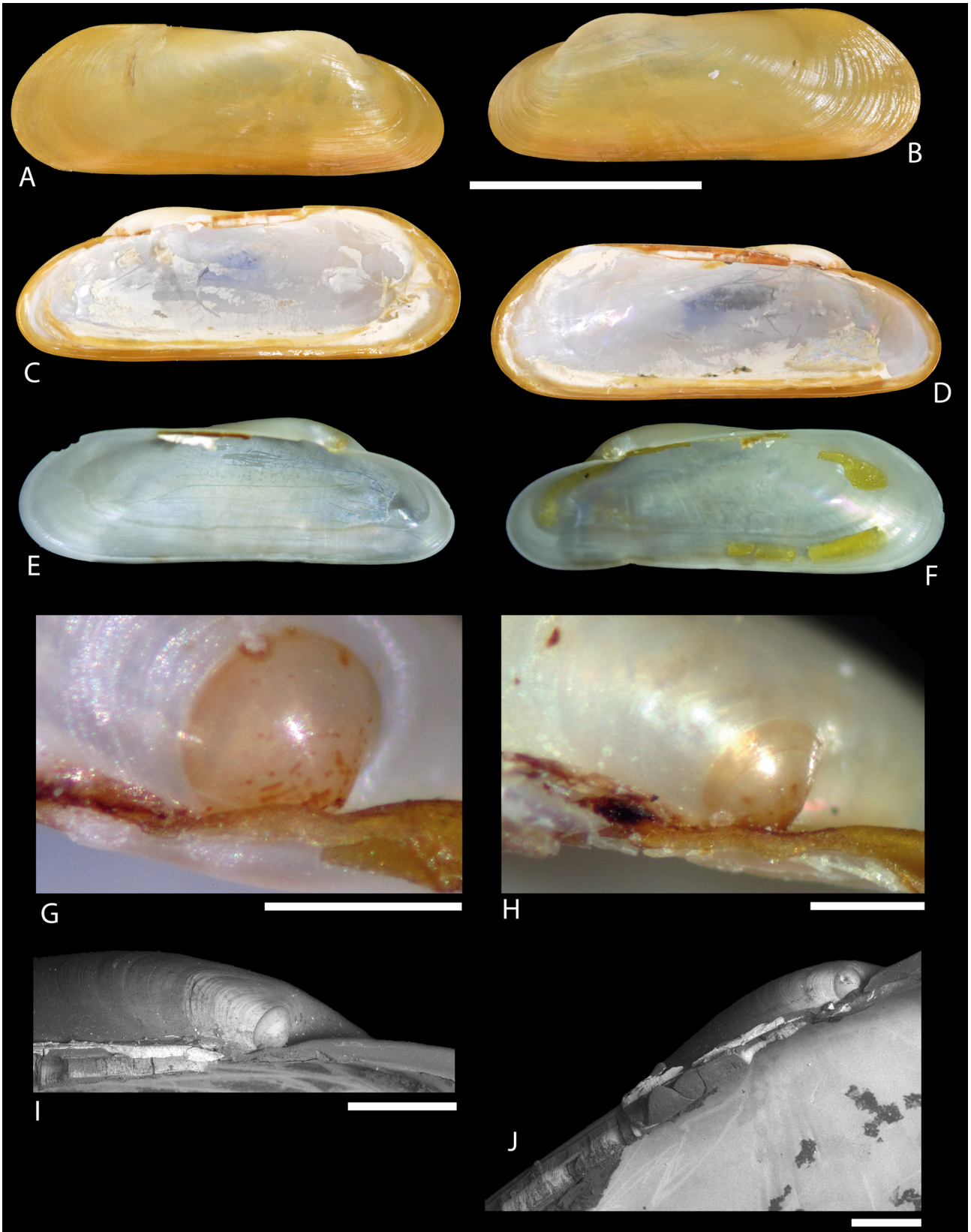


FIGURE 2. A–J. *Adipicola leticiae* new species. A–D. Holotype, CNP-Inv 2229. E–J. Paratype CNP-Inv 2233. E–F. internal view of Paratype 2233. G–H. Prodissoconch 2 of paratype 2233. I–J. Detail of anterior end of ligament of Paratype 2233. Scale bars: A–F = 1cm; G–H = 400 μ m; I–J = 1 mm.

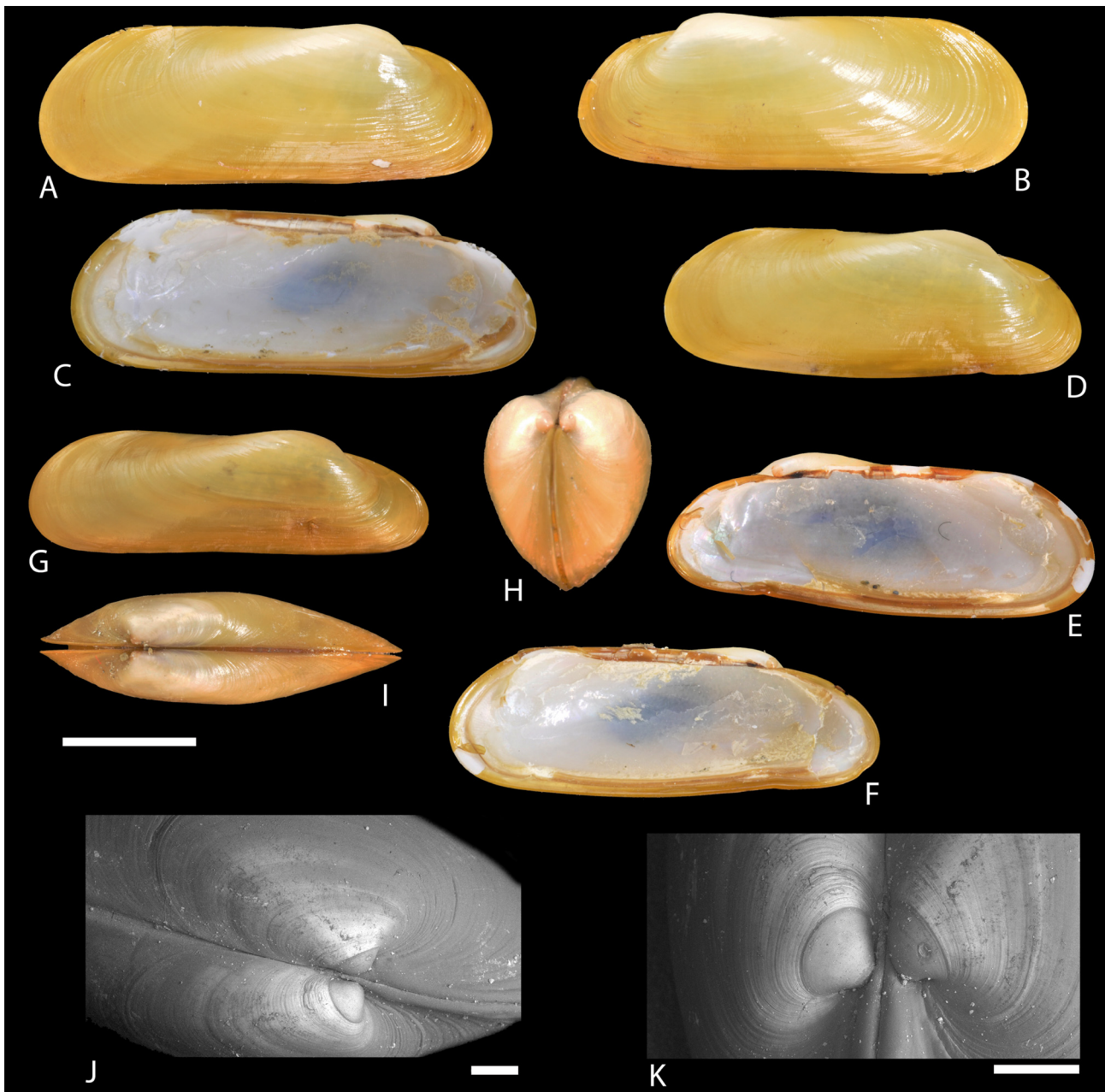


FIGURE 3. A–K. *Adipicola leticiae* n. sp. A–C. Paratype CNP-Inv 2230. D–F. Paratype, CNP-Inv 2231. G–I. Paratype, CNP-Inv 2232. J–K. Paratype CNP-Inv 2233. Scale bars: A–I= 1cm; J–K = 500 μ m.

The types of “*A.*” *longissima* are smaller than the present species and possess a pellucid shell with a sharper, anteriorly more elongated and overall arched shell outline (Figs 5I–J). “*Adipicola*” *simpsoni* is characterized by a more elliptical, posteriorly expanded shell (Figs 6A–D) in contrast to the more subrectangular shape of our species. This is also reflected by different H/L and B/L ratios (Table 2).

The holotype of *Gigantidas crypta* (Dall, Bartsch & Rehder, 1938), previously placed in *Adipicola* by Dell (1987), is only about 4 mm long and has a slightly elevated and much forward-placed umbo. The shell outline is oval with a smaller posterior than anterior end and a slightly concave ventral margin. Much larger specimens of up to 52.9 mm were reported from Japan (Habe 1977; Habe in Koyama *et al.* 1981; Kurozumi 2000). According to genetic studies, the species must be placed in the genus *Gigantidas* Cosel & Marshall, 2003, related to *G. gladius* Cosel & Marshall, 2003 and the “*Bathymodiolus*” *childressi* group (Thubaut *et al.* 2013a).

Huber (2010) excluded Prashad’s *Modiolus dubius* from the genus *Idas* and placed it within *Adipicola* due to the absence of periostracal hairs and the non-glossy interior aspect. Our examination of the holotype and paratype (ZMA.MOLL.135265, ZMA.MOLL.135270) (Figs 5G–H) suggests otherwise. The holotype, from Rotti Island,

Indonesia, shows a rhomboidal shell outline with conspicuous periostracal hairs over posterior portions of the shell. In addition, it shows a well-developed concentric sculpture and elongate ligament from the beak to virtually the end of the dorsal posterior margin. These morphological features are more characteristic of *Idas*.

TABLE 2. Shell measurements and ratios of *Adipicola* species. Abbreviations: B, distance from anterior end to the anterior edge of the beak; H/L, height expressed as a percentage of the length; B/L, distance from anterior end of the shell to the beak expressed as a percentage of the length. * Data after Dell (1987).

Species	Material	Length (mm)	Height (mm)	B (mm)	B/L	H/L
<i>Adipicola leticiae</i>	Holotype	20	7	5	23,9	33,7
	Paratype 1	18	6	4	24,2	35,1
	Paratype 2	17	6	4	25,2	36,0
	Paratype 3	16	5	5	29,2	31,1
	Paratype 4	16	6	5	29,0	35,8
	Paratype 5	13	5	4	27,7	37,0
	Paratype 6	9	4	2	22,8	39,3
	Paratype 7	11	4	3	26,8	40,6
	Paratype 8	10	4	3	24,0	38,9
	Paratype 9	9	4	3	28,3	41,2
	Paratype 10	9	3	2	27,1	38,5
	Paratype 11	8	3	2	25,5	39,3
Paratype 12	9	4	2	21,1	42,5	
<i>A. osseocola</i> *	Holotype	24	9	6	24,6	37,3
	Paratype 1	28	9	8	28,1	32,7
	Paratype 2	24	9	6	26,4	36,2
	Paratype 3	19	8	5	24,3	39,7
<i>A. pelagica</i> *	Syntype 1	36	17	12	32,0	46,1
	Syntype 2	32	14	10	31,0	44,9
“ <i>A.</i> ” <i>simpsoni</i> *	Syntype 1	23	10	4	19,6	46,2
	Syntype 2	21	10	3	15,0	45,9
	Syntype 3	17	7	3	16,4	42,7
	North Sea	20	9	4	21,4	44,4
	Shetlands	19	8	4	19,4	42,5
	Shetlands	18	8	4	19,7	43,8
<i>T. pacifica</i> *	Holotype	27	11	6	22,6	42,6
	Japan 150 m	26	12	8	32,4	45,3
	Japan 150 m	15	7	4	25,0	48,0

Dell (1987) suggested that the types of *A. iwaotakii* (Habe, 1958) could belong to larger specimens of *A. crypta*. However, the genetic analysis by Thubaut *et al.* (2013b) places this species within *Gigantidas* and close to the *Bathymodiolus* “*childressi* group”.

Terua arcuatilis Dell, 1995, differs from *A. leticiae* **n. sp.** by having an arched rather than straight ventral margin, a longer ligament and a larger and more elongate shell (Figs 6E–F). *Terua pacifica* (Dall, Bartsch & Rehder, 1938) (Figs 6G–H) differs from the new species by having an arched ventral margin and a less elongate shell. Its collection sites in the Pacific off Oahu, Hawaii and southern Japan (Dell 1987; Habe 1977) also suggests that these are different species.

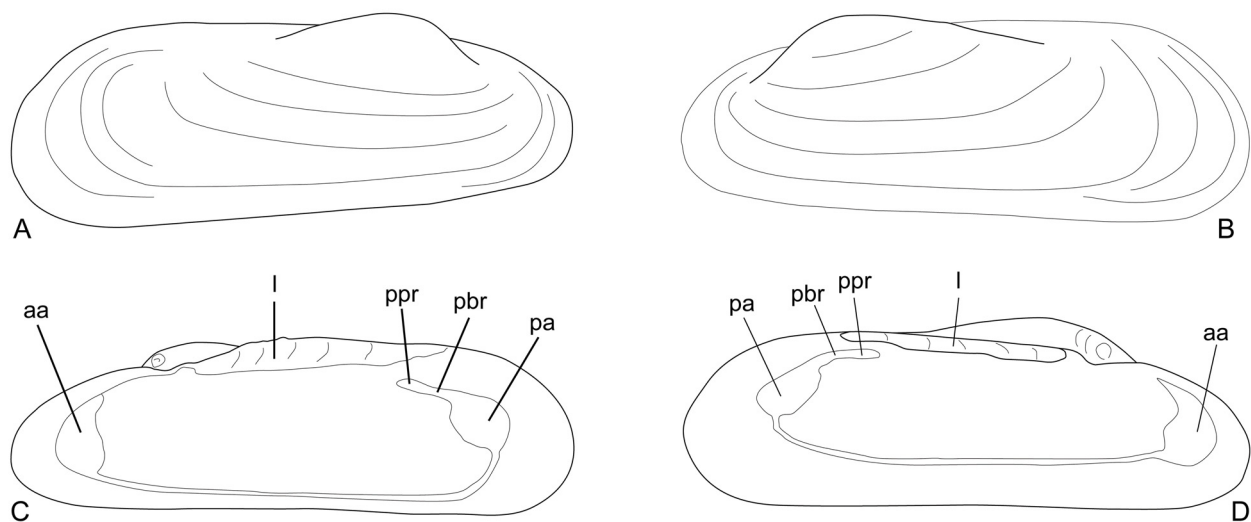


FIGURE 4. *Adipicola leticiae* n. sp. A–D. Paratype, CNP-Inv 2230. A–B. External view. C–D. Internal view, showing outline of the various muscle scars; aa: anterior adductor muscle; l: ligament; pa: posterior adductor muscle; pbr: posterior byssal retractor muscle; ppr: posterior pedal retractor muscle.

Discussion

The present study updates and contributes to the knowledge of deep water biodiversity of Mytilidae by the description of a new Bathymodiolinae species. Herein, we recognize six species within *Adipicola*, among them two Miocene species from Japan and Italy, respectively and *Adipicola leticiae* n. sp. The new species constitutes the first record of the genus reported as living in the southwestern Atlantic Ocean.

Recent genetic publications (Fujita *et al.* 2009; Génio *et al.* 2012; Lorion *et al.* 2010; Thubaut *et al.*, 2013b, among others) on *Adipicola* and related genera reveal that morphological characters are not enough to distinguish them. Thus, *Adipicola sensu lato* is used as a placeholder until more conclusive results resolve the biodiversity of Bathymodiolinae.

Specifically, new field work along the Argentine Sea should focus on the collection of life material for molecular biologic studies. However, this is a difficult task given that natural habitats of whale skeletons and other organic remains have an unpredictable patchy distribution. To counteract this difficulty, systematic sampling has been conducted in some areas such as in Papua New Guinea (Pante *et al.* 2012) and Japan (Kyuno *et al.* 2009). Also, experiments have been conducted by sampling purposefully sunk pieces of wood (Dean 1993; Ockelmann & Dinesen 2011; Rodrigues *et al.* 2014), whale carcasses (Fujiwara *et al.* 2007, 2010; Okutani *et al.* 2004) and cow bones (Génio *et al.* 2015), enabling studies to be conducted on colonization, population dynamics, and reproductive cycles. Such experimental work will undoubtedly contribute to the knowledge of deep-water mytilids.

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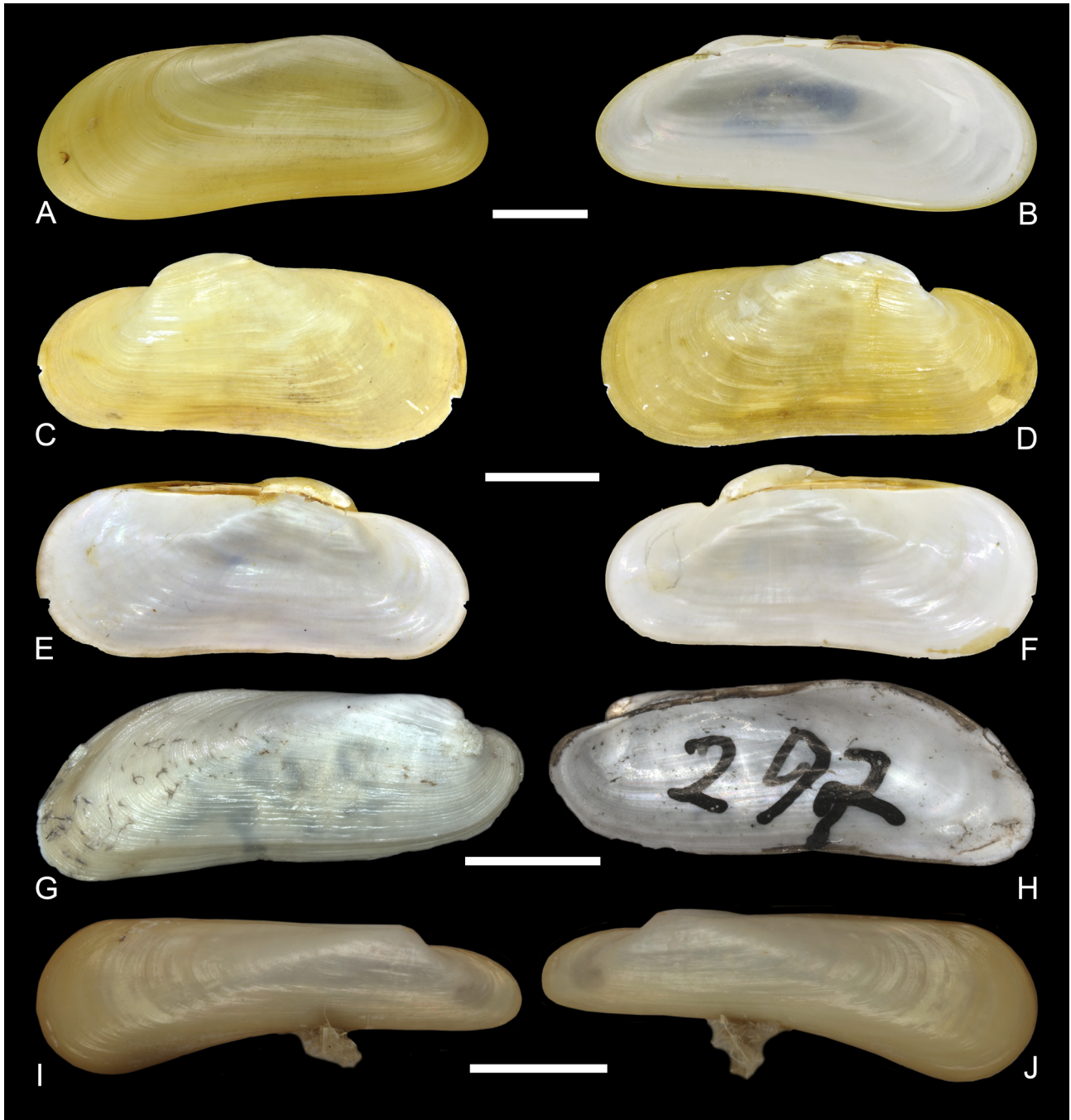


FIGURE 5. A–B. *Adipicola osseocola*, Holotype NMNZ M. 75026 (copyright Te Papa CC-BY-N-ND license). C–F. *Adipicola pelagica*, Syntypes NHMUK 1849.12.10.67–68. G–H. *Idas dubius*, Holotype ZMA.MOLL 135265, right valve. I–J. “*Adipicola*” *longissima*, Syntype ZMB 77803. Scale bars: A–B, I–J = 5 mm; C–F = 1 cm; G–H = 2 mm.

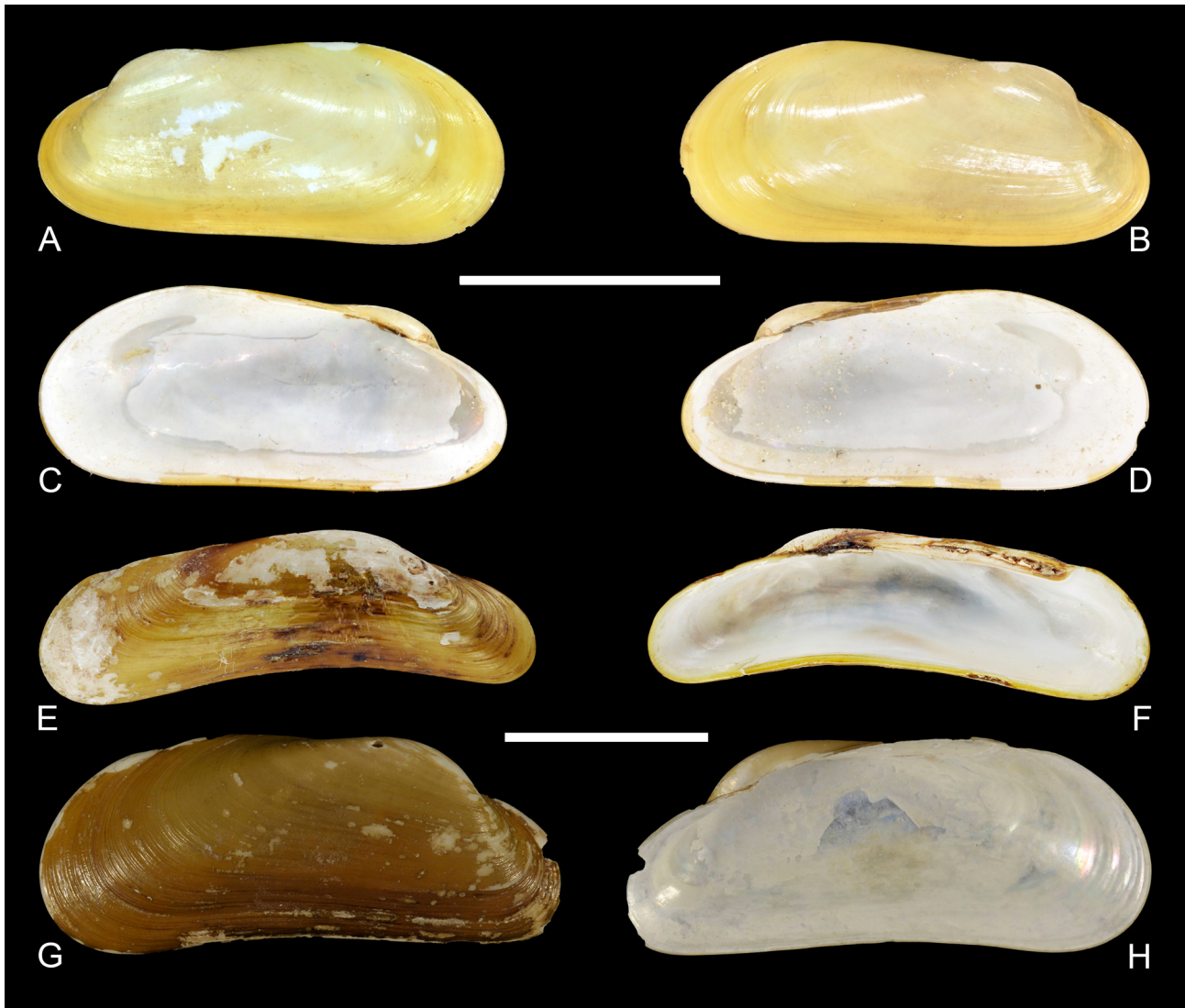


FIGURE 6. A–D. “*Adipicola*” *simpsoni*, Syntypes NHMUK 1900.10.16.19–21. E–F. *Terua arcuatilis*, Holotype NMNZ M. 089788 (copyright Te Papa CC-BY-N-ND license). G–H. *Terua pacifica*, Holotype USNM 173020 (copyright National Museum of Natural History, Smithsonian Institution). Scale bars: A–H = 1 cm.

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