Geologia Croatica
Journal of the Croatian Geological Survey
and the Croatian Geological Society

2023 | 76/1 | 37–46 | 7 Figs. |

www.geologia-croatica.hr

Taxonomic revision of the Lake Pannon cockle subgenus *Lymnocardium* (*Budmania*) BRUSINA, 1897

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doi: 10.4154/gc.2023.01

Article history:

Manuscript received March 11, 2022
Revised manuscript accepted November 28, 2022
Available online February 23, 2023

Keywords: Mollusca, Lake Pannon, Neogene, taxonomy, paleoecology, stratigraphy

Abstract

The lymnocardiine subgenus *Budmania* is characterized by the most unusual and spectacular morphology in the endemic mollusc fauna of the Late Miocene – Pliocene Lake Pannon. *Budmania* possessed extremely high, hollow, irregular keels on its ribs, a pattern that was long considered an adaptation to the fluid, muddy substratum. Eight species were described with this pattern between 1874 and 1973. Our revision, based on the type materials and a large number of additional specimens from several collections, revealed however, that only two species can be distinguished with certainty: *Lymnocardium* (*Budmania*) *ferrugineum* (BRUSINA, 1874) and *L.* (*B.*) *cristagalli* (ROTH, 1878). The former lived in the littoral zone of Lake Pannon, on a sandy substratum, whereas the latter inhabited the sublittoral zone with a muddy bottom. This habitat partitioning challenges the interpretation of the high, hollow keels as an adaptation to a soft, muddy substratum. The occurrence of both species seems to have been restricted to the period between 7.5-7.15 Ma.

1. INTRODUCTION

Long-lived lakes are often sites of endemic radiation in their various groups of biota. Well-known examples include molluscs (e.g., HAASE & BOUCHET, 2006; WESSELINGH, 2007), that sometimes develop spectacular morphologies in such lakes, e.g., Recent thalassoid snails in Lake Tanganyika (WILSON et al., 2004) or molluscs of Miocene Lake Pebas in South America (WESSELINGH et al., 2002). The Late Miocene – Pliocene Lake Pannon, a large, deep, brackish lake in the intra-Carpathian Pannonian Basin System, was also the habitat of a diverse endemic mollusc fauna (MÜLLER et al., 1999; NEUBAUER et al., 2016). This fauna included some forms with highly unusual morphologies, such as the up to 10 cm long, thick-shelled dreissenid mussel *Congeria ungulacaprae* (MÜNSTER, 1837) (known as “goat’s hoof” to the locals), or the limpet-shaped, profundal dweller lymnaeid snail *Valenciennius* ROUSSEAU, 1842 which could also grow up to 10 cm wide (e.g., AGER, 1963, 1993).

The most spectacular “freaks” from this lake, however, became widely known to the scientific public when Gyula (‘Julius’) Halaváts, a geologist of the Hungarian Royal Geological Institute, discovered a new fossil locality near the small village of Tirol, Bánság/Banat region, southeastern Pannonian Basin, in 1883 (HALAVÁTS, 1892; Fig. 1). [The name of the locality became known as Királykegye (Hungarian) and Königsgnade or Königsgnad (German), referring to the act of Franz I, Emperor of Austria, who settled exiled Tyrolian freedom fighters here in 1810.] HALAVÁTS (1892) found a clay layer that had been deposited in the sublittoral zone of Lake Pannon and contained a diverse and well-preserved fauna of endemic cardiids, dreissenids, and deepwater-adapted lymnaeids. The most interesting member of the fauna was a cockle with spectacularly high, irregular, keeled radial ribs. In many specimens, the extreme part of the keel formed a T-shaped swelling in cross section, similar to the head of a railway track profile. HALAVÁTS (1892) recognized this form as a new species and named it *Cardium* (*Adacna*) *semseyi*, in honor of Andor Semsey, a generous patron of earth sciences in Hungary. This fossil was recovered in apparently unrestricted quantity from the layer, and specimens from Tirol thus became treasured items in many fossil collections from Bucharest to London and from Vienna to Washington.

The extremely high, sometimes distally swollen, internally hollow keels with their multiple cavities challenged functional morphological interpretations. MARINESCU (1973) argued that the extreme size of the keels excludes any role in mechanical stregthening. He thought that the only adaptive significance of the keels was providing more stability to the large shells in a fluid mud. SAVAZZI & SÄLGEBACK (2004) also discarded the mechanical enforcing role of the high ribs, and concluded that this peculiar sculpture served anchoring functions, preventing sinking within the water-laden, soupy, muddy sediment.

Specimens of lymnocardiine cockles with extraordinarily high keels from Tirol and other localities were classified into eight species comprising a subgenus, *Budmania* BRUSINA, 1897. The authors of new species commonly failed to give clear differential diagnoses, and generally underestimated the high intraspecific variability, a pattern very characteristic of Lake Pannon endemic molluscs, including cardiids (e.g., MÜLLER & MAGYAR, 1992). Here, we revise these keeled lymnocardiines and discuss their palaeoenvironment, stratigraphic distribution, age, and possible evolutionary context.

2. TAXONOMIC HISTORY

In 1874, Croatian palaeontologist S. Brusina described a new species under the name *Cardium ferrugineum* from Remete (now a neighbourhood in the Maksimir district of Zagreb). His specimens were moulds (“steinkerns”) preserved in iron-stained sand, with the calcareous shell material completely dissolved (Fig. 2). Brusina did not depict the fossils, and gave only a very brief description:

"*Cardium ferrugineum* […] reaches the size of *C. Zagrabiense*, resembles *C. Neumayri* Fuchs from Matica north of Ploeşti in Wallachia [Romania], but it can be easily distinguished at first glance from all other forms by its 5, rarely 6 to 7 high, lamella-like ribs, and by the ribless posterior part of the shell. The ribs are very similar to those of the recent *C.* (*Tropicardium*) *costatum* L. […] from Guinea and Senegambia" (translated from German).

Four years later L. ROTH (1878) also published a description of a new species, *Cardium cristagalli*, from multiple localities in southwestern Hungary. His best-preserved specimens were found in the village of Kurd (Figs. 1, 3). ROTH (1878) compared his new species with Brusina's *C. ferrugineum*: "The species *Card. ferrugineum*, proposed by Brusina, as far as it can be judged from the very brief description, seems to be a close relative of *C. cristagalli* […]. The ribs [of *C. ferrugineum*] are, according to Brusina, very similar to those of *C.* (*Tropidocardium*) *costatum* L., so they seem to be slightly different from the ribs of my new species. […] I had the opportunity to compare the original specimens of this *Cardium* species living along the western coasts of Africa with my fossils. I found that although the ribs of the two forms are similar in general, they are significantly different if details are observed. As I do not possess a drawing of *C. ferrugineum*, I am not in the position to say anything about any similarity of ribs between *C. ferrugineum* and *C. cristagalli*" (translated from Hungarian). ROTH (1878) listed the additional localities around the Mecsek Mountains (southwestern Hungary) where he and his colleague Böckh collected *C. cristagalli*. Its moulds (steinkerns) from iron-stained sand were recovered in Hidas, Németürög (now part of Pécs), Bükkösd, Sormás, Cserdi, Zsibrik and Pusztafalu (now part of Lovászhetény), whereas its well-preserved shells were collected from bluish gray clay in Bakóca and Bükkösd. Roth observed that specimens found in clay were always larger than those recovered from sand. He gave drawings of two specimens: one from a sand layer in Kurd, and another, embedded into clay, from Bükkösd (Figs. 1, 3).

In 1884, Brusina described a new species, *Adacna meisi*, based on a single, well-preserved right valve from Zagreb–Okrugljak. He noted that "perhaps my steinkerns that I described as *Cardium ferrugineum* from Remete belong to this species, but those fossils do not provide solid evidence for such a conclusion" (translated from German).

BRUSINA (1884) also described the highly keeled *Adacna histiophora* from the clays of Zagreb–Okrugljak. In the description he referred to *Adacna cristagalli* Roth but did not present a comparison between the two species.

HALAVÁTS (1892) argued that his new species, *Cardium* (*Adacna*) *semseyi*, belonged to the same group as *Cardium cristagalli* ROTH and *Adacna histiophora* BRUSINA. "The Királykegye form is very closely related to both; they are all similar in their size, outline, number and spacing of radial ribs. The difference lies in the shape of the rib. The other two forms have evenly thin lamellae, whereas the Királykegye form displays a thickened head at the top of the rib, similar to the cross-section of a railway track" (translated from Hungarian). LŐRENTHEY (1893), however, remarked that some thickening in the top of the lamellae is present in his *L. cristagalli* specimens from Nagymányok, as well as in the Sormás and Bükkösd specimens (syntypes) of ROTH (1878).

HOERNES (1901) introduced the new name "*Limnocardium subferrugineum*" for two right valves from Tirol. He observed

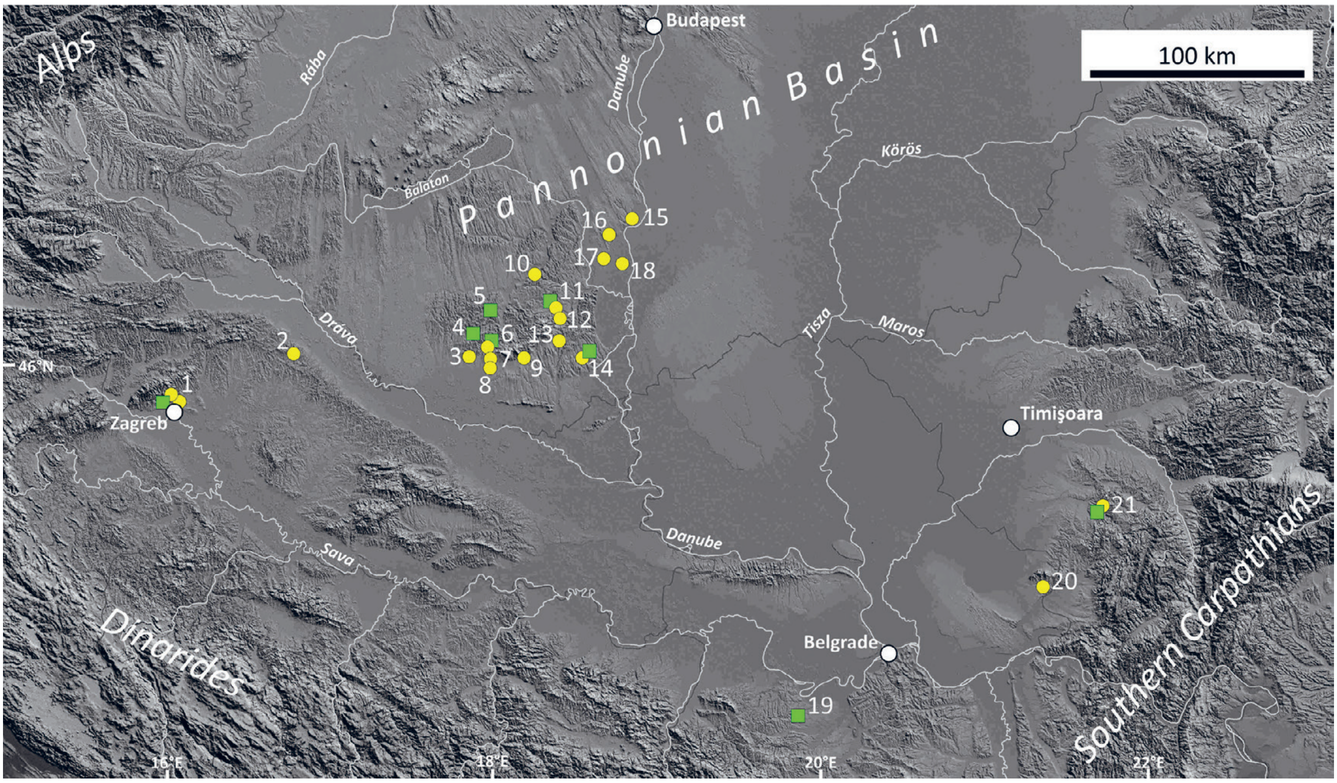

Figure 1. The southern Pannonian Basin with confirmed localities of *Lymnocardium* (*Budmania*) *ferrugineum* (dots) and *L.* (*B.*) *cristagalli* (squares). The geographic distribution of the two species is restricted to the southern part of the basin where they largely overlap, and mark the position of the shelf in Lake Pannon between ca. 7.6 and 7.1 Ma ago. 1) Zagreb (Remete and Okrugljak), 2) Jagnjedovac, 3) Nyugotszenterzsébet, 4) Ibafa, 5) Bakóca, 6) Bükkösd, 7) Cserdi, 8) Szentlőrinc, 9) Pécs–Cserebogár-dűlő, 10) Kurd, 11) Nagymányok, 12) Hidas, 13) Lovászhetény–Pusztafalu, 14) Himesháza, 15) PAET-34P, 16) PAET-29P, 17) PAET-27, 18) PAET-30, 19) Novaci, 20) Kuštilj, 21) Tirol.

that "they are very closely related to the Remete steinkerns described by Brusina as *Cardium ferrugineum*; they possibly belong together"(translated from German).

HOERNES (1901) claimed that *L. semseyi* is connected to *L. cristagalli* with transitional forms, and any distinction between the two forms would be arbitrary. He also claimed that there was no reason to distinguish *L. histiophorum* from *L. cristagalli*; the sail-like, triangular lamellae of the illustrated type specimen of *L. histiophorum* is presumably a pathological pattern which is not characteristic for all specimens of this species from Okrugljak. In spite of these observations, he argued in favour of keeping the names "*semseyi*" and "*cristagalli*" denoting varieties (subspecies) with extreme morphologies.

GORJANOVIĆ-KRAMBERGER (1902) synonymized *L. semseyi* with *L. histiophorum*, coming to the conclusion that *L. cristagalli* and *L. histiophorum* are two subspecies ("varieties") of the same, strongly variable species. He also argued that *L. subferrugineum* HOERNES is identical to *L. ferrugineum* BRUSINA.

ANDRUSSOFF (1903) went further: he claimed that *B. meisi*, *B. cristagalli* (the Kurd form), *B. histiophora* and *B. semseyi* represent "vicariant forms" of one and the same species, each with its own distinct geographical distribution.

In spite of these observations, all the above species names remained in use by subsequent authors. In fact, two new species names were introduced based on specimens from Tirol. MARINESCU (1973) described *Limnocardium* (*Budmania*) *aequicostata* and *L.* (*B.*) *obliquicosta*, claiming that their types were first considered "aberrant individuals" or specimens with "distorted growth" of *L. semseyi*.

BRUSINA (1897) erected the subgenus *Budmania* for the species "*Budmania histiophora*" and "*Budmania meisi*", without further explanation or description. HOERNES (1901) and GORJANOVIĆ-KRAMBERGER (1902) disagreed with the idea of erecting a new subgenus for these species, because the character of the ribs is highly variable in all these forms, and because *Lymnocardium hungaricum* and *L. zagrabiensis*, two species with moderately high ribs, were excluded from the subgenus. Later authors, however, used *Budmania* as a subgenus or genus for all lymnocardiines with extremely high, hollow ribs, i.e. for *L.* (*B.*) *ferrugineum*, *L.* (*B.*) *cristagalli*, *L.* (*B.*) *histiophorum*, *L.* (*B.*) *meisi*, *L.* (*B.*) *semseyi*, *L.* (*B.*) *subferrugineum*, *L.* (*B.*) *aequicostata*, and *L.* (*B.*) *obliquicosta* (e.g., MARINESCU 1973; STEVANOVIĆ 1990; BASCH 1990; SAVAZZI & SÄLGEBACK 2004).

3. MATERIAL

In our revision, we used specimens from the following collections: Croatian Natural History Museum, Zagreb (Hrvatski Prirodoslovni Muzej, HPM); Natural History Museum Vienna (Naturhistorisches Museum Wien, NHMW); Supervisory Authority of Regulatory Affairs, Budapest (Szabályozott Tevékenységek Felügyeleti Hatósága, formerly Geological Institute of Hungary, SZTFH); and the Hungarian Natural History Museum, Budapest (Magyar Természettudományi Múzeum, MTM). Information on specimens was obtained from the collection of the University of Graz (Universität Graz, UG). Literature data was utilized from materials deposited in the Geological Institute of Romania – National Museum of Geology, Bucharest (Institutul Geologic al României – Muzeul National de Geologie, IGR-MNG).

4. TAXONOMIC DECISIONS AND THEIR JUSTIFICATION

Much confusion in the literature came from the fact that Roth's nominal species *Cardium cristagalli* had a composite nature. ROTH (1878) failed to recognize that, in addition to size, there are several other consistent morphological differences between the sand- and clay-associated specimens of *C. cristagalli*. In specimens from sand, the shell has a triangular or, rather, a quarter circle outline, the hinge is strongly curved in an S-shape, the posterior field is smooth, and all radial ribs curve anteriorly (as they run from the umbo towards the ventral margin). In contrast, specimens from clay sediments have an outline resembling a semi-circle, the hinge is straight to slightly sigmoidal, and the posterior field is covered with ribs that curve posteriorly.

Based on these consistent diagnostic features recognizable even in steinkerns and posterior fragments, the original syntypes of *C. cristagalli* (Fig. 3) belong to two different species: the smaller, sand-associated form is identical with *Lymnocardium* (*B.*) *ferrugineum* (BRUSINA, 1874), whereas the larger, clay-associated form indeed represented a species that was new to science in 1878. Later literature refers to either the Kurd form or the Bükkösd form, or both as *C. cristagalli*, causing ambiguities in identification.

In order to avoid further confusion, we designate the specimen depicted by ROTH (1878, his fig. 2), found in clay at Bükkösd, as the lectotype of *L. cristagalli*. We are entitled to do so particularly because the first scholar to further advocate this species name, LŐRENTHEY (1890, 1893), applied the name for the Bükkösd morphotype when identifying newly found specimens from Nagymányok. The Kurd specimens of ROTH (1878, his fig. 1) are identified as *Cardium ferrugineum* BRUSINA, 1874 herein.

We share BRUSINA'S (1884) original idea about the identity of his *Cardium ferrugineum* and *Adacna meisi*. Thus, following the notion of HOERNES (1901) and GORJANOVIĆ-KRAMBERGER (1902), we regard both *A. meisi* and *L. subferrugineum* as subjective junior synonyms of *Cardium ferrugineum* BRUSINA.

We also agree with HOERNES (1901) and GORJANOVIĆ-KRAMBERGER (1902) that *C. cristagalli*, *A. histiophora* and *C.* (*A.*) *semseyi* represent one highly variable species. We further argue that the diagnoses of *L.* (*B.*) *aequicostata* and *L.* (*B.*) *obliquicosta* by MARINESCU (1973) do not justify the erection of these new taxa. The very few features that MARINESCU (1973) mentions when comparing his new species to *L.* (*B.*) *semseyi* are not sufficient to distinguish his type specimens from other specimens of *L.* (*B.*) *semseyi*. The photographic illustrations do not provide such features either, and the author explicitly claims (in the case of *L.* (*B.*) *obliquicosta*) that there is a specimen that shows transitional character towards *L.* (*B.*) *semseyi*. In our view, Marinescu's type specimens only represent extreme morphological variants of *L.* (*B.*) *semseyi*. As a consequence, we claim that *Adacna histiophora*, *Cardium* (*Adacna*) *semseyi*, *Limnocardium* (*Budmania*) *aequicostata* and *Limnocardium* (*Budmania*) *obliquicosta* are all junior subjective synonyms of *Cardium cristagalli*.

Systematic palaeontology

Genus *Lymnocardium* STOLICZKA, 1870
Type species: *Cardium haueri* HÖRNES, 1861; OD

Subgenus *Budmania* BRUSINA, 1897
Type species: *Adacna histiophora* BRUSINA, 1884; SD, COSSMANN (1898)

***Lymnocardium* (*Budmania*) *ferrugineum* (BRUSINA, 1874)**

1874 *Cardium ferrugineum* BRUS. – BRUSINA, p. 138.

in part 1878 *Cardium cristagalli* ROTH nov. sp. – ROTH, p. 54, pl. 4, fig. 1 (excl. fig. 2.)

1884 *Adacna ferruginea* BRUSINA – BRUSINA, p. 138.

1884 *Adacna Meisi* BRUSINA – BRUSINA, p. 146, pl. 28, fig. 36.

1897 *Budmania Meisi* – BRUSINA, p. 35, pl. 18, figs. 7, 8.

1901 *Limnocardium subferrugineum* nov. form. – HOERNES, p. 89, pl. 2, fig. 1; pl. 3, fig. 2.

1902 *Limnocardium* (*Budmania*) *Meisi* BRUS. – GORJANOVIĆ-KRAMBERGER, p. 9, pl. 2, fig. 3.

1902 *Limnocardium ferrugineum* BRUS. – GORJANOVIĆ-KRAMBERGER, p. 11, pl. 1, figs. 1–6.

1903 *Limnocardium Meisi* BRUSINA – ANDRUSSOFF, p. 71, pl. 6, figs. 17–21.

1903 *Limnocardium crista galli* ROTH – ANDRUSSOFF, p. 72, pl. 7, figs. 10–12.

1933 *Limnocardium meissi* BRUS. – ŠUKLJE, p. 16, pl. 1, fig. 1.

non 1934 *Limnocardium ferrugineum* BRUS. – POLJAK & ŠUKLJE, p. 17, pl. 2, fig. 1.

1968 *Limnocardium ferrugineum* BRUS. – POPOVIĆ, p. 361, pl. 3, figs. 1–3.

1973 *Limnocardium* (*Budmania*) *ferrugineum* (BRUSINA) – MARINESCU, p. 21, pl. 6, fig. 2.

1990a *Limnocardium* (*Budmania*) *meisi* BRUSINA – BASCH, p. 553, pl. 2, figs. 7–9.

1990b *Limnocardium* (*Budmania*) *meisi* (BRUSINA) – BASCH, p. 54, pl. 16, figs. 3–5; pl. 17, fig. 5.

in part 1990b *Limnocardium* (*Budmania*) *ferrugineum* (BRUSINA) – BASCH, p. 55, pl. 18, figs. 1–5, 7 (excl. figs. 6, 8)

1992 *Lymnocardium cristagalli* (ROTH) – BUJTOR, p. 240, pl. 1, figs. 1, 2.

2015 *Lymnocardium ferrugineum* – SZTANÓ et al., p. 340, fig. 10e.

2018 *Lymnocardium ferrugineum* – KOVÁCS et al., p. 339, pl. 1, figs. H, I.

2022 Lymnocardium ferrugineum – RADIVOJEVIĆ et al., p.1561, fig. 7c

Type locality: Zagreb–Remete (district of Maksimir).

Type material: syntypes (12 specimens) in HPM (5270-435/1-4, 5271-436.1-3, 5272-437.1-5).

Remarks: The syntypes of *L. ferrugineum* hold some uncertainty, because their original labels were lost. BRUSINA (1874) did not originally specify the number of specimens that served as a basis for the description of the species, but 10 years later he claimed that there were 16 steinkerns of *L. ferrugineum* in the Zagreb museum from Remete (BRUSINA 1884). GORJANOVIĆ-KRAMBERGER (1902), who revised the subgenus *Budmania*, wrote that "I had not only Brusina's originals at my disposal, but also sufficient comparative material". We infer from this remark that all the Remete specimens of *L. ferrugineum* in HPM, 4 of which were photographed and figured by GORJANOVIĆ-KRAMBERGER (1902), are the syntypes of this species.

Of the paralectotypes of *cristagalli* that belong to *ferrugineum*, some injured shells from Kurd (Pl.3145–3150, 3152; Fig. 4/A, B) and steinkerns from Hidas (Pl.3037, 3039, 3041, 3042),

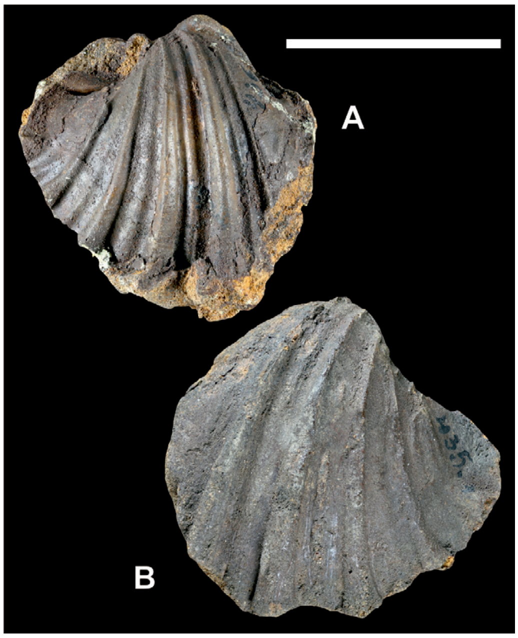

Figure 2. *Lymnocardium* (*Budmania*) *ferrugineum* (BRUSINA, 1874), syntypes from Zagreb–Remete. A: HPM 5271-436.3; B: HPM 5270-435. Scale bar: 3 cm.

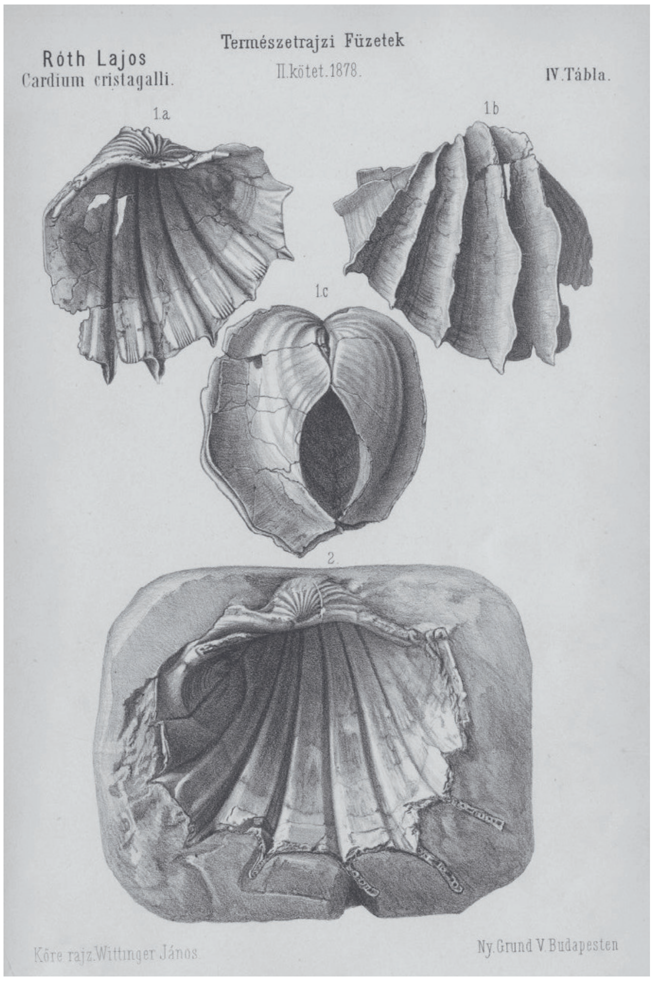

Figure 3. The first illustration of specimens of *Lymnocardium* (*Budmania*). This plate by ROTH (1878) clearly shows the difference between the two species of the subgenus. Although ROTH (1878) considered both depicted specimens belonged to *Cardium cristagalli*, we identify the upper specimen (1 a-c) from Kurd as *L.* (*B.*) *ferrugineum*. The lower specimen (2) from Bükkösd is designated herein as the lectotype of *Lymnocardium* (*B.*) *cristagalli*.

Bükkösd (Pl.2791–2793), Cserdi (Pl.2843), and Lovászhetény–Pusztafalu (Pl.4360) are available at SZTFH.

The holotype of *Adacna meisi* is reposited in the HPM (5011-176/1, holotype by monotypy; MILAN et al. 1974; BASCH 1990). Further specimens from Zagreb-Okrugljak are available in Zagreb (HPM 5003-168.1-4; 5010-175.1-5; 3161/87; Fig. 4F) and Vienna (NHMW 1889/0002/0003; 1889/0002/0004; 1889/0002/0006; 1888/0014/0031; Figs 4E, G, H).

According to HOERNES (1901), the two syntypes of *Lymnocardium subferrugineum* from Tirol were reposited in the collection of the University of Graz, but they are presumed lost (B. Hubmann, pers. comm. 2014). Further specimens from Tirol are

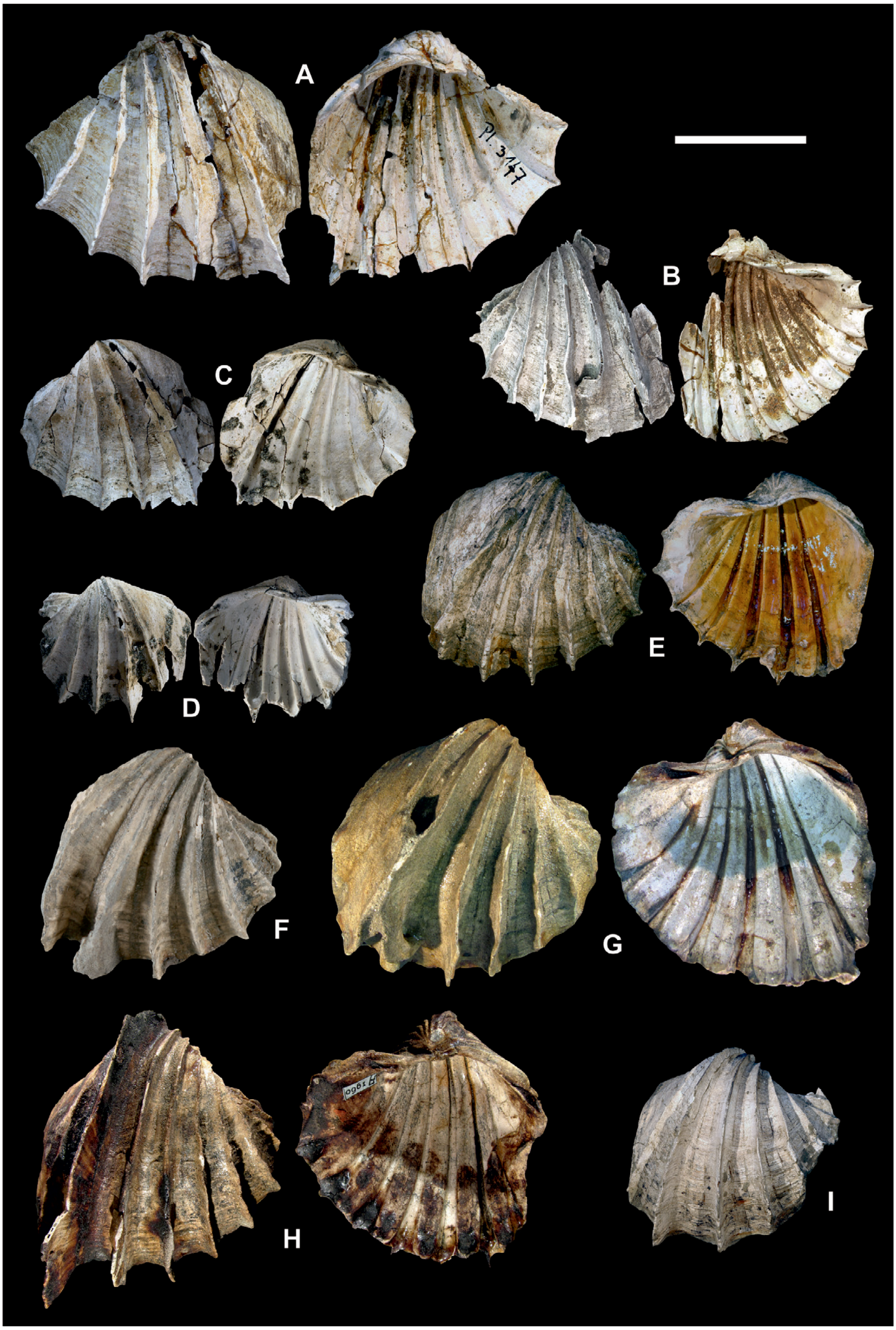

Figure 4. *Lymnocardium* (*Budmania*) *ferrugineum* (BRUSINA, 1874). A, B: Kurd (SZTFH Pl.3147 and 3150); C, D: PAET-29P (MTM); E, G, H: Zagreb–Okrugljak (NHMW 1889/0002/0006; 1889/0002/0003; 1889/0002/0004); F: Zagreb–Okrugljak (HPM 175.1); I: Tirol (NHMW 1900/0009/0050). Scale bar: 3 cm.

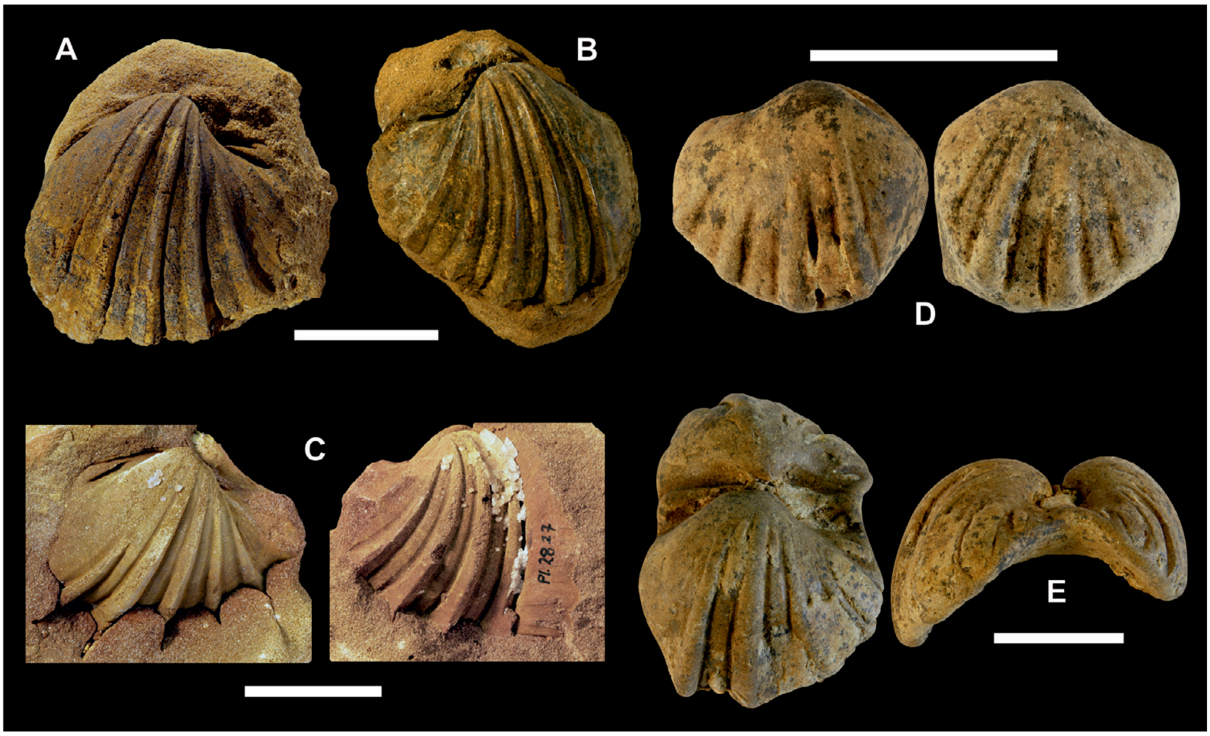

Figure 5. *Lymnocardium* (*Budmania*) *ferrugineum* (BRUSINA, 1874). Steinkerns from the Mecsek Mts. A, B: Nyugotszenterzsébet (MTM); C: Szentlőrinc (SZTFH Pl.2827); D, E: worn steinkerns ("pebbles"), Himesháza (MTM). Scale bars: 3 cm.

kept in Vienna (NHMW 1900/0009/0050; Fig. 4I), Zagreb (HPM 4810-2450.2., GORJANOVIĆ-KRAMBERGER 1902), and Bucharest (IGR-MNG, MARINESCU 1973).

Distribution: Confirmed occurrences (i.e. properly illustrated publications and collection materials studied here) include those from Zagreb–Remete (GORJANOVIĆ-KRAMBERGER, 1902; BASCH, 1990b); Kurd (ROTH, 1878; ANDRUSSOFF, 1903); Zagreb–Okrugljak (BRUSINA, 1884, 1897; BASCH, 1990a, 1990b; ANDRUSSOFF, 1903); Tirol/Királykegye/Königsgnad (HOERNES, 1901; GORJANOVIĆ-KRAMBERGER, 1902; MARINESCU, 1973); Jagnjedovac (ŠUKLJE, 1933); Kuštilj, (POPOVIĆ, 1968; RADIVOJEVIĆ et al., 2022); Nyugotszenterzsébet (BUJTOR, 1992); Bükkösd (SZTANÓ et al., 2015); Nagymányok (KOVÁCS et al., 2018); Himesháza (BUDAI et al., 2019); Szentlőrinc ("*L. cristagalli*" by STRAUSZ, 1953, SZTFH); Pécs–Cserebogár-dűlő (possibly the same location as "Németürög" in ROTH 1878; MTM); Cserdi (SZTFH, MTM); Hidas (SZTFH, MTM); Pusztafalu (now part of Lovászhetény, SZTFH); and drill cores from near Paks (PAET-27, 29P, 30, 34P; MTM) (Fig. 1).

Lymnocardium (*Budmania*) *cristagalli* (ROTH, 1878)

in part 1878 *Cardium cristagalli* ROTH nov. sp. – ROTH, p. 54, pl. 4, fig. 2 (excl. fig. 1.)

1884 *Adacna histiophora* BRUSINA – BRUSINA, p. 144, with text-fig.

1890 *Adacna cristagalli*, ROTH – LŐRENTHEY, p. 41, pl. 1, fig. 1.

1892 *Cardium* (*Adacna*) *Semseyi* nov. sp. – HALAVÁTS p. 26, pl. 1, figs. 1–5.

1893 *Limnocardium cristagalli* RÓTH – LŐRENTHEY, p. 121, pl. 5, fig. 4.

1897 *Budmania histiophora* BRUS. – BRUSINA, p. 34, pl. 18, figs. 4–6.

1901 *Lymnocardium Semseyi* HALAV. – HOERNES, pl. 1, figs. 1, 2; pl 2, fig. 3; pl. 3, fig. 1.

1901 *Lymnocardium cristagalli* ROTH – HOERNES, pl. 2, fig. 2; pl. 3, fig. 3.

1902 *Limnocardium* (*Budmania*) *histiophorum* BRUS. – GORJANOVIĆ-KRAMBERGER, p. 7, pl. 2, fig. 1.

1903 *Budmania histiophora* BRUSINA – ANDRUSSOFF, p. 74, pl. 7, figs. 2, 3, 6.

1903 *Budmania Semseyi* HALAVATS – ANDRUSSOFF, p. 78, pl. 7, figs. 1, 4, 5, 7–9.

Figure 6. *Lymnocardium* (*Budmania*) *cristagalli* (ROTH, 1878). Lectotype from Bükkösd (SZTFH Pl.2789); width of the shell: 74 mm. The handwritten inscription says "drawn specimen", with reference to Fig. 2 of ROTH (1878) (see Fig. 3 above).

1943 *Budmania cristagalli* ROTH – GILLET, p. 82, pl. 6, figs. 9, 9a.

? 1951 *Limnocardium* (*Budmania*) *histiophora* BRUS. – STEVANOVIĆ, p. 243, pl. 7, fig. 1.

1973 *Limnocardium* (*Budmania*) *semseyi* (HALAVÁTS) – MARINESCU, p. 22, pl. 6, figs. 3, 4; pl. 7, figs. 1–9.

1973 *Limnocardium* (*Budmania*) *aequicostata* sp. n. – MARINESCU, p. 24, pl. 8, fig. 4.

1973 *Limnocardium* (*Budmania*) *obliquicosta* sp. n. – MARINESCU, p 25, pl. 8, figs. 1, 3.

? 1990 *Limnocardium* (*Budmania*) cf. *histiophora* BRUS. – STEVANOVIĆ & ŠKERLJ, p. 171, pl. 1, figs. 12, 13.

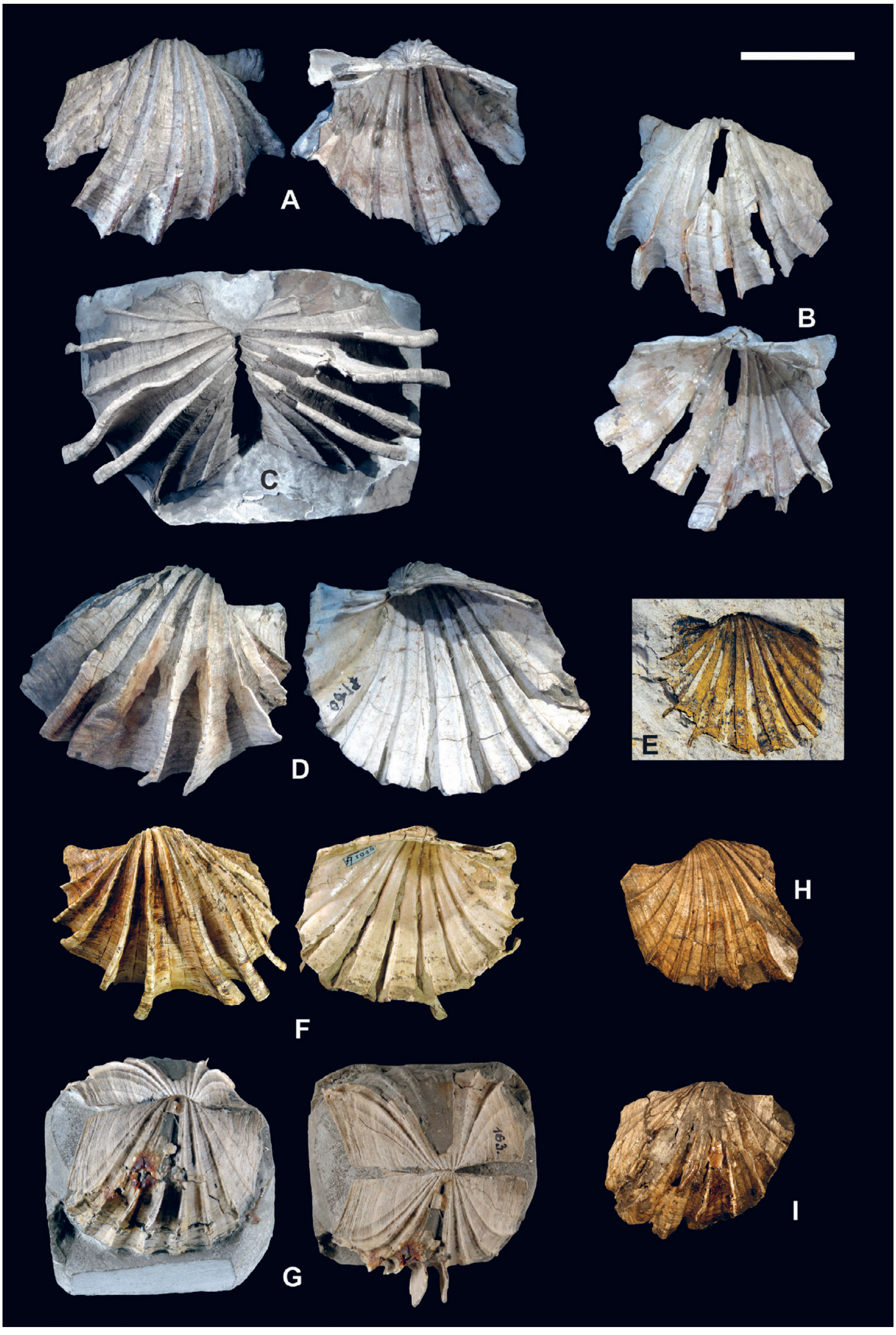

Figure 7. Specimens of *Lymnocardium* (*Budmania*) *cristagalli* (ROTH, 1878). A–D: Syntypes of *L. semseyi* (HALAVÁTS, 1892) from Tirol/Királykegye (SZTFH Pl.60); E: steinkern from Ibafa (MTM); F: Tirol/Königsgnad (NHMW 1900/0009/0057); G: lectotype of *L. histiophorum* (BRUSINA, 1884) from Zagreb–Okrugljak (HPM 4998-163); H, I: Zagreb–Okrugljak (NHMW 1888/0014/0029a, b). Scale bar: 3 cm.

1990 *Limnocardium* (*Budmania*) *histiophora* BRUSINA – STEVANOVIĆ, p. 481, pl. 6, fig. 4.

1990a *Limnocardium* (*Budmania*) *histiophora* BRUSINA – BASCH, p. 553, pl. 2, fig. 6.

1990b *Limnocardium* (*Budmania*) *histiophorum* (BRUSINA) – BASCH, p. 53, pl. 16, figs 6, 7; pl. 17, figs. 1–4.

2000 *Lymnocardium* (*Budmania*) *semseyi* (HALAVÁTS) – GEARY et al., p. 470, figs. 5/3, 4.

2004 *Budmania semseyi* (HALAVÁTS) – SAVAZZI & SÄLGEBACK, p. 228, figs. A–D, F, H–O.

2004 *Budmania* cf. *aequicostata* (MARINESCU) – SAVAZZI & SÄLGEBACK, p. 228, fig. G.

2007 *Lymnocardium* (*Budmania*) *semseyi* – WESSELINGH, p. 294, fig. 18.

2015 *Lymnocardium cristagalli* – SZTANÓ et al., p. 340, fig. 9b.

2019 *Lymnocardium cristagalli* (ROTH) – BUDAI et al., p. 2011, figs. 8k, 8l.

Type locality: Bükkösd, Mecsek Mts.

Type material: Lectotype, designated herein (Pl.2789; Fig. 6) and paralectotypes (Pl.3144, 3153 from Bakócza; Pl.2790 from Bükkösd) in SZTFH.

Remarks: Although MILAN et al. (1974) indicated the originally figured specimen of *L. histiophorum* as a holotype, it was a syntype because BRUSINA (1884) based his description on two specimens. The better preserved syntype (HPM 4998-163; Fig. 7G) is designated herein a lectotype, because the other synytpe, an imprint with shell fragments (BRUSINA, 1884), could not be identified and confirmed in HPM. Further specimens from Okrugljak are available in Zagreb (HPM 160-167, 169-174, altogether 30 specimens) and in Vienna (NHMW 1888/0014/0029; Fig. 7H,I).

The syntypes of *L. semseyi* from Tirol are reposited in SZTFH (Pl.60; Fig. 7A-D). Further specimens from Tirol are available in HPM, NHMW (Fig. 7), SZTFH, MTM, IGR-MNG, UG, Naturalis – Leiden (WESSELINGH, 2007), Natural History Museum – London (SAVAZZI & SÄLGEBACK, 2004), Smithsonian Natural History Museum – Washington, etc.

According to MARINESCU (1973), the holotype of *L. aequicostata* is in his own collection, whereas two paratypes are available in HPM (2465.1 and 2465.2), labelled as *L. rothi*.

The holotype of *L. obliquicosta* is reposited in IGR-MNG (3347), whereas paratypes were selected from the collection of NHMW (without numbers) and from the collection of the author of the species (also without numbers), plus a specimen in IGR-MNG (3391) (MARINESCU, 1973).

Distribution: Confirmed occurrences (i.e. properly illustrated publications and collection materials studied here) include those from Bükkösd (ROTH, 1878); Bakóca (SZTFH); Zagreb–Okrugljak (BRUSINA, 1884, 1897; ANDRUSSOFF, 1903; GORJANOVIĆ-KRAMBERGER, 1902; BASCH, 1990a, 1990b); Nagymányok (LŐRENTHEY, 1890, 1893); Királykegye/Königsgnad/Tirol (HALAVÁTS, 1892; HOERNES, 1901; ANDRUSSOFF, 1903; GILLET, 1943; MARINESCU, 1973; GEARY, et al. 2000; SAVAZZI & SÄLGEBACK, 2004; WESSELINGH, 2007); Novaci (STEVANOVIĆ, 1990); Ibafa (SZTANÓ et al., 2015); Himesháza (BUDAI et al., 2019) and, possibly, Blatno (STEVANOVIĆ & ŠKERLJ, 1990) (Fig. 1).

5. DISCUSSION

5.1. Environment and adaptation

Although specimens of *Lymnocardium* (*B.*) *ferrugineum* are known from the classic sites of Zagreb–Okrugljak and Tirol where *L.* (*B.*) *cristagalli* is common, the two species usually occur in different sedimentary rocks and with different accompanying species. *Lymnocardium* (*B.*) *ferrugineum* is typically found in fine - very fine sands, which are interpreted to have been deposited in shallow-water, littoral and deltaic environments (SZTANÓ et al. 2015; KOVÁCS et al. 2018; BUDAI et al. 2019; RADIVOJEVIĆ et al. 2022). The most common associated species, such as *Congeria triangularis* PARTSCH, *Dreissenomya schroeckingeri* (FUCHS), *Dreissena serbica* BRUSINA, *Prosodacnomya dainellii* (BRUSINA), *Lymnocardium szaboi* LŐRENTHEY, *L. pelzelni* (BRUSINA), *L. ochetophorum* (BRUSINA), *Pseudocatillus simplex* (FUCHS), *Viviparus* sp. and others are considered shallow-water dwellers (e.g., STEVANOVIĆ, 1951; POPOVIĆ, 1968; MÜLLER & SZÓNOKY, 1990; MÜLLER & MAGYAR, 1992; BUJTOR, 1992; SZTANÓ et al., 2015; KOVÁCS et al., 2018; BUDAI et al., 2019).

In contrast, *Lymnocardium* (*B.*) *cristagalli* commonly occurs in clays and silts, deposited below the wave-base, in the sublittoral zone of Lake Pannon (SZTANÓ et al., 2015; BUDAI et al., 2019). The associated species include, for example, *Congeria rhomboidea* HÖRNES, *C. zagrabiensis* BRUSINA, *Lymnocardium majeri* (HÖRNES) and *Valenciennius reussi* (NEUMAYR) (BRUSINA, 1884; HALAVÁTS, 1892; POPOVIĆ, 1968; BUDAI, 2019), i.e. forms that were adapted to the sublittoral depth of Lake Pannon (KORPÁS-HÓDI, 1983; LENNERT et al., 1999; CZICZER et al., 2009).

Lymnocardium (*B.*) *ferrugineum* and *L.* (*B.*) *cristagalli* thus inhabited different environments. The specimens of *L.* (*B.*) *ferrugineum* that have been recovered from the offshore deposits of Zagreb–Okrugljak and Tirol may have been transported from the shallow to the deeper environment, although no signs of mechanical wear were observed in their shells. *Lymnocardium* (*B.*) *cristagalli*, however, does not occur in shallow-water sediments. This relatively strict habitat partitioning between the two coeval species strongly challenges the interpretation of the high, hollow keels as an adaptation to fluid, muddy substratum (MARINESCU, 1973; SAVAZZI & SÄLGEBACK, 2004).

5.2. Geographical distribution, stratigraphy and age

The subgenus *Budmania* is geographically restricted to the southern part of the Pannonian Basin (Fig. 1); when it first appeared, the northern part of the basin had already been infilled by sediments (MAGYAR, 2021).

Lymnocardium (*B.*) *ferrugineum* occurs together with *Prosodacnomya dainellii* (BRUSINA) in several localities (Kurd, Nyugotszenterzsébet, Cserdi and Paks (PAET drill cores), according to ROTH, 1878, BUJTOR, 1992, and our own observations), therefore its stratigraphic range seems to be restricted to the *P. dainellii* Zone (MÜLLER & MAGYAR, 1992; MAGYAR, 2021). The only report of its co-occurrence with the younger *Prosodacnomya vutskitsi* (BRUSINA) came from Jagnjedovac (ŠUKLJE 1933). In that paper, however, *Prosodacnomya vutskitsi* and *P. dainellii* are treated as a single species, thus leaving the biostratigraphic assignement (*P. dainellii* Zone or *P. vutskitsi* Zone) uncertain.

In the magnetostratigraphically dated and seismically correlated PAET drill cores at Paks, the lowermost occurrence of

Lymnocardium (*B.*) *ferrugineum* is in PAET-29P, 207.7 m, which corresponds to an age of 7.5 Ma. The uppermost occurrence in the Paks cores is in PAET-34P, 177.6 m, having an age of 7.15 Ma (KELDER et al., 2018; MAGYAR et al., 2019).

Lymnocardium (*B.*) *cristagalli*, a sublittoral dweller, occurs together with *Congeria rhomboidea* Hörnes and is thus restricted to the *Congeria rhomboidea* Zone (8–?4.5 Ma; MAGYAR & GEARY, 2012; MANDIC et al., 2015). *Lymnocardium* (*B.*) *cristagalli* was not found in the Paks PAET cores, and its occurence was not magnetostratigraphically dated in other locations either. The first appearance and last occurrence of this species is thus difficult to assess. In some transgressive successions, however, *L.* (*B.*) *cristagalli* appears directly above the basal shallow-water deposits with *Prosodacnomya dainellii* and *Lymnocardium ferrugineum* (Bükkösd, Nagymányok; cf. ROTH, 1878; LŐRENTHEY, 1890, 1893; SZTANÓ et al., 2015; KOVÁCS et al., 2018), whereas in others, its occurrence is directly followed by regressive deltaic sediments with *L. ferrugineum* (Vršac Mts., Himesháza; HALAVÁTS, 1892; POPOVIĆ, 1968; BUDAI et al., 2019). In both cases, its first appearance in the succession is very close to that of *L.* (*B.*) *ferrugineum*, suggesting a largely overlapping stratigraphic range of the two species.

The geographic distribution of *Budmania* thus reflects the position of the shelf of Lake Pannon between ca. 7.5 and 7.15 Ma (Fig. 1).

5.3. Evolutionary relationships

BRUSINA (1897) introduced the new subgenus *Budmania* for *Lymnocardium* (*B.*) *histiophorum* (= *L.* (*B.*) *cristagalli*) and *Lymnocardium* (*B.*) *meisi* (=*L.* (*B.*) *ferrugineum*). Although not stated explicitly, the shared feature of the two species that justified their distinction as a new subgenus was the spectacularly high, hollow keel. Because the two species lived in different environments, the evolution of the keel is therefore difficult to interpret as an adaptive trait that evolved independently in unrelated lineages. The characteristic and complex keel with its multiple cavities is probably a shared derived character (synapomorphy) between the two species and indicates their monophyletic origin.

The currently available data on the stratigraphic distribution of the two species do not provide evidence as to which of them appeared earlier. *Lymnocardium* (*Budmania*) *ferrugineum*, however, shows a striking morphological similarity to *Lymnocardium* (*Lymnocardium*) *inflatum* (GORJANOVIĆ-KRAMBERGER, 1899) in size, shape, number of ribs, curved hinge and smooth posterior field. The only obvious difference is the lack of high keels in *L.* (*L.*) *inflatum*. Although POLJAK & ŠUKLJE (1934) reported the co-occurrence of *L.* (*L.*) *inflatum* and *L.* (*B.*) *ferrugineum* from Glogovnica, in our view all the Glogovnica specimens belong to *L.* (*L.*) *inflatum*, thus no sympatric occurrence of the two species is known.

Lymnocardium (*L.*) *inflatum* is stratigraphically restricted to the shallow-water *Lymnocardium* (*L.*) *decorum* Zone (Orešac: STEVANOVIĆ, 1951, 1990) and the younger *Prosodacnomya carbonifera* Zone (Kötcse: MÜLLER & MAGYAR, 1992). The magnetostratigraphically dated and seismically correlated age of its occurrence in the PAET-26 drill core is 7.8-7.9 Ma (MAGYAR et al., 2019).

Based on the above data, we hypothesize the following phylogeny for the subgenus *Budmania*. *Lymnocardium* (*L.*) *inflatum* evolved anagenetically into *L.* (*B.*) *ferrugineum* sometime between 7.8 and 7.5 Ma in the littoral zone of Lake Pannon. Soon after, *L.* (*B.*) *cristagalli* appeared in the deeper, offshore environment, probably through allopatric speciation from *L.* (*B.*) *ferrugineum*. Both *Budmania* species were likely to have become extinct before 7.15 Ma, because their occurrence in younger layers has not yet been confirmed.

6. CONCLUSIONS

Two out of the eight species names, introduced for various specimens of the subgenus *Budmania*, such as *Cardium ferrugineum*, *Cardium cristagalli*, *Adacna meisi*, *Limnocardium subferrugineum*, *Adacna histiophora*, *Cardium* (*Adacna*) *semseyi*, *Limnocardium* (*Budmania*) *aequicostata and Limnocardium* (*Budmania*) *obliquicosta*, are accepted as valid species names: *Lymnocardium* (*Budmania*) *ferrugineum* (BRUSINA, 1874) and *L.* (*B.*) *cristagalli* (ROTH, 1878). Both species seem to have been restricted in time to between 7.5–7.15 Ma. *L.* (*B.*) *ferrugineum* probably evolved from *L.* (*L.*) *inflatum* and gave rise to *L.* (*B.*) *cristagalli*.

L. ferrugineum was a shallow-water dweller in Lake Pannon, whereas *L. cristagalli* populated offshore, sublittoral environments. The widely held notion that the spectacularly high, keeled ribs of these cockles reflect adaptation to soft muddy substrate thus cannot be maintained.

ACKNOWLEDGEMENT

Our work on the museum collections was supported by Klára PALOTÁS, László MAKÁDI, Bálint SZAPPANOS (SZTFH); Oleg MANDIC, Mathias HARZHAUSER (NHMW); Katarina KRIZMANIĆ and Marija BOŠNJAK (HPM). Martin GROSS and Bernhard HUBMANN kindly provided information on the UG collection. For taxonomic and ICZN issues, we were advised by Philippe BOUCHET (Muséum National d'Histoire Naturelle, Paris) and Barna PÁLL-GERGELY (ELKH Agrártudományi Kutatóközpont, Budapest). Reviewers Simon SCHNEIDER and Oleg MANDIC are thanked for their large effort to improve the original manuscript. This research was funded by the National Research, Development and Innovation Office (NKFIH) project 143787. This is MTA-MTM-ELTE Paleo contribution No. 368.

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