Palaeobiology, palaeoecology and stratigraphic significance of the Late Miocene cockle *Lymnocardium sopronense* from Lake Pannon

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Abstract: Stratigraphic subdivision of the Upper Miocene deposits in the Pannonian Basin has been traditionally based on the endemic mollusc species of Lake Pannon. The cockle species *Lymnocardium soproniense* Vitális, apparently evolving through a sympatric speciation event in the sublittoral zone of Lake Pannon about 10.2–10.3 Ma, attained wide geographical distribution in the Pannonian basin and thus may serve as a good stratigraphic marker. *Lymnocardium soproniense* was one of the few large-sized cockles in Lake Pannon, most closely related to its ancestor, *L. schedelianum* (Fuchs), and to another descendant of the latter, *L. variocostatum* Vitális. According to the $\delta^{18}O$ stable isotope record of its shells, the large size of *L. soproniense* was coupled with an extended life time of more than 10 years, probably reflecting a stable lake environment with increased resource availability and decreased predation. The species lived in quiet offshore conditions, below the storm wave base, where clay was deposited from suspension and the influence of currents was negligible. The base of the *Lymnocardium soproniense* Zone in the sublittoral deposits of Lake Pannon is defined by the first occurrence of the species, whereas the top of the zone is marked with the base of the overlying *Congeria praerhomboidea* Zone, defined by the FAD of *C. praerhomboidea*.

Key words: Late Miocene, Pannonian Basin, Lake Pannon, molluscs, endemism, palaeoecology, stable isotopes.

Introduction

Lymnocardium soproniense Vitális, 1934 is one of the ca. 200 species of non-marine cockles that were described from the deposits of Lake Pannon (Müller et al. 1999; Geary et al. 2000). This lake occupied the Pannonian basin in the Late Miocene and Early Pliocene as a relict of the Paratethys Sea (Harzhauser & Piller 2007). The stratigraphic subdivision of its thick sedimentary pile has been traditionally based on the prolific endemic mollusc fauna of the lake (for a summary, see Magyar & Geary 2012). Of the many cockle species of Lake Pannon, some possess a narrow stratigraphic span coupled with a wide geographical distribution; these species are considered to be good stratigraphic markers.

Lymnocardium soproniense is one such species, and it is used to designate the sublittoral *L. soproniense* Zone (Magyar et al. 1999, 2007; Magyar & Geary 2012). This species, however, is usually known from poorly preserved and/or fragmentary specimens, it was often confused with other large Lake Pannon cockles, and remained poorly documented in the palaeontological literature. In this paper we discuss its taxonomic position, geographical distribution, palaeoecology, phylogenetic relationships, and stratigraphic significance. The palaeoecological and palaeobiological interpretations are based on sedimentological facies analysis and $\delta^{18}O$ stable isotope profiles of shells.

Materials and methods

For this study we used the fossil mollusc collections of the Geological and Geophysical Institute of Hungary (MFGI, Budapest), the Hungarian Natural History Museum (TTM, Budapest), the Bakony Natural History Museum (TTM-BTM, Zirc), and the Naturhistorisches Museum Wien (NHMW, Vienna). Field work was conducted in the brickyard claypit of Mályi (northern Hungary, Fig. 1), the only outcrop known to us where *Lymncoardium soproniense* can be studied and collected from the embedding sediments today. We measured the outcrop and interpreted the sedimentological features in order to assess the palaeoenvironment in which *L. soproniense* lived.

Stable isotope data from *Lymnocardium soproniense* and its relatives were gathered as part of a larger study on cardiid bivalves from Lake Pannon (Johnson 2016). Shells were sampled by using a 0.5 mm bit to drill a series of grooves parallel to growth lines and spaced ~1 mm apart along the entire height of the shell. Samples were analysed at the University of Arizona's Environmental Isotope Laboratory using a KIEL-III device coupled to a Finnegan MAT 252 gas-ratio mass spectrometer at a precision of ±0.1 ‰ for $\delta^{18}O$. The data pertaining to *L. soproniense* and its closest relatives (*L. schedelianum, L. variocostatum*) are summarized and discussed below.

Systematic palaeontology

Class **BIVALVIA** Linné, 1758
Family **CARDIIDAE** Lamarck, 1809
Subfamily **LYMNOCARDIINAE** Stoliczka, 1870–1871
Genus ***Lymnocardium*** Stoliczka, 1870–1871

Type species: *Cardium haueri* M. Hörnes, 1862 from the Upper Miocene of Árpád (Pécs, Hungary)

Lymnocardium soproniense Vitális, 1934

1915. *Limnocardium Penslii* Fuchs — Papp S., p. 254, pl. 3, fig. 6. [misidentification]
*1934a. *Limnocardium soproniense* n. sp. — Vitális, p. 705, pl. 7, figs. 1–4.
1934b. *Limnocardium soproniense* n. sp. — Vitális, p. 77, pl. 1, figs. 1–4. [redescription]
1971. *Limnocardium soproniense* Vit. — Bartha, pl. 29, figs. 1,4.
1971. *Limnocardium (Pannonicardium) mihaili* sp. n. — Mihaila and Marinescu, p. 43, fig. 1, pl. 1, figs. 1–3.
2007. *Lymnocardium soproniense* — Magyar et al., p. 280, fig. 5.

Type specimen. Lectotype. MFGI, Pl. 97 (Fig. 2a, b), left valve.

Lymnocardium soproniense was first described by I. Vitális (1934a). Although this large bivalve species was very common in the brickyard claypits of Sopron/Ödenburg (Fig. 1), full and intact specimens were difficult to collect, thus Vitális chose to photograph a museum specimen; the depicted individual had been collected from the claypit of the Lenk brickyard (MFGI, Pl. 97., Fig. 2a, b). Boda (1964) indicated this specimen as a "holotype", but according to ICZN (1999, Art. 74.1 and 74.5), it represents the lectotype of the species.

The pictures published by Vitális (1934a, b), however, were not the first representation of this species in the literature. Papp (1915) published the photograph of a *L. soproniense* specimen erroneously identified as "*Limnocardium penslii* Fuchs" from Szilágynagyfalu (today Nuşfalau, Romania; Fig. 1), from sandy marl exposed in a trench cut into the hillside SE of the village.

In 1971, Mihaila and Marinescu described a Pannonian mollusc fauna from Sabolciu/Mezőszabolcs, valley of Crisul Repede/Sebes-Körös (Fig. 1), containing a new cockle species "*Limnocardium (Pannonicardium) mihaili* sp. n.". The holotype and paratype specimens of the new species, however, were collected from the village of Felcheriu/Felkér by A. Mihai (after whom Mihaila and Marinescu named the new species). The authors regarded the Sabolciu specimens as syntypes. Based on the description, drawing and photographs of *L. mihaili*, the Felcheriu specimens fully correspond to *L. soproniense*.

Subsequent picture representations of *L. soproniense* include a left valve (Bartha 1971) and a right valve of an articulated specimen (Magyar et al. 2007, p. 281), both from Sopron.

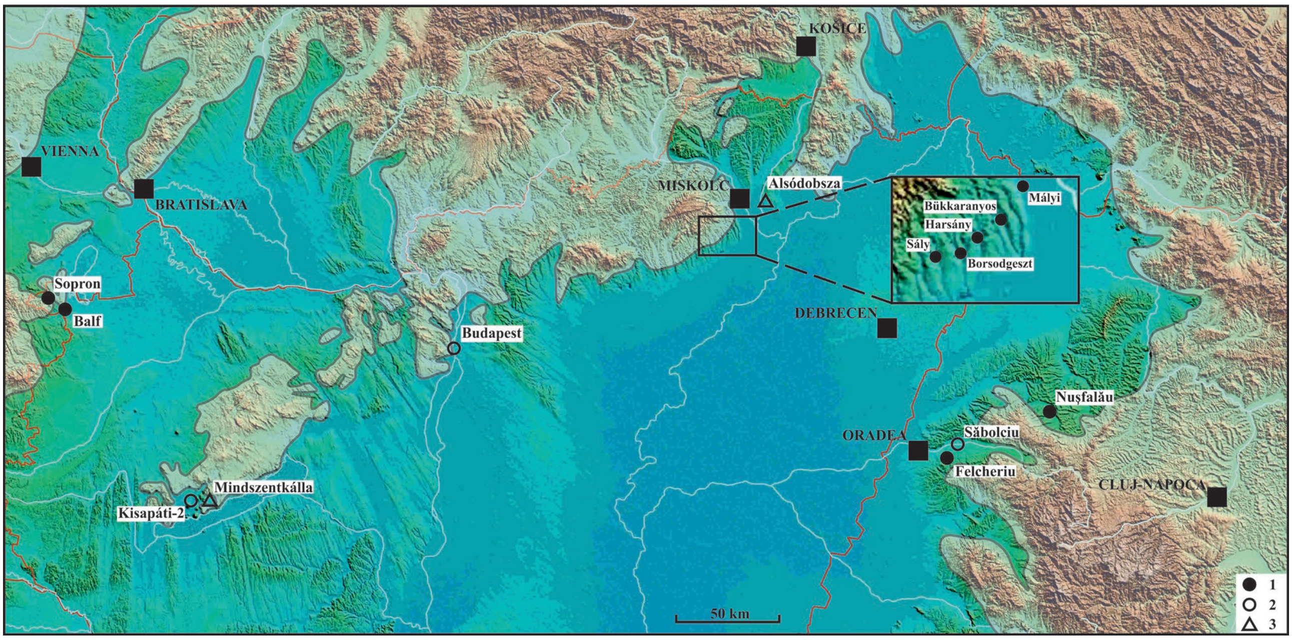

Fig. 1. Localities of *Lymnocardium soproniense* in the northern Pannonian Basin. **1** — confirmed occurrence; **2** — uncertain occurrence; **3** — no occurrence (mistaken identifications in the literature). Inset map shows a zoomed detail of the study area south of Miskolc.

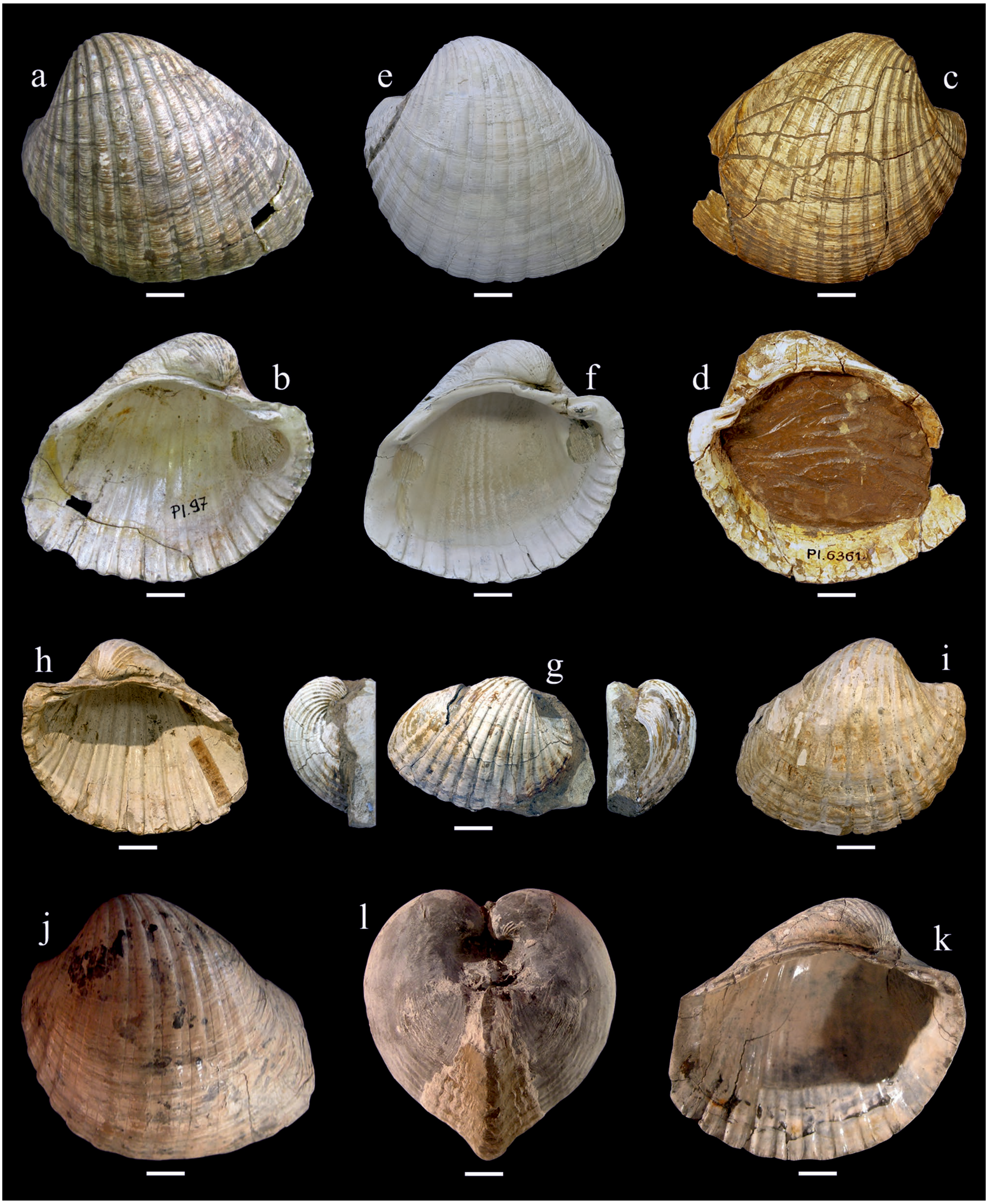

Fig. 2. Specimens of *Lymnocardium soproniense* from Sopron (a–i) and Mályi (j–l). **a–d** — a left valve (a,b; MFGI Pl. 97, lectotype of the species) and a right valve (c,d; MFGI Pl. 6361) from Sopron, Lenk brickyard, donated to the Hungarian Royal Geological Institute by L. Károlyi in 1914; **e, f** — a left valve depicted (and probably collected) by Bartha (1971) from Sopron, Balfi út brickyard (MFGI Pl. 2016.1.1); **g** — a right valve of a juvenile specimen from Sopron (TTM-BTM 2014-123-1); **h, i** — a right valve from Sopron (TTM M57/815); **j, k** — a left valve from Mályi brickyard (collection of I. Cziczer); **l** — a partial shell and "steinkern" of an articulated specimen from Mályi (collection of I. Cziczer). Scale bars 1 cm.

Type locality and type stratum. Sopron/Ödenburg, Hungary, Szák Formation, Upper Miocene, Pannonian Stage. The brickyard claypits of Sopron, mentioned by Vitális (1934 a, b, 1951), have been closed and re-cultivated by today. The only outcrop which was described in some detail in the geological literature is the Balfi út claypit. Stratigraphic columns of the outcrop were given by Bartha (1971), Korpás-Hódi (1994), and most recently by Barna et al. (2010). According to the latter, the lower 4.5 m of the more than 10 m high outcrop consisted of greyish-blue bioturbated clay with variable silt content and dispersed molluscan shells. Silt content gradually increased from 4.5 to 9 m, and this interval consisted of rhythmic depositions of clay, silt, and very fine sand. Parallel lamination, cross-lamination, small-scale graded bedding and plant remains were common in the fine sand and silt. The fine-grained sequence was capped by coarse-grained silt, sand, and fine-grained gravel layers that displayed cross-bedding, cross-lamination, and scour-and-fill structures and erosional surfaces. The entire sequence was interpreted as reflecting the transition from a sublittoral lacustrine environment to a distributary channel and mouth bar (Barna et al. 2010). According to Bartha (1971, p. 100), *Lymnocardium soproniense* occurred in the lower, clayey part of the section (Szák Formation).

Comparison. *Lymnocardium soproniense* is morphologically very close to *L. schedelianum* (Fuchs), and also to *L. variocostatum* Vitális. When they are preserved as internal moulds (steinkerns), it is very difficult or sometimes impossible to tell the three species apart. The diagnostic difference is in their rib architecture (Fig. 3). *L. schedelianum* has prominent radial ribs (Fig. 3a). In *L. soproniense*, the ribs are not prominent but quite flat, and the intercostal spaces are filled with shell material so that they are even with the ribs, giving the entire shell a smooth appearance (Fig. 3b). In *L. variocostatum*, the ribs in the central and rear areas of the valve are wide and flat, and the intercostal spaces are reduced to a shallow groove (Fig. 3c).

Remarks. Prior to the description of *Lymnocardium soproniense* as a new species by Vitális (1934a), its specimens were identified as, or were considered to have been related to, various other large Lake Pannon cockles. For instance, the specimens collected by L. Roth in Balf were first labelled as "*Cardium schmidti* (Hörnes)". Later the curator of the museum of the Hungarian Royal Geological Institute, Gy. Halaváts, corrected the labels of these specimens to "*L. dumicici* Gorjanovic-Kramberger" (see in Vitális 1934 a, p. 707). Papp (1915) described his *L. soproniense* specimen from Szilágynagyfalu as *L. penslii* (Fuchs). Even after Vitális described *L. soproniense* as a new species, and discussed all the morphological traits that distinguish *L. soproniense* from *L. schmidti*, *L. croaticum* (Brusina), and *L. dumicici*, Strausz (1942) expressed his opinion that *L. soproniense* is identical to *L. variocostatum* Vitális, which is, according to him, a subspecies of *L. penslii*. Mihaila and Marinescu (1971) assigned *L. mihailii* (= *L. soproniense*) into *Pannonicardium,* a subgenus erected by Stevanović (1951) for *L. dumicici, L. schmidti*, and *L. penslii*. On the other hand, A. Papp (1953) thought that *L. soproniense* is very closely related to *L. schedelianum*, therefore he regarded Sopron/Ödenburg as a *L. schedelianum*-bearing locality (Papp 1953, p.198).

Fig. 3. Rib structure of *Lymnocardium schedelianum* (**A**; Wien-Hennersdorf, TTM), *Lymnocardium soproniense* (**B**; Sopron, MFGI), and *L. variocostatum* (**C**; Bicske, TTM-BTM). Scale bars represent 5 mm.

Distribution. The localities where *Lymnocardium soproniense* has been found so far are clustered in several areas in the northern part of the Pannonian Basin (Fig. 1). The most abundant material is from Sopron and its vicinity. The second-richest material was collected from the SE margin of the Bükk Mts., northern Hungary (in the vicinity of Miskolc). A few specimens have been documented from three localities in the northwestern foreland of the Apuseni Mts. in Romania (vicinity of Oradea/Nagyvárad). Finally, museum materials indicate occurrences of the species in Budapest and in the Balaton region, but these are considered uncertain and require future confirmation (see Appendix).

Lymnocardium soproniense in the Mályi outcrop

The claypit of Mályi brickyard

The only outcrop known to us where *Lymnocardium soproniense*-bearing sediments are exposed today is the brickyard claypit of Mályi in the vicinity of Miskolc, northern Hungary. The outcrop, located in the northern outskirts of the village, exposes a 20–25 m thick homogeneous, bluish-grey, fossiliferous clay/argillaceous marl, overlain rather sharply by a coarsening upward series of white, fine sand, gravelly sand, and conglomerate (Fig. 4). The clay is fully bioturbated; the only indication of bedding is represented by accumulations of randomly oriented mollusk shells, first of all disarticulated valves of small (juvenile) individuals of *Congeria czjzeki* Hörnes. Many of these beds are poorly cemented with iron oxide-hydroxides, and limonitic concretions also occur with shells in their cores. These beds do not contain sand, gravel or any other coarse material that would indicate vigorous currents, therefore the varying abundance of shells is probably related to the original living conditions rather than post-mortem transport and accumulation. Scattered shells also occur in the clay; most of the large *L. soproniense* and *Congeria ungulacaprae* Münster specimens were found in such position. The abundance of molluscs apparently decreases upwards. The uppermost 2 m of the clayey interval is grey-yellow variegated clay, overlain by 2 m yellow siltstone. This change in colour is related to ground waters percolating in the overlying sand.

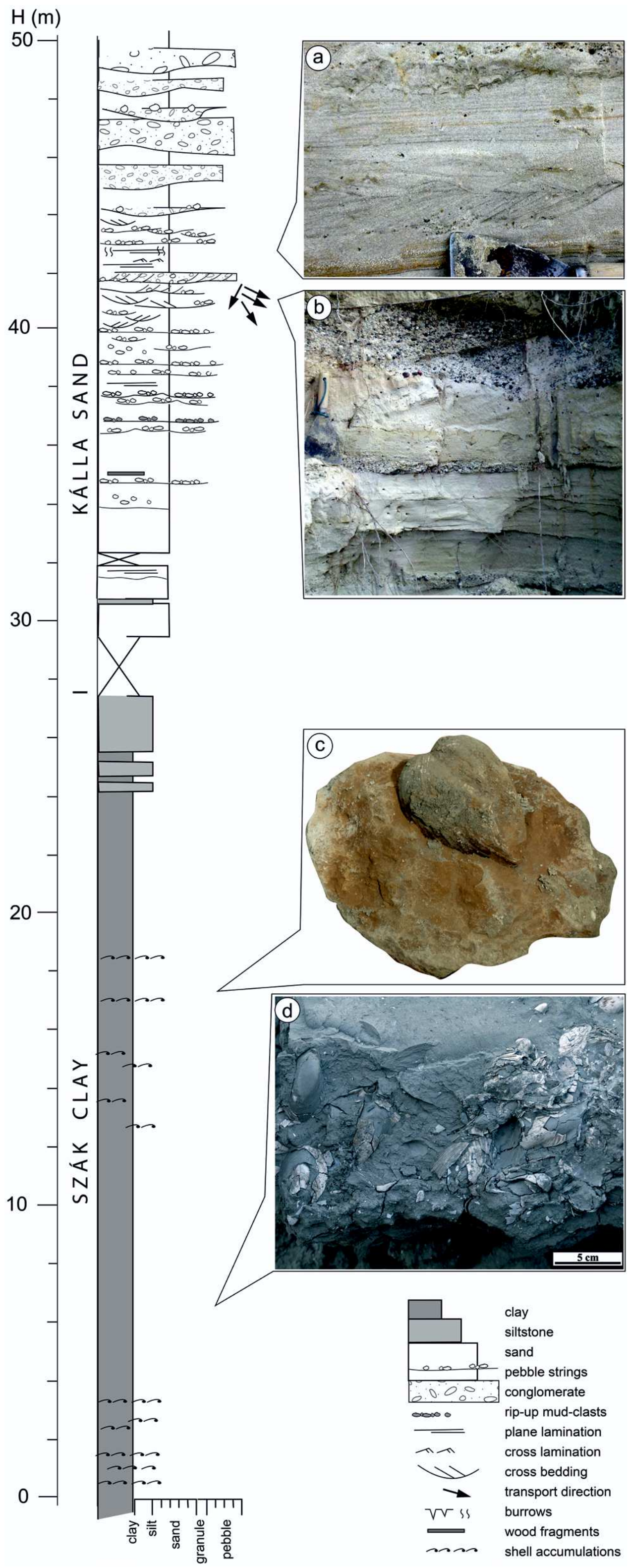

Fig. 4. Stratigraphic column of the Mályi outcrop. **a** — cross- and plane lamination with small vertical burrows in fine-grained sand; **b** — trough cross-bedding in sand, pebbly sand points to southward transport; **c** — articulated valves of *Lymnocardium soproniense*, embedded into clay in life position; **d** — shell-bed with *Congeria czjzeki* in the blue clay. Spade is 10×22 cm for scale (a, b).

The transition of silt to sand was covered by debris in the outcrop, but morphology of the terraces suggests a sharp transition. The white, fine-grained sand is moderately to well-sorted, attaining a total thickness of 20 m. Much of the sand lacks structure, mostly due to bioturbation. Plane lamination, cross-lamination, decimetre-scale cross-bedding, shallow and wide erosional scours rarely occur. The scours and cross-bedding are paved by granule to small-grained pebbles. The abundance and thickness of these cm-scale pebbly layers increase upwards. Some small, v-shaped burrows, large pebble-filled vertical burrows, carbonaceous material (wood fragments) and granule-size rip-up mud clasts also can be found. The uppermost metres of the outcrop consists of pebbly sand and sandy gravel, made up of well-rounded "pearl" gravel.

The clay was deposited from suspension settling in quiet offshore conditions (i.e. below storm wave-base). The overlying sands and gravels are products of shallow, nearshore waters above wave-base. Most of the structures indicate shallow currents, but the swash-zone of breaking waves is also clearly demonstrated. We cannot distinguish deposits of a prograding wave-dominated coast from those of a small, coarse-grained deltaic lobe. No large-scale architecture (i.e. foresets) support the latter. The sharp transition reveals a pronounced shift of facies from offshore to nearshore (i.e. a regression). It points to a drastically increased rate of sediment input, which can be the result of either development of a delta entry nearby or a lake-level fall (or their combined effect). The clay is assigned to the Szák Formation (see Cziczer et al. 2009 and references therein), whereas the gravelly white sand belongs to the Kálla Formation (see Csillag et al. 2010 and references therein).

Palaeoecological interpretation

Environment. In the Mályi outcrop, the shells of *Lymnocardium soproniense* are most common in the lower layers that were deposited in a distal offshore environment. The unstratified, bioturbated clay was deposited from suspension in the sublittoral zone of Lake Pannon, which means below the storm wave-base. Shells are usually found with articulated valves, either in closed or open position (Fig. 4c). There are no indications of storm- or gravity-induced currents, a fact that may point to a flat depositional surface far away from sediment input. Water depth is difficult to reconstruct, but studies of the Szák Formation elsewhere and comparisons with the present-day Caspian Sea as an analogue of Lake Pannon suggest that the sublittoral argillaceous marl was deposited at 20–30 to ?80 m water depth (Korpás-Hódi 1983; Cziczer et al. 2009). *L. soproniense* becomes less common and finally disappears from the record as sediment input increased and water depth decreased up to and even above the wave-base.

Accompanying species. The most common accompanying mollusc species in Mályi include *Congeria czjzeki*, *C. ungula-caprae*, *Lymnocardium brunnense* Andrusov, *Caladacna steindachneri* (Brusina), and *Pisidium krambergeri* (Brusina)

(Fig. 5). The first three of these are also common at other localities in the vicinity of Miskolc and Sopron. In particular, *C. czjzeki* is known to be a characteristic form of sublittoral deposits. In the Sopron area, Balfi út outcrop, dominance of candoniid ostracods over cypridiids in the lower layers of the section also indicates a deeper water, offshore environment (Barna et al. 2010). All these patterns confirm that *L. sopronìense* was a sublittoral dweller.

Stable isotope records of *Lymnocardium soproniense* and closely related species

Ontogenetic ages and growth rates

Recent stable isotope work on various *Lymnocardium* species including *L. soproniense* offers additional palaeoenvironmental data as well as information about the longevity and growth rate of *L. soproniense* and its relatives (Johnson 2016). Stable oxygen isotope profiles in mollusc shells typically consist of quasi-sinusoidal patterns that have been interpreted as annual cycles (e.g., Dettman & Lohmann 1993; Dettman et al. 1999; Andreasson & Schmitz 2000; Goodwin et al. 2001; Schmitz & Andreasson 2001; Ivany et al. 2004; Ivany & Runnegar 2010). Winters are recognized from high $\delta^{18}O$ ratios, whereas summers produce low $\delta^{18}O$ ratios.

The profile of a large (~90 mm in height) *Lymnocardium soproniense* from Sopron (Fig. 6) contains ~10 winter-summer cycles, indicating at least 10 years of growth (Johnson 2016). Shell growth may slow or stop seasonally if temperatures exceed the tolerances of the species, or during a reproductive event when the animal reallocates resources (Dettman et al. 1999). The seasonal signal may also be obscured by low seasonality of the ambient temperature — potentially buffered by depth — and/or seasonality in the $\delta^{18}O$ values of lake water, which may destructively interfere with temperature effects. Later in ontogeny, the growth rate slows, which makes it more difficult to detect annual cycles using isotopes due to

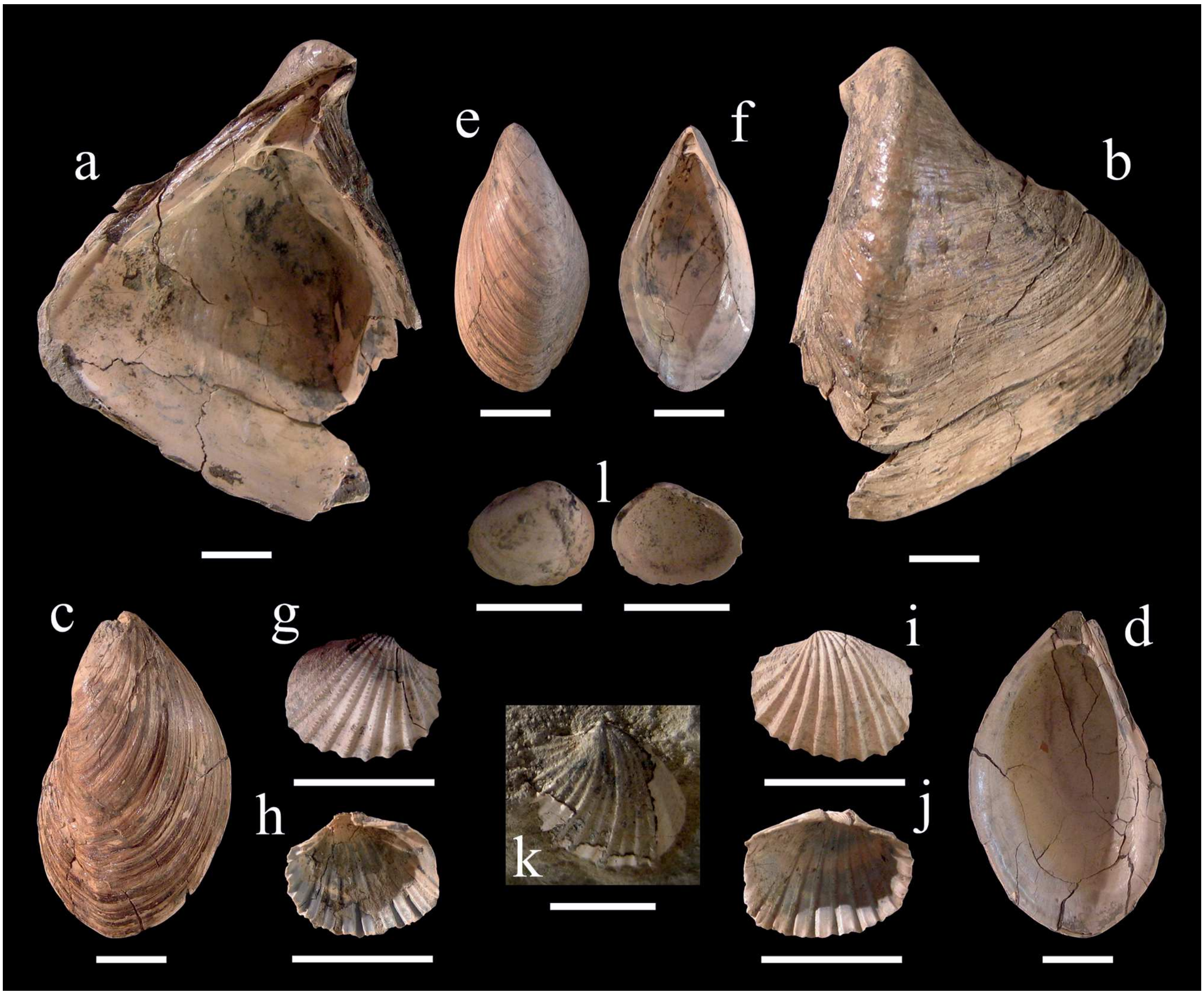

Fig. 5. Mollusc species accompanying *Lymnocardium soproniense* in the Mályi outcrop. **a,b** — *Congeria ungulacaprae* Münster; **c–f** — *Congeria czjzeki* Hörnes; **g–j** — *Lymnocardium brunnense* Andrusov; **k** — *Caladacna steindachneri* (Brusina); **l** — *Pisidium krambergeri* (Brusina). All specimens are from the collection of I. Cziczer. Scale bars 1 cm.

time-averaging of samples (Goodwin et al. 2001, 2003). High-resolution microsampling can mitigate this time-averaging by greatly increasing the sampling density (Dettman et al. 1999; Patterson & Cheatham 1999; Surge et al. 2001; Wurster & Patterson 2001; Schöne et al. 2004, 2005; Ivany & Runnegar 2010), but these methods require time and resources not available in the collection of these data (Johnson 2016). Given these considerations, 10 years is a minimum ontogenetic age of the Sopron shell. Maximum rate of growth for the Sopron shell was 16 mm/yr based on the best-preserved year within the shell.

The growth rates and ontogenetic ages of the two most closely related cockle species, *Lymnocardium schedelianum* and *L. variocostatum,* have been estimated and compared to *L. soproniense* using the same method (Fig. 7; Johnson 2016). The studied shells of *L. schedelianum* are smaller (~40 mm in height) and have a maximum growth rate of 17 mm/yr based on the best-resolved year from 5 individuals. The studied *L. variocostatum* is of similar size to *L. soproniense*, although the shell presented here was broken near the umbo. Because of this breakage, the initial ~30 mm of shell is missing. The complete individual should be ~80 mm in height. The best-preserved year from this specimen indicates a growth rate of 13 mm/yr. Among these three species, body size and growth rate appear unrelated.

Ontogenetic age and body size do seem to be related among *Lymnocardium soproniense*, *L. schedelianum*, and *L. variocostatum* (Johnson 2016). The smaller *L. schedelianum* have the shortest lifespan, with only 2 to 4 years detected by isotope analysis. Although the *L. variocostatum* shell was broken, 6 years were detected in 53 mm of shell growth; a complete specimen would likely contain ~8 years. *L. soproniense*, the largest specimen, appears to have the longest lifespan (at least 10 years).

Geary et al. (2012) observed that the Pannonian snail *Melanopsis* also seemed to achieve increased body size through increased longevity. They proposed that the reproductive advantage of larger body size coupled with an increase in resource availability and/or a decrease in predation drove this evolutionary trend in *Melanopsis*. Perhaps lymnocardiids were also able to take advantage of a stable lake environment by undergoing more reproductive events and at larger body size via longer lifespans (Johnson 2016).

Palaeoenvironmental interpretation

Environmental conditions are reflected in the stable oxygen isotope composition of shell carbonate. The amplitude or intrashell range in $\delta^{18}O$ values is related to seasonal variations in temperature and $\delta^{18}O_{water}$, although these factors can be difficult to distinguish (Dettman & Lohmann 1993; Ivany et al. 2004) especially from a single shell. Mean shell values, however, are useful for habitat comparisons. For example, in closed lakes there is a gradient in $\delta^{18}O$ values from lower values near-shore (under the influence of freshwater) to higher values off-shore (where water is better mixed and more

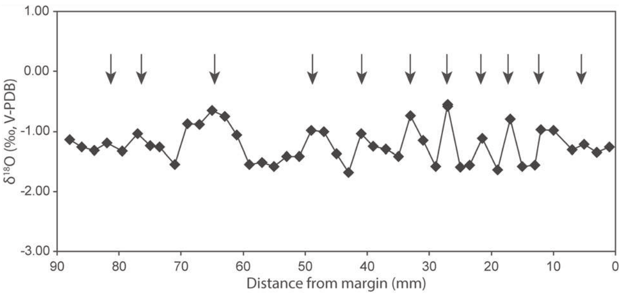

Fig. 6. Stable oxygen isotope profile of *Lymnocardium soproniense* from Sopron (MTM, M.571815) arranged with ontogenetically youngest values at left, and oldest values at right (Johnson 2016). Arrows indicate local maxima, interpreted as winter signals.

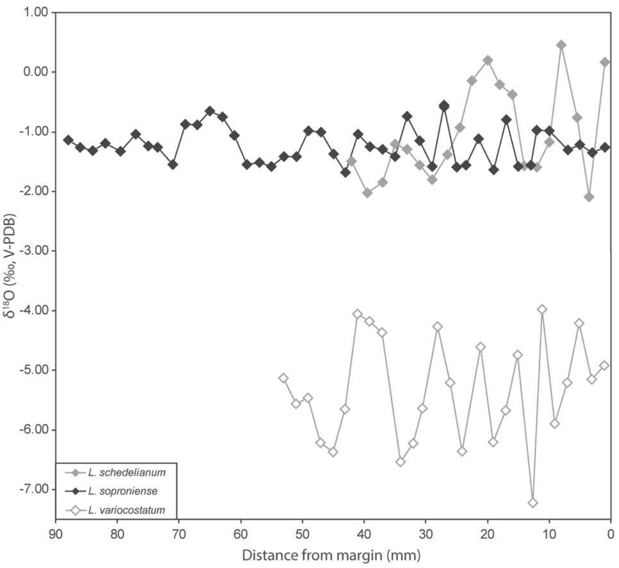

Fig. 7. Stable oxygen isotope profiles of *Lymnocardium schedelianum* from Wien-Vösendorf (NHMW coll.), *L. soproniense* from Sopron (MTM, M. 571815), and *L. variocostatum* from Dáka (private collection). Profiles are arranged with ontogenetically youngest values at left, and oldest at right. The profile of *L. variocostatum* is incomplete due to missing shell. Modified from Johnson (2016).

evaporated) (Talbot 1990; Goodwin et al. 2003). This contrast is observed between high mean $\delta^{18}O$ values of sublittoral *Lymnocardium schedelianum* (–1.6 to –1.0 ‰) and lower mean values of littoral *L. variocostatum* (–5.4 to –2.8 ‰). *L. soproniense* has a mean $\delta^{18}O$ value of –1.2 ‰, which is very similar to that of *L. schedelianum*, and supports a similar sublittoral habitat (Fig. 8).

Phylogeny and stratigraphy

Stratigraphic record of Lymnocardium soproniense and its relatives

Of the closely related species of *Lymnocardium schedelianum, L. soproniense,* and *L. variocostatum*, *L. schedelianum* appears first in the stratigraphic record. Its oldest occurrences are known from the well-studied outcrops of southern Vienna (Vösendorf, Hennersdorf, Laaerberg; Papp 1953), where it occurs both in sublittoral clays and in sandy shoreface deposits (Papp 1951; Schultz 2003). Based on the evaluation of their vertebrate fossils, these layers are correlated with the middle part of Zone MN9, and dated about 10.4 Ma (Harzhauser et al. 2004; Fig. 9).

Lymnocardium soproniense enters the fossil record somewhat later, and it is restricted to sublittoral clays. Molluscs from the overlying littoral deposits in Sopron and its vicinity contain a series of species that are common in younger deposits but missing in the Vienna basin, and vertebrates from the same deposits indicate uppermost MN9 to lowermost MN10 Zones (Harzhauser et al. 2004). Based on the normal magnetic polarity measured in the Balfi út claypit, the Sopron occurrence of *L. soproniense* is thus correlated with the upper part of C5n, and dated about 10 Ma (Magyar et al. 2007; Fig. 9). Apparently, *L. soproniense* replaced *L. schedelianum* in the sublittoral zone of Lake Pannon about 10.2–10.3 Ma, and from that time the latter became confined to the littoral zone. In eastern Austria (Burgenland), *L. schedelianum* occurs in the littoral deposits (e.g., Oggau, Grösshöflein; Magyar et al. 2000), whereas *L. soproniense* characterizes the coeval sublittoral sediments (Sopron; Fig. 9).

Finally, *Lymnocardium variocostatum* is known from littoral sands, correlated with Zone MN10, and dated roughly 9.5–9.0 Ma (*Lymnocardium ponticum* zone; Szilaj et al. 1999; Magyar et al. 2000, 2007). This species seems to have replaced *L. schedelianum* in the littoral zone of Lake Pannon at some time between 9.7 and 9.5 Ma (Fig. 9).

Evolutionary history of the Lymnocardium soproniense lineage

Based on the stratigraphic and palaeoecological patterns discussed above, the following scenario is considered most probable for the phylogenetic relationship of the three species. A sympatric speciation event in *Lymnocardium schedelianum* led to the appearance of *L. soproniense* in the sublittoral zone of Lake Pannon, and subsequent habitat partitioning between *L. soproniense* and *L. schedelianum*; the first was confined to the sublittoral, whereas the latter was limited to the littoral zone of the lake. Later, the now littoral *L. schedelianum* evolved into *L. variocostatum*, possibly anagenetically, as no common occurrence of the two species has been found so far (Fig. 9).

Definition of the Lymnocardium soproniense Interval Zone

Although *Lymnocardium soproniense* is not a very common species, it appears in widespread localities of the Pannonian Basin, apparently with very similar accompanying fauna. This feature makes it a valuable biostratigraphic marker, therefore its first occurrence is used to define the base of the *L. soproniense* mollusc zone in the sublittoral sediments of Lake Pannon (Magyar et al. 1999, 2007; Magyar & Geary 2012).

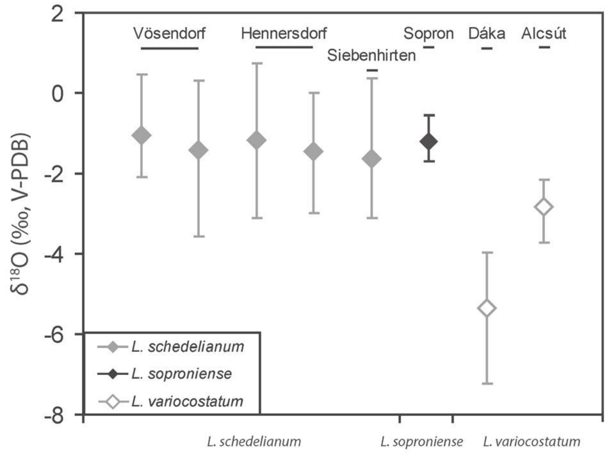

Fig. 8. Mean and range of within-shell $\delta^{18}O$ values of *Lymnocardium schedelianum* (NHMW coll.), *L. soproniense* (MTM, M. 571815), and *L. variocostatum* (private coll.). Data are arranged by species (at bottom) and locality (at top), and do not necessarily indicate relative stratigraphic positions. Both *L. variocostatum* shells were incomplete, potentially affecting within-shell range. Data from Johnson (2016).

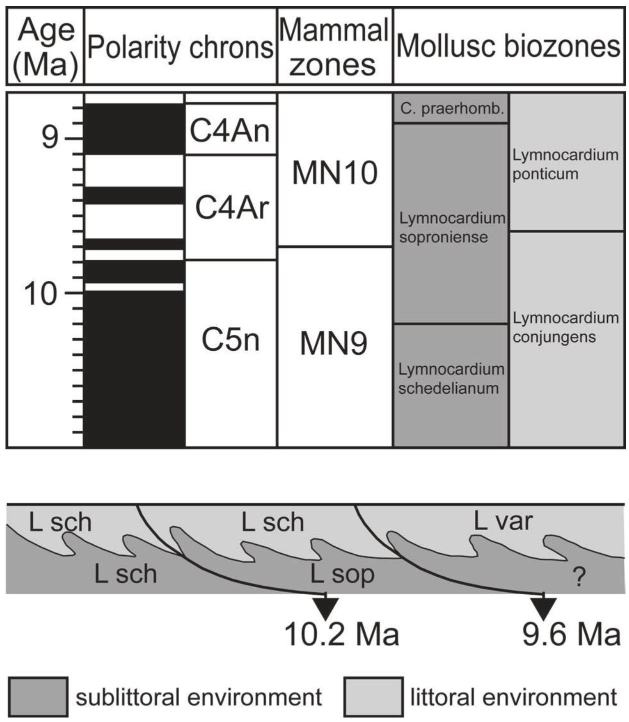

Fig. 9. Stratigraphic correlation of the *Lymnocardium soproniense* Interval Zone to the Geomagnetic Polarity Time Scale and the European mammal zonation (Hilgen et al. 2012). **L sch** — *L. schedelianum*, **L sop** — *L. soproniense*, **L var** — *L. variocostatum.*

The last occurrence of *Lymnocardium soproniense* in the stratigraphic record is more difficult to establish. The age of the uncertain Budapest occurrences is estimated at 8–9 Ma (Magyar et al. 2006). For practical reasons we suggest marking the top of the *L. soproniense* Zone with the base of the overlying *Congeria praerhomboidea* Zone, defined by the first appearance datum of *C. praerhomboidea* at ca. 8.9 Ma

(Magyar et al. 1999; Magyar & Geary 2012), regardless of whether *L. sopronіense* itself occurs in younger deposits or not (Fig. 9).

Conclusions

Lymnocardium soproniense was a Late Miocene brackish-water cockle living in the quiet offshore environment of Lake Pannon. It evolved from *L. schedelianum* some 10.2–10.3 million years ago by attaining larger size and increased longevity (>10 years). The species was widely distributed in the northern part of the Pannonian basin, and it is well represented in museum collections. Although full and intact specimens of this fossil are rare, it can be distinguished from other species even when found in small fragments. Consequently, it is a good biostratigraphic marker in the sublittoral deposits of Lake Pannon.

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Appendix

Review of collection and literature data on the distribution of *Lymnocardium soproniense*

Sopron/Ödenburg and Vicinity

There are many specimens of *Lymnocardium soproniense* from various claypits of Sopron and from a well in Balf (17 m depth from the surface) in the collection of the MFGI, obtained between 1872 and 1971. This material includes a beautiful pair of valves from Sopron, Lenk brickyard, donated to the institute by L. Károlyi in 1914 (the original label of these specimens was written and signed by L. Roth). The left valve is the type of the species (Pl. 97; Fig. 2a,b), photographed by Vitális (1934a,b), whereas the right valve is slightly damaged and partly filled with sediment (or glue?) in the inner part (Pl. 6361; Fig. 2 c,d). The relatively large collection of F. Bartha from the Balfi út claypit contains an outstandingly well-preserved left valve (Bartha 1971; Pl. 2016.1.1; Fig. 2e,f), along with some large and quite complete but sediment-filled specimens (Pl. 6336, 6337, 6354, 6355, 6359) and many shell fragments (Pl. 6332, 6341, 6344, 6345, 6347).

The Hungarian Natural History Museum (TTM) also has a relatively large collection of *L. soproniense* from Sopron, including specimens that were purchased from the legacy of I. Vitális (M57/807-817, M64/1200). In this material, however, there is only one right valve which is a complete and fully cleaned specimen (M57/815; Fig. 2 h,i). The Bakony Natural History Museum (TTM-BTM) in Zirc also houses a few nice though not fully intact specimens (Fig. 2g).

Vicinity of Miskolc

While mapping the southwestern hilly region of the Bükk Mts. between 1932 and 1934, Z. Schréter, geologist of the Hungarian Royal Geological Institute, collected fossils from shallow test holes (Schréter 1939) and deposited them in the MFGI collection. The best-preserved specimens are from Bükkaranyos (MFGI Pl. 4535, Pl. 4613, Pl. 4614); although the shells are broken and dissolved, the diagnostic rib pattern of *Lymnocardium soproniense* can be recognized in some of them. However, specimens from Borsodgeszt (Pl. 4627), Harsány (without inventory number), Sály (Pl. 4569), and Mályi (Pl. 4602) are poorly preserved; the shells are usually partly or entirely dissolved. They are identified as *L.* cf. *soproniense* (Schréter 1939, p. 520; Fig. 1).

Better-preserved specimens in the area were collected after the brickyard claypit in Mályi was opened. Apart from a steinkern (*L.* cf. *soproniense*, Pl. 4603), the museums have shelly specimens from this outcrop (Pl. 6438 and a specimen without inventory number in the collection of the MFGI; M. 68.32 in the collection of the TTM; and several specimens in the private collection of I. Cziczer, including an intact left valve (Fig. 2j,k).

Bartha (1971) mentioned the occurrence of *L. soproniense* from Alsódobsza, but these specimens, deposited in the collection of the MFGI, belong to *L. schedelianum* (Fig. 1).

Vicinity of Oradea/Nagyvárad

We have no information on the whereabouts of Papp's (1915) specimen from Nuşfalau. Mihaila and Marinescu (1971) claim that the holotype of *Lymnocardium mihaili* from Felcheriu is reposited in the Geological Institute in Bucharest, but no mention is made of the whereabouts of fossils collected by Mihaila and determined by Marinescu from Sabolciu (Mihaila and Marinescu 1971). As the latter material has not been depicted, we cannot confirm the presence of *L. soproniense* in Sabolciu (Fig. 1).

Budapest

In the TTM collection, there is a beautiful specimen of *Lymnocardium soproniense* (M57/38) preserved in clay with double and open valves. According to the label and the original sticker on the specimen, it was collected by Ferenc Kubinyi in 1849 from Budapest-Rákos. This locality and the immediately neighbouring Kőbánya outcrops are well-known from the palaeontological literature (see Magyar et al. 2006 and references therein), but no mention is made of fossils that could be identified with *L. soproniense*.

In the collection of the MFGI, however, there are two specimens from Budapest-Kőbánya (Pl. 2864), determined as *"Limnocardium* cfr. *schmidti"* by Bartha, that might be related to *L. soproniense*. Both specimens are articulated valves; one is a steinkern, the other with shells but compressed and broken. The latter has 18 ribs, the structure of which resembles that of *L. soproniense*.

This scarce material indicates that *L. soproniense* might have lived in the area, but further data are needed to strengthen that claim (Fig. 1).

Balaton

Bartha (1971, p. 101) reported *Lymnocardium soproniense* from the Kisapáti-2 borehole at 18–35 m depth (Fig. 1). The core sample (18.50–18.70 m) is deposited in the collection of the MFGI (Pl. 6327). It contains *Congeria czjzeki* specimens and a poorly preserved fragment of a large *Lymnocardium* species in fine-grained sediments. The sediment and the accompanying species make it probable that the large species is indeed *L. soproniense*, but its rib architecture is not visible, thus the determination remains highly uncertain.

Magyar (1988) depicted large *Lymnocardium* moulds (steinkerns) from Mindszentkálla as "*Lymnocardium* cf. *soproniense*" (Fig. 1). Although the preservation of these fossils, deposited in the TTM, does not allow distinction between *L. soproniense* and the closely related species *L. variocostatum* and *L. schedelianum*, the accompanying species — such as *Congeria pancici* Pavlović, *Unio atavus* Partsch, and *Melanopsis fossilis* (Martini-Gmelin) — as well as the shoreface depositional environment of the embedding pebbly sandstone – suggest that these large cockles probably belong to *L. schedelianum*. The entire association is typical of a littoral "Burgenland fauna" (Magyar et al. 2000; Csillag et al. 2010).