

Continuous record of the evolution of lacustrine cardiid bivalves in the late Miocene Pannonian Lake

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A biometric study was performed on populations of lacustrine cardiid bivalves in stratigraphically ordered samples from the deposits of a late Miocene lake, which are exposed close to Lake Balaton in Hungary. The lineage can be subdivided into several chronospecies: it starts from *Lymnocardium decorum ponticum* and leads to the genus *Prosodacnomya* which is considered to belong to another subfamily than *Lymnocardium*. The evolutionary process was gradual, microevolutionary, anagenetic, and possibly peramorphic. Certain populations displayed ecophenotypic changes that were similar in their nature to the observed evolutionary ones. The shells exhibit a gradual fusion of the central ribs, resulting in a smooth central zone in late populations. The process could be an adaptation to conditions present in shallow regions of an endorheic lake with frequently displaced shoreline where ploughing was more important than digging. The smooth central zone leads to decreased friction during ploughing. The estimated time span of the evolution is between one and three million years.

Key words: gradual evolution, anagenesis, Miocene, Pannonian Lake, cardiid bivalves.

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Introduction

Endemic lacustrine molluscs are frequent objects of evolutionary studies (Neumayr & Paul 1875, Williamson 1981, Geary 1990). In general, lakes do not inherit their molluscs from other lakes (Taylor 1988: p. 514). Instead, lacustrine faunae are mainly recruited from fluvial ones, but also from shallow standing waters such as marshes or oxbow ponds, and in

rare cases from marginal marine habitats. Such migrations to lakes always involve profound changes in life conditions.

For fluvial forms the lake offers a wide array of new potential niches. Organisms living in a river are subjected to a constant downstream drift, thus they need to have the ability to counteract it and even to propagate upstream. In most cases this necessity rules out planktonic larvae and favours a smooth, streamlined shell. Constraints of this type are released in lakes. Probably these factors lead to adaptive radiations characteristic of 'ancient' lakes, very often evoking the appearance of forms with spinose or ridged shells.

Pulmonate molluscs originating from shallow standing waters may also profoundly change in their biology and morphology when finding themselves in a lacustrine environment. Some lakes of marine origin (e.g. the Aral, the Caspian, and the Pannonian lakes) inherited a set of species derived from marginal marine euryhaline ancestors. In the lakes they found new conditions, which released them from certain earlier pressures and imposed upon them new ones, such as the elimination of certain predators and competitors, lack of noticeable tides, and a change from chloride- to hydrocarbonate-dominated water chemistry.

The late Miocene Pannonian Lake (Kázmér 1990) harboured one of the most diverse endemic lacustrine faunae ever known, including several hundreds of described molluscan species, dozens of endemic genera, and some endemic subfamilies (Papp *et al.* 1985, Stevanovic *et al.* 1990). Even one endemic family (Lymnocardiidae Stoliczka 1871) is recognized by some authors, although we prefer to keep this taxon on subfamily level. This lake was a remnant of the central Paratethys (Sarmatian) sea.

Obvious errors committed in early studies of molluscan evolution in the Pannonian Lake were due mainly to incorrect stratigraphic decisions (Neumayr & Paul 1875). Unfortunately, these discouraged further attempts in evolutionary studies in the Pannonian Lake fauna. Some authors, however, continued to propose precursor-descendant relationships (e.g. Papp 1953, Taktakishvili 1987). Recently Geary (1990) studied the evolution of the Pannonian Lake *Melanopsis*.

In the present study we describe a continuous change in shell morphology from the subspecies *Lymnocardium decorum ponticum* to *Prosodacnomya vutskitsi*. We interpret this as reflecting a gradual, anagenetic evolution. This evolution is expressed in the smoothing of the ribbed surface and in the changes of the overall shape of the shell. The evolution observed took place in a time span estimated as one to three million years. Our biometric study points to the usefulness of Brusina's (1902) and Stevanovic's (1951) species concept. The smoothing of the shell surface probably had an adaptive value in facilitating ploughing which might be part of an escape strategy against lowering of the lake level.

The studied and figured material is deposited in the collection of the Natural History Museum, Budapest (Természettudományi Múzeum Föld-és Őslénytár, H-1088 Budapest, Múzeum krt. 14-16, abbreviated TTM).

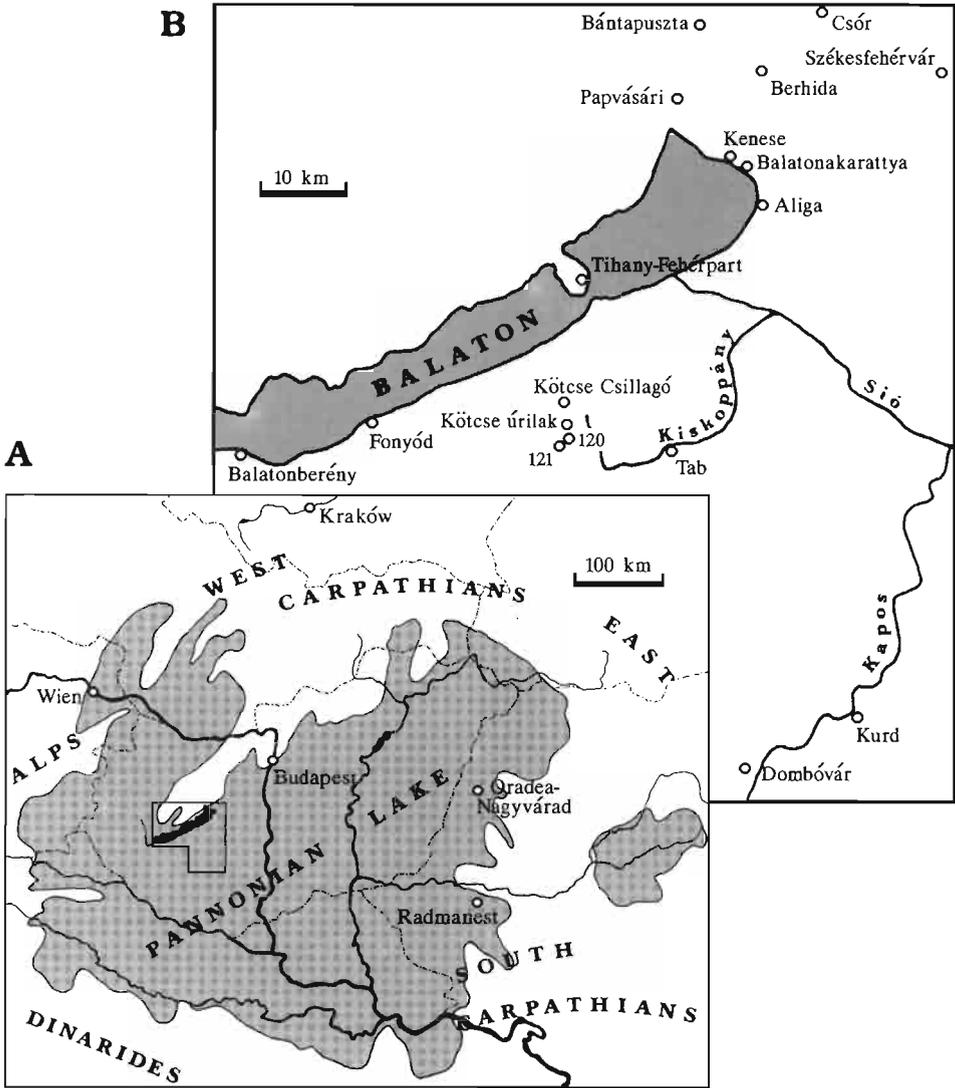


Fig. 1. □A. Extend of the Pannonian Lake sediments and location of the studied areas. □B. Localities in the Balaton Lake area.

Methods

Variations in the shell morphology was studied in samples from sections, situated mainly in the vicinity of Lake Balaton. Most samples were collected by us from layers the thickness of which did not exceed ten centimeters, showing no signs of reworking. Thus they probably represent very short time intervals, virtually instances.

Three kinds of measurements were taken:

- (1) the largest well preserved specimens from all samples were measured for all parameters (Fig. 5, 6),
- (2) changes in the form of ribs during ontogeny were measured in randomly selected samples (Fig. 7, 8, 9),
- (3) from two localities, yielding well preserved specimens, including juvenile ones, we measured parameters describing shell shape in all sufficiently well preserved specimens (Fig. 10).

All measurements were taken with a micrometer eyepiece. Rib profiles were studied in tangential views, by turning the specimens around their longitudinal axis under the microscope.

Previous taxonomy of the lineage studied

Our study encompasses six forms described by four authors:

Lymnocardium decorum decorum (Fuchs 1870)

Lymnocardium decorum ponticum (Halaváts 1902)

Lymnocardium aff. *serbicum* (Brusina 1902)

Prosodacnomya dainelli (Brusina 1902)

Prosodacnomya vutskitsi (Brusina 1902)

Prosodacnomya carbonifera (Stevanovic 1951)

Except for *L. decorum ponticum*, *L. aff. serbicum* and *P. carbonifera* we included topotype material in our study. Most Hungarian authors (Halaváts 1903, Lörenthey 1906, Strausz 1942) preferred to give molluscan species quite a broad meaning, arguing that transitional forms do exist. Thus they united several species of Brusina (1902). Here we accept, however, the approach of Brusina (1902), Stevanovic (1951), and Basch (1990) because their narrower taxa rather well correspond to present concepts about chrono(sub)species (Dzik 1990: p. 282) and were proven to be useful by our biometric study (see below).

Genera *Lymnocardium* and *Prosodacnomya* are generally assigned to two separate subfamilies, respectively Lymnocardiinae Stoliczka 1871 and Prosodacninae Andreescu 1974 (Müller & Magyar in press).

Localities and stratigraphy

Our study is based mainly on material collected in the vicinity of the Lake Balaton (Fig. 1), especially near the village of Kötöcs, where the stratigraphic order of the localities is the clearest (Müller & Magyar in press). Other localities, yielding the bulk of the *Lymnocardium* material, are scattered in a broad area, thus their stratigraphy is less obvious than that of the Kötöcs localities. In spite of this, using Lörenthey's (1906) zonation (Fig. 2, Müller & Magyar in press), we could arrange them in stratigraphic order.

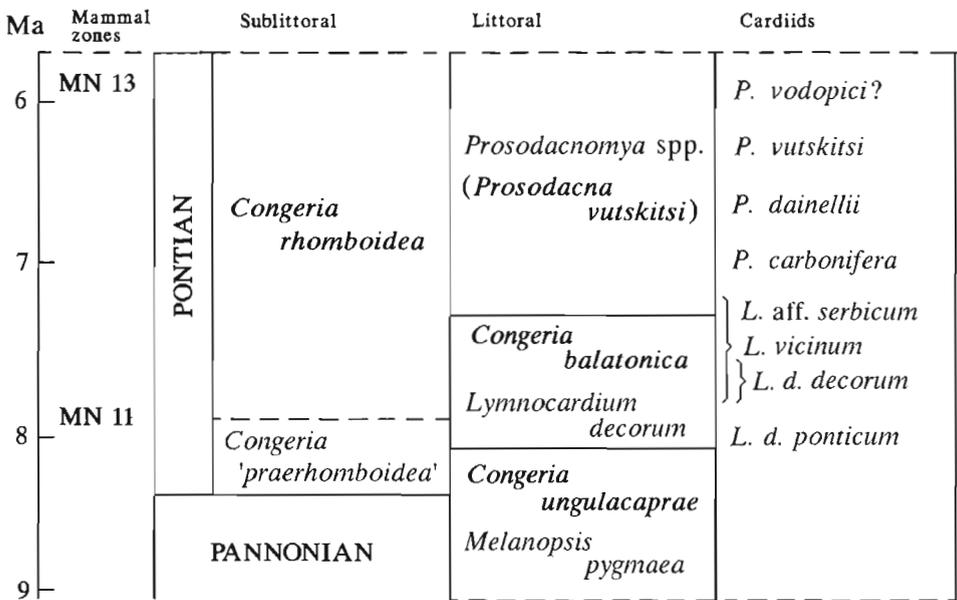


Fig. 2. Stratigraphic scheme for the Pontian (sensu Stevanovic 1951) of the Balaton region. Lórenthey's (1906) zonemarkers bold.

In Bántapuszta (sand-pit near the ancient Roman dam) and in Csór (Strausz 1942: p. 30) *Lymnocardium decorum ponticum* occurs near the base of the *Congeria balatonica* - *Lymnocardium decorum* Zone, close to the top of the *Congeria unguicaprae* Zone (Fig. 2). This is also true for the borehole Berhida 3 (Kókay *et al.* 1992), where at depths of 129 and 110 meters this form occurs above *C. unguicaprae*-bearing layers. Specimens at 92 m in this borehole already show traits of *L. decorum decorum*. The stratigraphic position of other *L. decorum ponticum* localities are more questionable: borehole Székesfehérvár 5, (depth 181 m) and Oradea (Nagyvárad) Fughiu (Wanek 1978).

Localities of *Lymnocardium decorum decorum* are, in an approximate stratigraphic order: Papvásári hill near Berhida, two layers; Kenese-Üdül-ötelep, railroad cut; Balatonakarattyá-Csittényhegy, layer 'a' of Halaváts (1903); Tihany-Fehérpart, four layers (Müller & Szónoky 1990: Fig. 63); Balatonberény (Strausz 1942: p. 34); and Fonyód, Lórenthey's (1906: p. 27) 'II. Horizont'. The age of Radmanesti, type locality of *L. decorum* and *L. vicinum*, seems to be slightly older than that of Tihany-Fehérpart (Gillet & Marinescu 1971), but probably it is a strongly condensed section which encompasses a longer interval.

Outcrops and the stratigraphy of the Kötöcse area are described by Müller & Magyar (in press).

Magnetostratigraphic study of the borehole Berhida 3 (Kókay *et al.* 1992) reveals that the transition from *Lymnocardium decorum ponticum* to

L. decorum decorum falls slightly above the top of anomaly 4a (about 7.8 to 8.0 Ma). Using magnetostratigraphic and seismic data the transition from *Lymnocardium decorum* to *Prosodacnomya dainellii* can be estimated to have taken place between 7.0 and 7.7 Ma (Pogácsás *et al.* in press). Some Tihany-Szarkád specimens of *Prosodacnomya carbonifera* are embedded in a block of silt from a basalt agglomerate, the age of which was estimated by radiometric methods (Balogh *et al.* 1986, Balogh personal communication) as 7.5 Ma. The age of a borehole sample with *Prosodacnomya vutskitsi* from the Szarvas area has been estimated as 6.0 to 6.4 Ma (magnetostratigraphic and seismic data).

The Tihany-Fehérpart exposure with *Lymnocardium decorum* yielded mammalian teeth most probably belonging to MN 11 Mammal Zone (Kordos 1989), while Hatvan clay-pit, situated stratigraphically above *Prosodacnomya vutskitsi*-bearing layers, is probably of MN 13 age (Kordos, personal communication 1990). Thus in all probability all localities studied in this paper belong to the Turolian stage (MN 11 to 13), an interval between 9 (or 8.2) and 5.2-5.4 million years ago (Berggren 1987).

This way the stratigraphic order of the studied taxa can be determined reliably at least for the Balaton area as follows, from below upwards: *Lymnocardium decorum ponticum* (Fig. 3A), *L. decorum decorum* (Fig. 3B-G), *L. aff. serbicum* (Fig. 3H, I), *Prosodacnomya carbonifera* (Fig. 3J-N, Fig. 4A-D), *P. dainellii* (Fig. 4E, F), *P. vutskitsi* (Fig. 4G, H).

Ecology and palaeogeography

All the Hungarian localities included in this study belong to Jámbor's (1980: p. 195) Tihany Formation. Its facies indicates that it was deposited on a delta plain with intercalations formed on an upper part of a delta front. Thick layers of fossil-depleted variegated silts with sandy lenses dominate. These lenses contain thin, generally only few cm thick intercalations with fossils (Müller & Szónoky 1990). Most layers yielding *Lymnocardium decorum* or *Prosodacnomya* spp. are grey silts or fine sands, with *Unio*, several species of pulmonates, small spinose *Melanopsis*, *Bithynia*, *Viviparus* and *Theodoxus*. These are characteristic of Korpás-Hódi's (1983: p. 130) *Melanopsis sturii* - *Theodoxus* sp. association, which points to a marginal, extremely shallow water facies, usually deposited in lagoons or in protected shallow areas overgrown with algae.

Lymnocardium decorum and *Prosodacnomya* are sometimes present in coquinas of deeper water origin (Tihany-Fehérpart layer 2, Müller & Szónoky 1990; Kötcse 120, Müller & Magyar in press) but in these cases shells were accumulated from a broad scale of ecological settings.

The Tihany Formation, bearing *Lymnocardium decorum* or *Prosodacnomya*, can be traced in similar facies from the Lake Balaton region to the vicinity of the Mátra mountains in northern Hungary (Szentés 1943, Korpás-Hódi personal communication). Though a detailed study of this

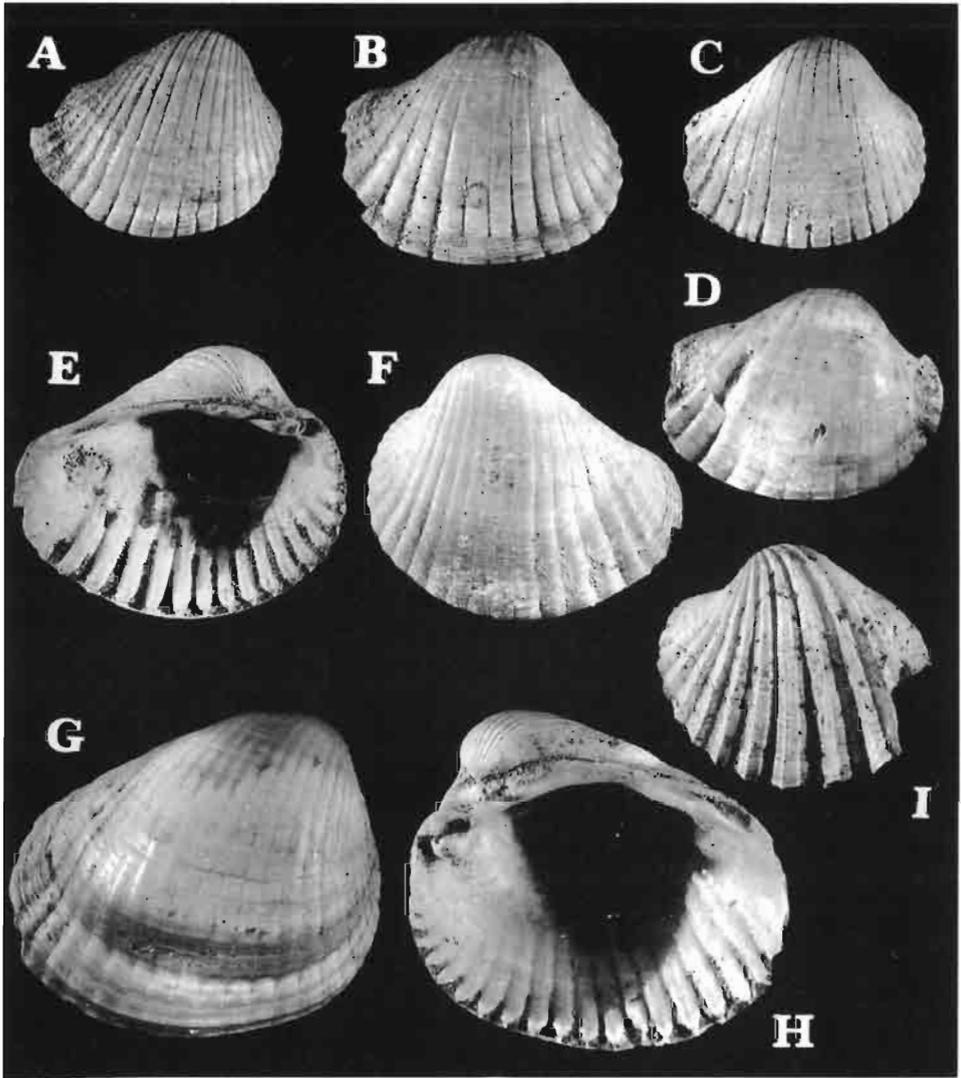


Fig. 3. □A. *Lymnocardium decorum ponticum* (Halaváts 1902), Bántapuszta, sandpit near to the ancient Roman dam, TTM M91 422. □B-D. *Lymnocardium decorum decorum* (Fuchs 1870), Fonyód, Lörenthey's (1906) 'II. Horizont', TTM M91 423. □E. *Lymnocardium decorum decorum* (Fuchs 1870), Kötse, Csillagó claypit, layer 9A, TTM M91 424. □F, G. *Lymnocardium decorum decorum* (Fuchs 1870), Kötse, Csillagó claypit, layer 9H, specimen with almost fused central ribs, TTM M91 425. □H, I. *Lymnocardium* aff. *serbicum* (Brusina 1902), Kötse, Csillagó claypit, layer 20, specimen in Fig. I with almost fused central ribs, TTM M91 426. □J-N. *Prosodacnomya carbonifera* (Stevanovic 1951), Kötse, loc. 121, specimen in Fig. J with open intercostae, exceptional for this locality, specimen in Fig. L with high ribs (M-N, same specimen), TTM M91 427. All $\times 2$.

material was precluded by its scarcity, the spatial distribution of the species seems to be the same as in the Kötöcse area. The whole region was a 300 km long northeastern shoreline of the lake, where interconnected delta systems prograded S-SE-ward (Pogácsás *et al.* in press). A similar pattern seems to be present all around the lake, in Slovenia (Stevanovic & Škerlj 1990), Croatia (Basch 1990), Serbia (Stevanovic 1990), and in Romania (Wanek 1978, Gillet & Marinescu 1971): *Lymnocardium decorum* occurs near the margins while *Prosodacnomya* species, quite in the order of their inferred chronology, deduced from observations made in the Balaton area, occur in increasingly basinward positions (Müller & Magyar in press: Fig. 6). This spatial distribution reflects the actual progradational directions.

Biometrics

All the seven characters measured show clear unimodal frequency distribution in all samples sufficiently big to draw conclusions in this respect. Number of individuals in samples from boreholes was too low (3 to 5) to make estimations of frequency distributions, but their characters fit among those observed on larger ($n > 12$, usually 24 or 36) samples, collected in exposures. Six of the characters reflect changes which can be correlated with geological age (Fig. 5, 6). The most conspicuous change noted is the smoothening of the central zone of the shells as expressed in two characters, reflecting fusion and lowering of the ribs. In *Prosodacnomya* species the fusion of the ribs is complete in the central regions, while the anterior and posterior regions remain almost as strongly ribbed as in *Lymnocardium decorum*. In juvenile specimens of *Prosodacnomya* species, up to a shell length (H) of about 3 to 5 mm, the intercostal flats remain open, thus the ribbing is identical with specimens of similar size of *Lymnocardium decorum* (Fig. 4F, H, 8). In Fig. 6 it can be seen how the intercostal flats become increasingly narrower with geological time (ratio k/b), and disappear completely in specimens from locality Kötöcse 121, except for a single one. Simultaneously the ribs become relatively lower (ratio m/b , Fig. 6). Ratio m/b changes conspicuously during the ontogeny, repeatedly in both directions, especially in forms close to the *Lymnocardium/Prosodacnomya* transition, in Kötöcse 121 and slightly less so in Csillagó 20 (Fig. 9). In contrast, a trend is observed in *Prosodacnomya dainellii* (Kötöcse úrilak; Fig. 7) toward a stabilisation of the rib shape, while *P. vutskitsi* (Tab; Fig. 7) exhibits only slight variations in this respect during growth, except in its juvenile stage.

The relative width of central rib or costation index (ratio b/H , Fig. 6) shows a slightly more complicated pattern. *Lymnocardium decorum ponticum* starts with narrow ribs, later these become wider, while beginning with the transition to *Prosodacnomya* a continuous trend is observable toward more and more narrow ribs. Though the b/H ratio is highly variable

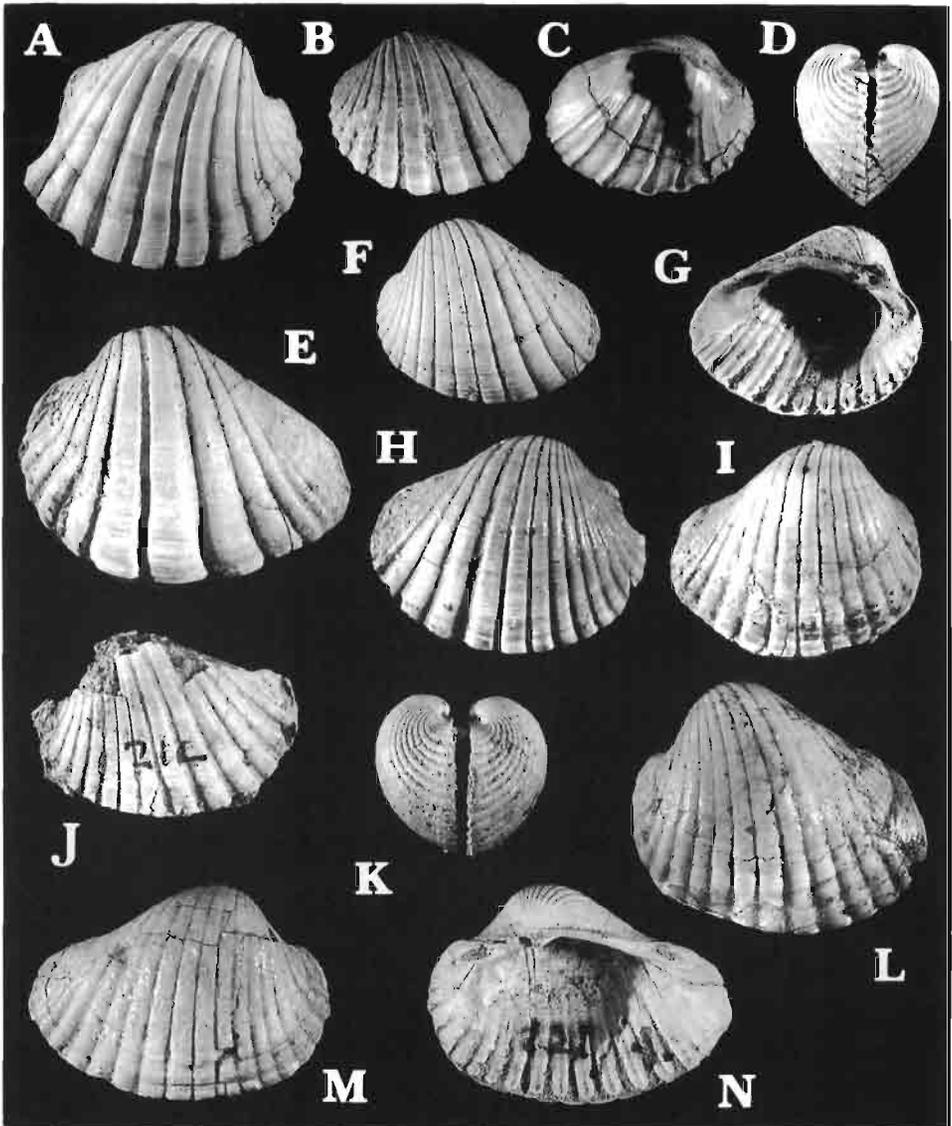


Fig. 4. □A-D. *Prosodacnomya carbonifera* (Stevanovic 1951), Kötse, loc. 121, ribs tend to fuse in these specimens. All specimens, especially that in B, show repeated changes in height of ribs during growth, TTM M91 427. □E, F. *Prosodacnomya dainellii* (Brusina 1902), Kötse, úrilak, TTM M91 428. □G, H. *Prosodacnomya vutskitsi* (Brusina 1902), Tab, claypit next to the railway station, layer 1, TTM M91 429. □I. *Lymnocardium vitcinum* (Fuchs 1870), Kötse, loc. 120, TTM M91 430. All $\times 2$.

between and within localities and samples, in individuals it is obviously fixed.

Characters describing the shape of the shell, relative height (M/H), relative width (V/H), and degree of prosogyration (B/H) exhibit a gradual change with geological time, especially clearly in the Kötse section (Fig. 5).

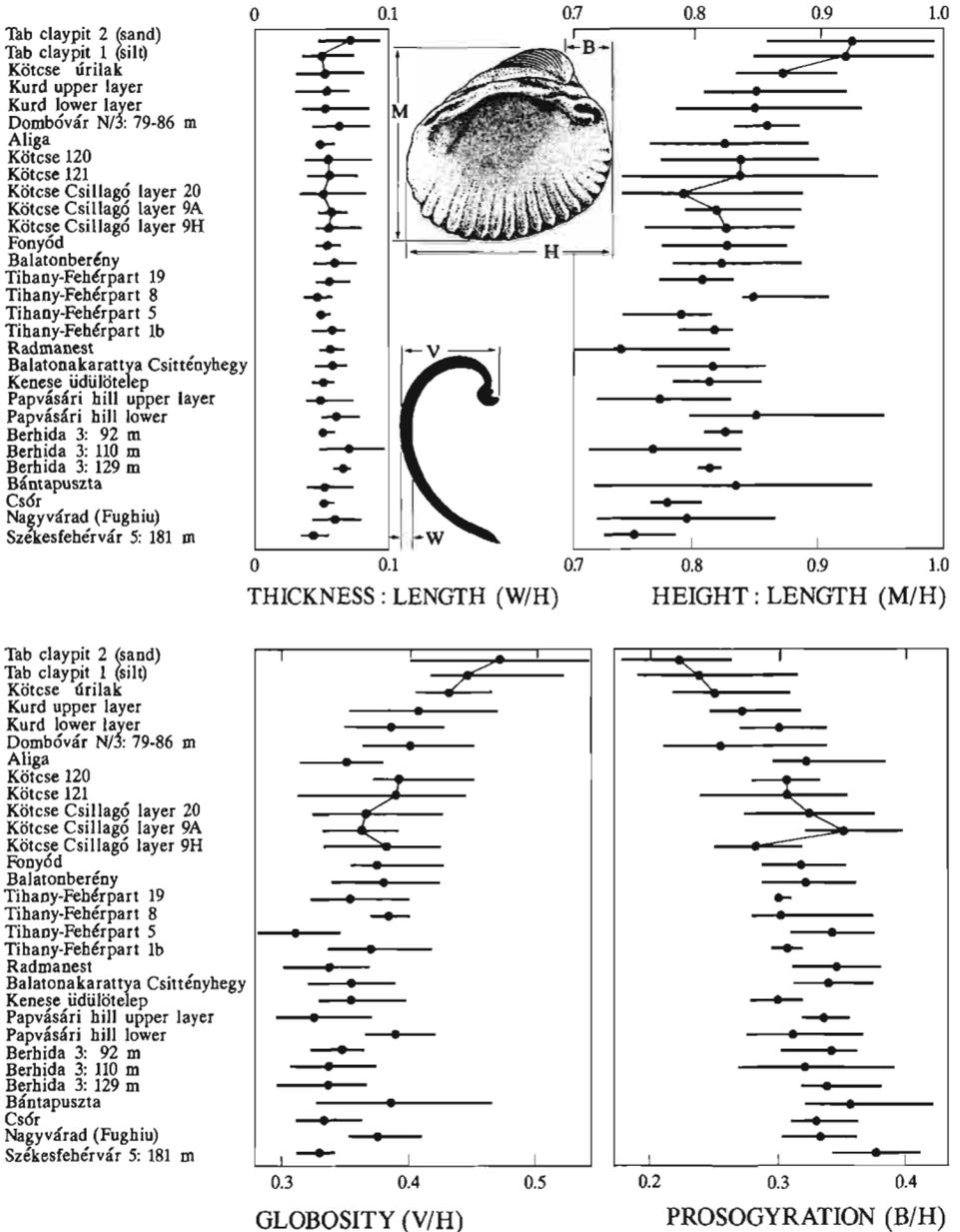


Fig. 5. Changes in shell morphology in the *Lymnocardium-Prosodacnomya* lineage. Samples in clear superposition order are connected by line; stratigraphic order of the remaining ones has been inferred from geological and paleontological data (see also Fig. 1). Arithmetic means indicated by circles, range of values by lines. Coordinates for measurements of shell length and height were respectively parallel and perpendicular to the line determined by the lateral teeth. Ratios based on means of measurements done on three ribs located at the mid-length of the shell.

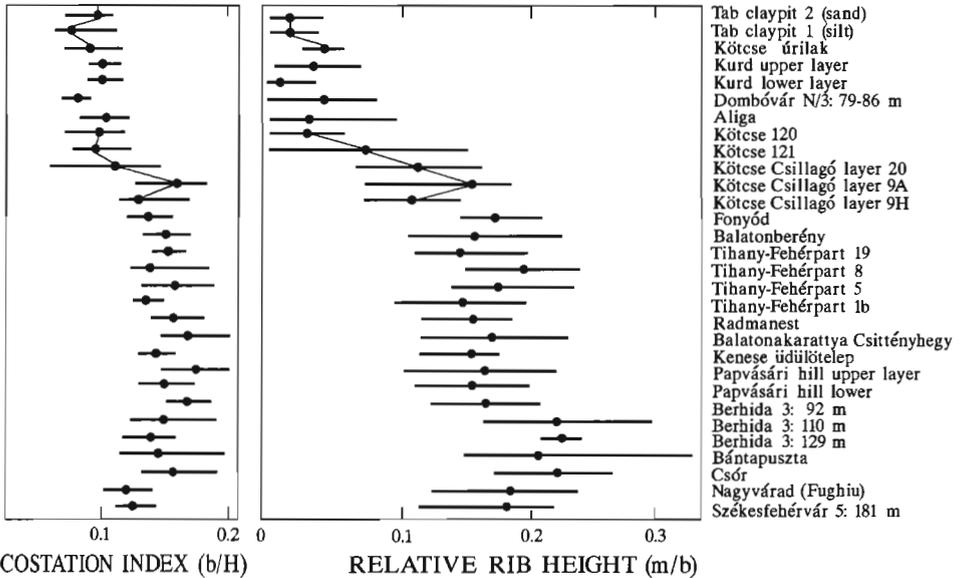
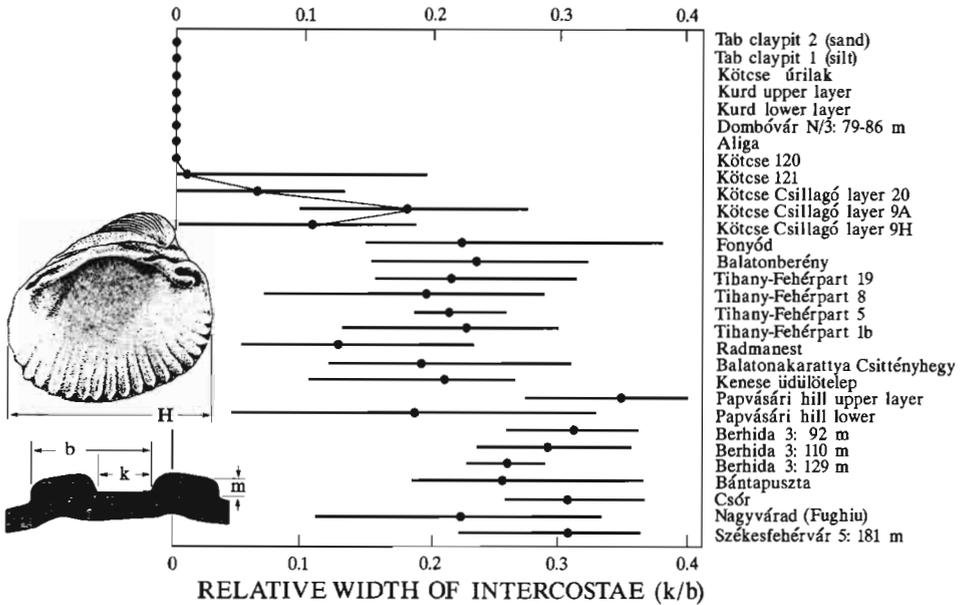


Fig. 6. Changes in shell ornamentation in the *Lymnocardium-Prosodacnomya* lineage. Samples from Székesfehérvár 5 to Berhida 3: 110 m represent *Lymnocardium decorum ponticum*, those from Berhida 3: 92 m to Kötcese Csillagó layer 9A *Lymnocardium decorum decorum*, Kötcese Csillagó layer 20 is *Lymnocardium aff. serbicum*, Kötcese 121 to Aliga is *Prosodacnomya carbonifera*, Dombóvár N/3 to Kötcese úrilak is *Prosodacnomya dainelli*, and Tab claypit samples represent *Prosodacnomya vutskitsi*.

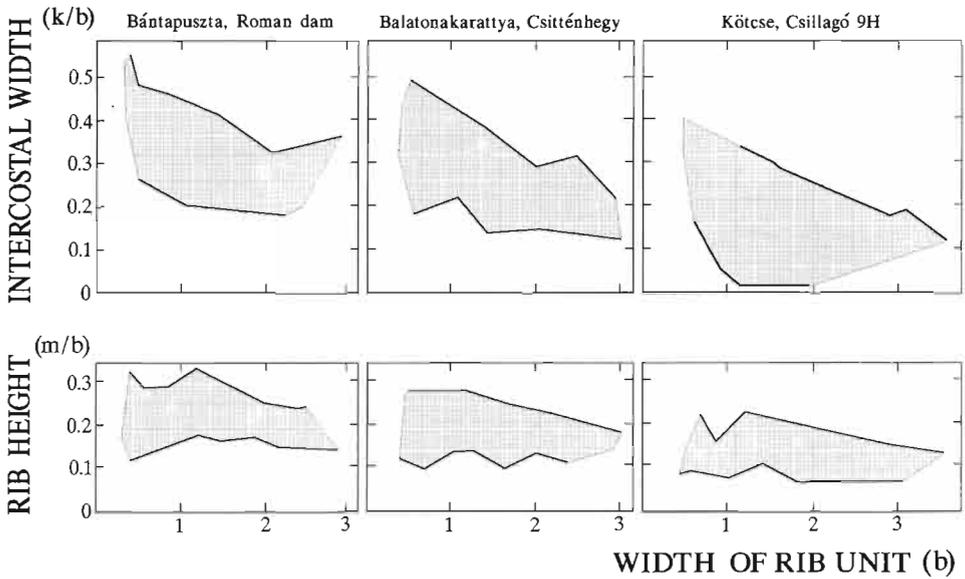


Fig. 7. Evolution of ontogeny of costation in *Lymnocardium* part of the *Lymnocardium-Prosodacnomya* lineage. Ontogenetic changes in relative width of intercostae (k/b), and relative height of ribs (m/b). Width of central ribs + intercostae (b) is taken as a measure of individual age.

Changes of the thickness of the wall (W/H , Fig. 5) seem not to have any temporal trend, but are probably ecophenotypically controlled. In the two samples from Tab clay-pit, the specimens of the silty layer have much thinner shells than those of a sandy layer, deposited probably from more agitated water. A similar pattern is reported by Andreescu (1977: p. 14) for *Prosodacna* species of the Dacian basin.

Materials from two localities (Csillagó 9H and Tab 2, Fig. 10) were studied for changes of the shape parameters during growth. Though dispersion is high due to individual variability, it is clear that ontogenetic change observed in the Tab 2 sample is similar to the evolutionary one. Young specimens of *Prosodacnomya vutskitsi* are low, narrow, and moderately prosogyrate, quite like specimens of similar size of *Lymnocardium decorum*.

We did not study the hinge in any detail. Strausz (1970) already stated that there is no significant difference between hinges of '*Lymnocardium decorum*' and '*Prosodacna vutskitsi*'. The anterior lateral tooth All tends to be larger in *Prosodacnomya* than in *Lymnocardium decorum*, but individual variability is high. In the likely descendants of *Prosodacnomya*, i.e. in *Prosodacna* species, this tooth grows to an enormous size at the expense of the other teeth (Andreescu 1977).

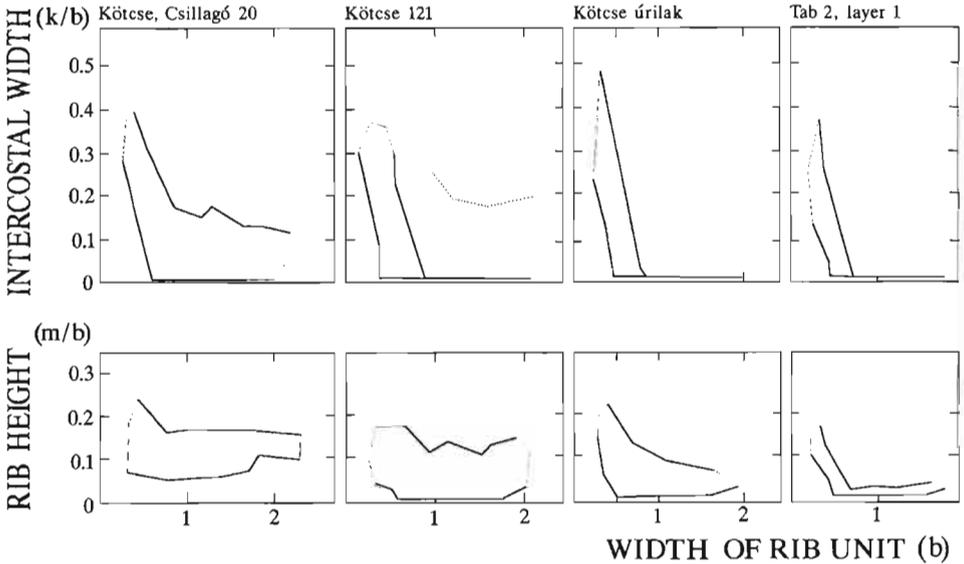


Fig. 8. Evolution of ontogeny of costation in *Prosodacnomya* part of the *Lymnocardium-Prosodacnomya* lineage. Ontogenetic changes in relative width of intercostae (k/b), and relative height of ribs (m/b). Width of central ribs + intercostae (b) is taken as a measure of individual age.

Patterns of the process

A virtually continuous profound morphological change in time was observed in shells collected from increasingly younger layers of the Balaton area and the Kötse section. We interpret this change as an evolutionary process linking populations classified as *Lymnocardium decorum ponticum* with *Prosodacnomya vutskitsi* through intermediate forms. This transformation, microevolutionary in all its aspects, led to a change, generally accepted as being on subfamily level.

In late populations the rib structure is quite stable, while in earlier ones it is variable, especially in forms close to the *Lymnocardium/Prosodacnomya* transition. Notable variations in sediment and in the accompanying fauna do not affect the rib structure of *Prosodacnomya vutskitsi*.

The most conspicuous change observed, the smoothening of the ribs, was clearly under an ecophenotypic control in individuals from localities Kötse 121 (Fig. 4A-D, 7) and Csillagó 20 (Fig. 4E), but similar changes occur in many *Lymnocardium decorum* specimens, too. The only plausible explanation for a repeated change of rib form (Fig. 9) during growth is that it was controlled by external factors.

The fact that evolutionary changes have a similar character to ecophenotypic ones is probably not accidental. Johnson (1981 personal

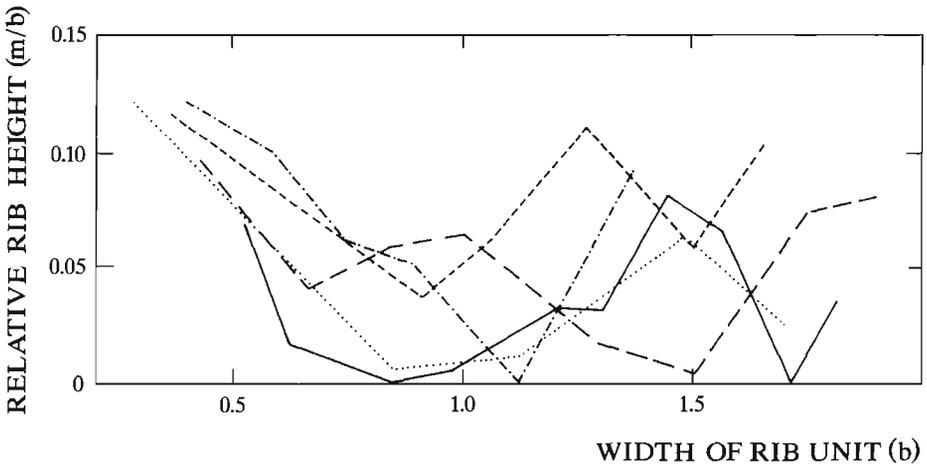


Fig. 9. Change of relative height of ribs (m/b) during growth of particular individuals from Kötöcsé 121.

communication 1991; Johnson & Lennon 1990: p. 482) thinks that; 'ecophenotypically controlled' traits in developmentally flexible species may later be genetically stabilized by an adaptive process, irrespective of whether or not in the life of the individuals the ontogenetic change had an adaptive significance. Johnson adds that this process may even accelerate the evolution by providing 'ready-made' pathways. So evolution may have involved the 'genetic assimilation' of ecophenotypic variation (Waddington 1957; Matsuda 1982).

The evolution described seems to reveal a heterochronic, peramorphic nature. This is most clear with the ribs: young specimens of *Prosodacnomya* have *Lymnocardium decorum*-like ribs. Shape parameters in *Prosodacnomya vutskitsi* seem to obey a similar rule.

Adaptive significance

Most cardiids are active and fast shallow burrowers but jumping as an escape mechanism and ploughing as a directed locomotion are also frequent patterns of motor activity (Savazzi 1985). Most Pannonian lake cardiids beyond doubt retained this mode of life, since substantial changes in locomotion would have led to profound changes in shell form (Savazzi 1985: p. 293), yet most *Lymnocardium* species retained the basic cardiid structure.

Savazzi (1982) demonstrated experimentally that ribs, especially central and anterior ones, are essential for the fast burrowing of cardiids. Smoothing of central ribs in *Prosodacnomya* species is very likely

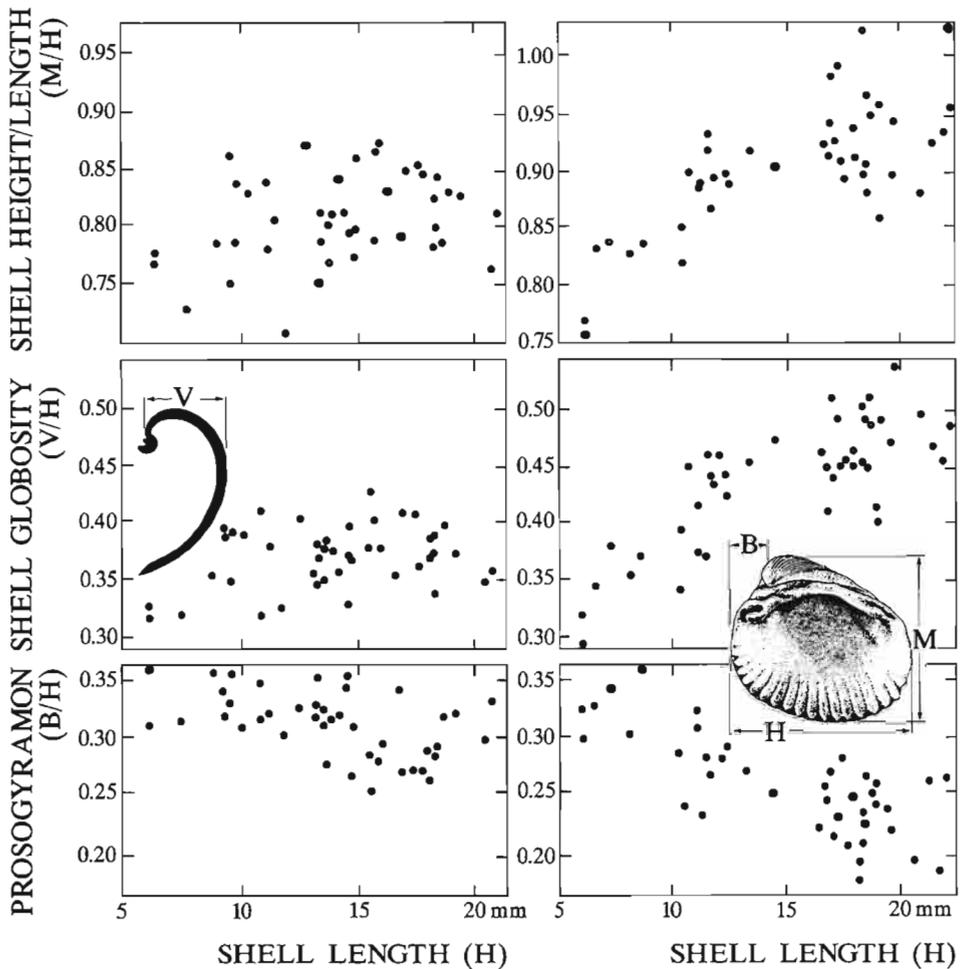


Fig. 10. Ontogenetic changes of shell morphology in a population of *Lymnocardium decorum* from Csillagó 9H and *Prosodacnomya vutskitsi* from Tab, layer 2.

disaptive (Baum & Larson 1991) in respect to burrowing, which strongly suggests a decrease of importance of burrowing in the habits of the taxon.

As to a possible adaptive value of smoothening of the ribs, we suggest tentatively that it might have had a role in facilitating another important locomotory pattern: ploughing. During ploughing, only the central ribs are in contact with the sediment, while the anterior and posterior ones are emergent. Thus smoothening of central ribs could effectively decrease friction. It should be remembered that only the central ribs smoothen in *Prosodacnomya*, while anterior and posterior regions remain ribbed similarly to various *Lymnocardium* spp.

In a branching event, *Lymnocardium vicinum* (Fuchs 1870), characterized by sharp, high central ribs (Fig. 4I), split off from the *L. decorum*

lineage. This species shared its environment with a number of other cardiids, in a sublittoral setting, while *L. decorum* lived in much shallower, marginal parts of the lake, typically as the only cardiid in its associations. The morphological difference of the two forms probably reflects diverging requirements imposed by their respective environments.

The mostly endorheic Pannonian Lake underwent frequent and abrupt changes of water level, documented by the frequent changes in facies of shallow water deposits, and resulting in drifts of shorelines (cf. chapter 'Localities'). These changes were seasonal or multiannual, in either case they reflected variations in water balance. On the other hand, tides must have been negligible in the lake.

Marked and fast replacements of shorelines on flat shores can be fatal to a great number of littoral organisms. Under such conditions ploughing might be an effective escape strategy, in contrast to digging which might even be dangerous during extended dry periods. Evidently in deeper waters, for instance for *Lymnocardium vicinum*, this factor has had only slight or no importance.

Spatial and temporal characteristics of the evolution

From scattered data we may conclude that the evolution of *Prosodacnomya* took place in a uniform way along the shoreline of the Pannonian Lake. Though we can not prove rigorously that transformations were coeval in all places, it seems that the evolution was lakewide, anagenetic. Peripheral isolates, if they existed at all, played a limited role in the process.

As has been stated in the stratigraphic part, the pace of the evolutionary process can be estimated only roughly. The estimated time span of the process is between one and three million years. Within this span no major change in the pace is observable, but the available data do not permit a detailed analysis of the evolution as a function of geological time.

Further fate of the lineage

Prosodacnomya did not die out with *P. vutskitsi*. *Prosodacna vodopici* (Brusina 1902) may be regarded as a further step in the evolution, restricted to a small area in northern Serbia and Croatia where the last vestiges of the Pannonian Lake might have been located. *Prosodacna* species of the late Pontian and Pliocene of the Dacian and Euxinian basins are also probable descendants of *Prosodacnomya* (Andreescu 1977), which, possibly by a temporary overflow of the Pannonian Lake, could emigrate and survive the final desiccation of the lake. Another genus, *Eupatorina* (= *Pseudoprosodacna*) is probably also closely related to the studied genera, possibly having been derived from a branching of *Prosodacnomya* in the Dacian or Euxinian lakes.

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Összefoglalás

Tavi szívkagylók (Cardiidae) folyamatos fejlődése a Pannon-tóban

A késő miocénben, a Pannon-tóban gazdag endemikus puhatestű fauna fejlődött, mintegy 5-6 millió éven át. A fauna részben édesvízi eredetű, részben a szarmata tengerből származik.

Egy, a Cardiidae családhoz tartozó alaksort vizsgáltunk, mely a *Lymnocardium decorum ponticum* alfajtól a *Prosodacnomya vutskitsi* fajhoz vezetett. A *Prosodacnomya* és a *Lymnocardium* nemzetségeket külön alcsaládba sorolják.

Hét biometriai jellemzőt vizsgáltunk. A fejlődés során a teknő búbja fokozatosan előbbre tolódott, a kagylók magasabbak és szélesebbek, gömbölyűbbek lettek. A legfeltűnőbb változás azonban a középső mező bordáinak elsímulása.

Különböző módszerek (radiometria, mágnesrétegtan, emlősrétegtan) adatai alapján megbecsültük a fejlődés időtartamát: ez egy és három millió év között volt.

A fejlődés fokozatos, anagenetikus jellegű volt. Egyes populációkban olyan ökofenotipikus változásokat mutattunk ki, melyek jellege az evolúciós változásokhoz hasonló volt: az egyénfejlődés során a bordák magassága többszörösen változott.

A teknők síma felszíne valószínűleg elősegítette a vízszintes mozgást (szántást), míg a beásás valószínűleg veszítette a jelentőségéből. A Pannon-tó hosszú ideig lefolyástalan volt, tehát a víz szintjét a vízmérleg határozta meg. Így az éghajlatingadozások hatására a partvonal gyakran eltolódott, ennek bizonyítéka a sekélyvízi összletek gyakran változó fáciese. A partvonal-eltolódások ellen a gyors szántás hatásos menekülési stratégia lehetett.

Streszczenie

W basenie międzykarpackim istniało w późnym miocenie przez 5-6 milionów lat wielkie jezioro z bogatą fauną małczaków o pochodzeniu morskim (sarmackim) i słodkowodnym, która podlegała endemicznej ewolucji.

Przedmiotem szczegółowych biometrycznych badań przedstawionych w niniejszym artykule była ewolucja małżów z rodziny Cardiidae począwszy od *Lymnocardium decorum ponticum* do *Prosodacnomya vutskitsi*. Rodzaje *Lymnocardium* i *Prosodacnomya* zaliczane są do dwu różnych podrodzin. W trakcie ewolucji wierzchołek muszli przesunął się stopniowo ku przodowi, a muszle stawały się coraz wyższe i grubsze. Najbardziej jednak

uderzająca zmiana polegała na spłaszczeniu i zaniku żeberk środkowego pola muszli.

Dane radiometrii i magnetostratygrafii w powiązaniu z biostratygrafią opartą na ssakach wskazują, że ewolucja od *L. d. ponticum* do *P. vutskitsi* trwała co najmniej 1, a nie więcej niż 3 miliony lat. Ewolucja miała charakter stopniowy, anagenetyczny. W pewnych populacjach zmienność ekofenotypowa była podobna do efektów przemian ewolucyjnych: wysokość żeberk kilkakrotnie zmieniała się w trakcie ontogenezy.

Gładka powierzchnia muszli prawdopodobnie ułatwiała horyzontalne przemieszczanie się (orkę) małża, natomiast zakopywanie w miarę przemian ewolucyjnych traciło zapewne na znaczeniu. Pannońskie jezioro długo miało charakter bezodpływowy, toteż zmieniający poziom wody regulowany był wyłącznie przez bilans wodny. Linia brzegowa często przesuwała się przy zmianach klimatu. Orka mogła więc być skuteczną strategią przetrwania w niestabilnych warunkach środowiskowych.

Ewolucja tej gałęzi sercówek kontynuowała się dalej w pozostałych z wielkiego jeziora pannońskiego mniejszych zbiornikach wodnych północnej Serbii i Chorwacji. Ostatnim jej przedstawicielem jest tam *Prosodacna vodopici*. Zapewne również inni przedstawiciele tego rodzaju z późnego pontu i pliocenu są potomkami pannońskiej linii ewolucyjnej.