Abstract

The Late Miocene dreissenids of Lake Pannon – a long existing eastern-central European lake – bear witness to two very different modes of life, which allowed these bivalves to successfully settle in what appears to be an inhospitable environment. One guild is restricted to the genera Mytilopsis Conrad, 1858 and Sinucongeria Lörenthey, 1894. These representatives are extreme r-strategists which tend to produce temporal boom-and-bust populations during ‘time windows’ of improved ecological conditions. These opportunities are interpreted here to correlate with cyclic shifts in the epilimnion/hypolimnion relation and the corresponding oxygenation of bottom waters, events which are probably triggered by low-frequency orbital forcing. The second guild is composed solely of Congeria Partsch, 1836. The paradox of the proliferation of a single species, characterised by extreme size and weight, in a muddy, oxygen-deficient lake environment avoided by nearly all other molluscs points to a ‘hidden’ mechanism not accessible to other species. We tentatively link this mechanism with chemosymbiosis. Functional morphology in interplay with a highly sulphidic, over-saturated interstitial water support an interpretation of the large Congeria subglobosa as a successful ‘H₂S pump’ model.

Keywords: Dreissenidae; molluscs; settlement strategies; chemosymbiosis; Lake Pannon; sequence stratigraphy

1. Introduction

Lake Pannon formed at about 11.5 Ma at the Sarmatian–Pannonian boundary in place of the relic Paratethys Sea (Rögl, 1998). The vast brackish to freshwater lake covered the Pannonian Basin complex – a Neogene back-arc basin type of eastern-central Europe (Royden and Horváth, 1988) encircled by the Alps, the Carpathians and the Dinarids. The aquatic mollusc fauna of the long existing Lake Pannon is characterised by a high percentage of endemisms and conspicuous radiations (Müller et al., 1999). The development of the fauna was controlled by the gradual freshening of the water body as well as by geodynamic processes, resulting in profound changes in lake geometry (Magyar et al., 1999a). Aside from the highly evolved lymnocardiids (Cardiidae, Bivalvia), especially the manifold dreissenids display a
remarkable evolution. The study of this group, composed of the endemic fossil genera *Congeria*, *Sinucongeria* and *Dreissenomya*, and the extant *Mytilopsis* and *Dreissena*, reaches back to the early 19th century, starting with Partsch (1836). Since then, numerous systematic contributions have enriched our knowledge on the Central and Eastern European dreissenid lineages. Palaeoecological studies, however, such as those of Korpás-Hódi (1983), Szilaj et al. (1999), Mező et al. (1999) or Vrsaljko (1999), are comparatively rare and strongly focus on synecological aspects. In this paper strategies and mechanisms are emphasised which allow byssally attached, more or less hardground-dependent dreissenids to settle the pelitic substratum of Lake Pannon. These settlement strategies seem to be correlated at least partly with lake level fluctuations which caused phases of oxygen-deficient bottom conditions and changing sediment loads. These extreme and short-lived environmental changes favoured opportunistic species, which are typical within the dreissenids. K-strategists, however, could hardly compete within this unfriendly environment without developing special adaptations.

2. Dating and lithology

In the Vienna Basin the investigated mass occurrences are confined to the Middle Pannonian *Mytilopsis czjzeki* Zone and the *Lymnocardium schedelianum* Subzone according to the current biozonation introduced by Magyar et al. (1999b).

![Fig. 1. Correlation of the Lake Pannon stratigraphy (biozone calibration to the absolute time and magnetostratigraphic scales according to Magyar et al., 1999b) with the standard chronostratigraphic, biostratigraphic and magnetostratigraphic zonations (calibrations of MN-Zones according to Steininger et al., 1996, of magnetostratigraphic chrons and M/NN-zones according to Berggren et al., 1995). The shaded area indicates the time slice during which the herein described dreissenid assemblages proliferated.](image)
(Fig. 1) *Spiniferites paradoxus* Biochron sensu Magyar et al., 1999a). This interval, characterised by the co-occurrence of *Congeria subglobosa* Partsch, 1836 and *Melanopsis vindobonensis* Fuchs in Fuchs and Karrer, 1870, was originally introduced as Vienna Basin ‘Zone E’ by Papp (1951a). Currently, pelitic sediment of this zone is well exposed in the Vienna Basin at the section Hennersdorf, which served as base for this study (Fig. 2). The magnetostratigraphic dating of the section Hennersdorf allowed its correlation with the chron C5n (Magyar et al., 1999b). The corresponding sequence is characterised throughout the Vienna Basin by predominantly pelitic sedimentation, reflected in thick clay deposits which were exploited in numerous brickyards along the western margin of the basin. Sandy intercalations are rare and seem to be restricted to the basal parts. Today, only the pit Hennersdorf close to Vösendorf 10 km south of Vienna (Austria) is still accessible, whereas all others are filled by groundwater. One of the already abandoned pits at Vösendorf was intensively studied by Papp and Thenius (1954), who described more than 150 taxa of vertebrates and invertebrates. The development at Hennersdorf corresponds fully to that described by Papp and Thenius (1954) from Vösendorf. The succession illustrated in Fig. 3 starts with a currently unexposed 2-m-thick green clay layer without macrofossils; this is followed by up to 1 m sand with a diverse but allochthonous fauna including numerous molluscs and vertebrate remains. Upwards follow a few metres of blue-grey clay with in situ clusters of *Congeria subglobosa* Partsch, 1836 characterising the present bottom of the opencast pit at Hennersdorf. The base of the next unit is marked by a remarkable 4-cm-thick bivalve coquina, termed herein He 4; it is dominated by disarticulated shells of *Mytilopsis czjzeki* (Hörnes, 1867) and *Congeria zsigmondyi* Halavats, 1883. This marker bed underlies an about 8-m-thick green-blue-grey clay and silty clay unit intercalated by numerous thin layers made up of masses of predominantly articulated *Simucongeria primiformis* (Papp, 1951b) and scattered, disarticulated *Lymnocardium schedelianum* (Partsch, 1831) shells. The top of the Hennersdorf section is represented by about 7–8 m yellow-grey clay and silt which is practically barren of macrofossils except for a marker coquina bed (He 1) in

![Fig. 2. Geographic position of the studied section Hennersdorf in the Vienna Basin (Austria).](image-url)
its basal part. The He 1 bed is characterised by abundant *Mytilopsis spathulata* (Pantsch, 1836), *Melanopsis vindobonensis* and scattered *Congeria subglobosa* followed by various other melanopsids, dreissenids and lymnocardiids.

### 3. Palaeobiogeography

Although we deal here mainly with assemblages of the Vienna Basin, the remarkable dreissenid mass occurrences are not confined to this area, as indicated in **Fig. 4**. A similar mass occurrence of *Mytilopsis czjzeki* was documented by Jámbor et al. (1985) from the Dráva formation in the Balaton area (its shell outline is reminiscent of *Sinucongeria primiformis* and the two are often lumped together in the literature). There, the species is also extremely frequent in silty offshore deposits. The shells are still articulated and an appreciable transport from shallower settings can be excluded.

Korpás-Hódi (1983, 1985) also reported accumulations of *Mytilopsis czjzeki* from several localities in Hungary. She considered them as a constituent of the ‘*Congeria czjzeki–Paradacna abichi*’ association and of the ‘*Congeria banatica*’ association contributed additionally by *Congeria zsigmondyi*. As in the Vienna Basin, this assemblage is typically found in grey homogeneous clay and silt with traces of pyrite. The assemblage was interpreted as evidence for ploiohaline, nutrient-rich,
aphytal environments of the open lake at water depths between 15 and 60 m. From the northwestern Serbian Kolubara Basin, Stevanovic (1985a) reports mass occurrences of Mytilopsis czjzeki accompanied by abundant Congeria zsigmondyi; they stem from clays underlying sands bearing the index fossil Lymnocardium schedelianum. Sinucongeria primiformis is apparently also common in the basin. A quite similar occurrence – also with Lymnocardium schedelianum and in pelitic sediment – is documented by Skerlj (1985) from Slovenia. The typical Middle Pannonian (‘Serbian’) occurrence near Karagaca (SSE Belgrade) was originally documented by Pavlovic (1928). The faunal assemblages redescribed by Stevanovic (1985c) with Congeria subglobosa, C. zsigmondyi, Mytilopsis spathulata, M. czjzeki and also Sinucongeria? lithodomiformis highly resemble the studied one from Hennersdorf. Moreover, the corresponding assemblages are present in the adjacent Kreka Basin of NW Bosnia (Stevanovic, 1985b) as well as in the Eastern Slovakian Danube Basin (Fordinai, 1997). Finally, Marinescu (1985) cites a fauna of Congeria subglobosa, Congeria zsigmondyi and Mytilopsis czjzeki from ‘Zone E’ of the Romanian part of the Pannonian basin complex.

These assemblages are best and fully developed along the western and southern coasts of Lake Pannon (Fig. 4); the gap in the eastern part of the lake is probably related to a lack of available information. This indicates that the assemblages had a wide distribution throughout Lake Pannon. Thereby, Congeria subglobosa and Congeria zsigmondyi formed loose populations contrasting with the mass occurrences of the typical r-strategists Mytilopsis czjzeki and Sinucongeria primiformis. The mechanism which allowed these species repeatedly to settle the muddy bottom of the lake during the Middle Pannonian transgression in short-lived populations affected the entire lake ecosystem. This phenomenon cannot be explained by local conditions of the Vienna Basin.

4. Taxonomy and palaeoecology

The synoptic systematic presentations by Jeke-lius (1944) and Papp (1953) continue to serve as the foundation stones of our knowledge on the mollusc fauna of early Lake Pannon. More recently, the classification of the family Dreissenidae has been improved by Nuttall (1990), who introduced two subfamilies, i.e. Dreisseninae and Dreissenomyinae. The taxonomic concept applied in the present study follows that revision, if not noted otherwise. A comprehensive discussion of the herein mentioned taxonomic units – including synonymy, type species and taxonomic contents – is presented by Nuttall (1990).

4.1. Dreisseninae

The Dreisseninae comprise, in contrast to the Dreissenomyinae, typically byssate endobionts. They are represented by two modern genera, i.e. Mytilopsis and Dreissena. These are highly effective filter feeders that consume various kinds of seston. Both are documented to pass a planktrophic larval stage (Morton, 1969; Nuttall, 1990). Dreisseninae originated during Eocene times, probably from brackish Corbiculidae (Nuttall, 1990).

4.1.1. Mytilopsis

The genus Mytilopsis comprises the earliest representatives of Dreisseninae. It did not undergo major radiation until Miocene times. The initial important morphological diversification started in the Early Miocene (Kochansky-Devide and Sliskovic, 1978, 1981). The centre of origin was in the paralic to lacustrine system established on the peridinaric land forming the geographical barrier between the Paratethyan and Mediterranean regions (Rögl, 1998).

The subsequent, even more spectacular, radiation began in the Upper Miocene with the formation of Lake Pannon, which became established at the site of the finally isolated Central Paratethys Sea (Müller et al., 1999). Despite apparent homomorphic relationships between several taxa of both independent radiation events, it seems that the second Dreissenidae radiation again originated from a primitive Mytilopsis (Kochansky-Devide and Sliskovic, 1978; Nuttall, 1990). Hence, Mytilopsis gave rise in the Late Miocene not only
to modern *Dreissena* but also to the extinct Lake Pannon endemics *Congeria* and *Sinucongeria*.

The euryhaline *Mytilopsis*, in contrast to *Dreissena*, seems to comprise primarily brackish water taxa. Hence, the modern representatives inhabiting mangrove swamps of Western Africa tolerate salinities of up to 25% (Archambault-Guezou, 1976). According to ostracod data for the Lake Pannon *Congeria czjzeki* Zone, all herein discussed species could settle waters of 3–15% (Kovács et al., 1998).

4.1.2. *Dreissena*

Like the primitive mytiliform *Mytilopsis*, *Dreissena* is a byssate epibiont and typical r-strategist that massively colonises various primary and secondary hardgrounds. It developed from *Mytilopsis* by complete reduction of the apophysis, a protuberance of the septum acting as byssal/pedal retractor catchment (Nuttall, 1990).

In contrast to *Mytilopsis*, *Dreissena* is a typical inhabitant of fresh water riverine and lacustrine settings. Due to their role as natural hazards, *Dreissena polymorpha* (Pallas) and the quagga mussel *Dreissena bugensis* (Andrusov) are exceptionally well studied. These freshwater species tolerate only slightly brackish conditions. In their natural habitats they prefer salinities from 0.2–3.5% (Orlova et al., 1998, Liakhnovich et al., 1994), whereby some populations may tolerate levels up to 6.0%. Only the Caspian Sea representative *Dreissena rostriformis* (Deshayes) is apparently able to tolerate enhanced salinities, although values above 14% are lethal (Archambault-Guezou, 1976).

4.1.3. *Congeria*

*Congeria* is restricted by Nuttall (1990) to semi-epifaunal, byssate sediment recliners. The Middle Pannonian *Congeria subglobosa* represent its type species. The present study will demonstrate that it is a typical K-strategist. Nuttall (1990) was the first to point out the strange anomaly of the *Congeria* species within the dreissenid stock, reflected by unusually large and heavy shells: this feature is apparently restricted to the Lake Pannon representatives. The present study discusses this phenomenon in relation to chemosymbiosis.

All *Congeria* but especially its type species are characterised by an extremely thickened shell, which is a highly surprising feature for a mud recliner in an apparently oxygen- and nutrient-depleted environment. The most reliable explanation might be found in some kind of symbiosis with photo- or chemosynthetic bacteria providing the energy needed for such intensive mineralisation. Perhaps the installation of a symbiotic interaction will turn out to be the primary factor that led to the offshoot of the genus *Congeria*.

4.2. *Dreissenomyinae*

*Dreissenomyinae* are an endemic Paratethyan group of typically infaunal representatives that became extinct during Pliocene time. They are an Upper Miocene offshoot of primitive Dreisseninae, apparently related with the modioliform group including *Mytilopsis amygdalooides* and *M. czjzeki* (Papp, 1951b; Marinescu, 1977; Nuttall, 1990). The Middle Pannonian *Sinucongeria primiformis* stock represents its earliest representatives.

The *Dreissenomyinae* from the Macotian of the Dacian Basin have been recently shown to be not older than the Late Pannonian (Papaionopol et al., 1995; Magyar et al., 1999a).

The subfamily comprises only two genera, i.e. *Sinucongeria* and *Dreissenomya*, since Carinatoncegeria Stevanovic, 1990 with its type species *Congeria digitifera* Andrusov, 1897 is apparently not related (Vrsaljko and Sremac, 1999; Müller et al., 1999). They differ from typical Dreisseninae by a more or less well-developed dorsal shell margin. Moreover, a unique feature for *Dreissenomyinae* is the development of an infaunal mode of life of many species of *Sinucongeria* and *Dreissenomya* (Marinescu, 1977).

*Dreissenomya* and *Sinucongeria*, considered as subgenera of *Dreissenomya* by Marinescu (1977) and Nuttall (1990) are treated as genera in the present study. Both taxa are not only clearly morphologically defined, but developed adaptations to different modes of life. This treatment is fully consistent with the generic affiliation in other bivalve families (e.g. Pectinidae by Waller, 1991) and avoids the virtual monotypy state for the subfamily *Dreissenomyinae*.
4.2.1. Sinucongeria

The shell habitus as well as an integripalliate to slightly sinupalliate mantle scar in earliest Sinucongeria still coincides with modioliform Dreisseninae. Apparently, the first important morphological change in Sinucongeria appeared in the Late Pannonian with the rise of typical sinupalliate and infaunal forms. Accordingly, a shallow infaunal way of life which is characteristic of more highly evolved Sinucongeria did not develop before the Late Pannonian. Indeed, the present study provides clear evidence that the Middle Pannonian Sinucongeria primiformis was an epibiontic r-stratigist that was ecologically still close to primitive dreissenids.

4.2.2. Dreissenomya

Dreissenomya displays reduction of a characteristic dreissenid feature: the septum that is a ledge spanning the anterior interior shell margins, serving for anterior adductor and pedal/byssal retractor attachment. It is deeply sinupalliate already within the earliest representatives (Marinescu, 1977; Nevesskaya et al., 1993), pointing clearly to a deep infaunal way of life. It is stronger laterally compressed, less dorsally pointed and principally more thin-shelled than Sinucongeria.

Dreissenomya is most probably an offshoot of a primitive Sinucongeria, although the timing of its initiation is obscure. The presence of its earliest representatives (Sinucongeria zujovici and

Fig. 5. A ‘H2S pump’ candidate – Congeria subglobosa from the Pannonian stage type area (Vösendorf environ, ‘Zone E’, Middle Pannonian). (1) Ventral view of an articulated specimen from Hennersdorf included into a pyrite concretion; longitudinal axis (l.a.) = 81 mm. (2) Articulated specimen from the clay-pit S Leobersdorf; l.a. = 81 mm, ventral view showing the byssal/pedal gap (compare text). (3) Left valve from Vösendorf; l.a. = 62 mm; (a) exterior view. (4) Right valve from Vösendorf; l.a. = 70 mm; (a) interior view showing the central longitudinal ridge (compare text); (b) view perpendicular to posterior adductor insertion. (5) Right valve from Vösendorf showing extremely thickened ventral area; l.a. = 68 mm.
S. unionides) in the Middle Pannonian sediments is not confirmed reliably (Marinescu, 1977; Stevanovic, 1990).

5. Dreissenid assemblages

All herein studied bivalves are, at least as juveniles, byssally attached epibionts. The offshore environment of Lake Pannon, which is dominated by muddy bottoms of clay and silt devoid of pebbles and clasts, is a poor base for byssate bivalves. Nevertheless, the mass occurrences document the ability of some species to compete for the sparsely available hardsubstrata. The gregarious occupation cannot be related to the utilisation of micro-habitats, which were quite rare due to the uniform bottom conditions of the vast lake. Four types of epifaunal settlement strategies can be documented from the offshore clays of the Middle Pannonian. These can be defined as mixed gregarious (1 type), monospecific gregarious (2 types), and monospecific patchy (1 type) settlement. Two species represent the monospecific patchy settlement type: Congeria subglobosa and Mytilopsis spathulata. Both managed to form small clusters or nests on the muddy bottom but applied quite different strategies.

5.1. Congeria subglobosa – monospecific patchy assemblages

In the basal part of the clay pit, the large-sized, robust Congeria subglobosa (Fig. 5) is frequently
found in situ with valves articulated and the byssal/pedal gap pointing downward. It usually forms small, monospecific clusters of few specimens (3–5 individuals; Fig. 13b). Although closely adjoining, they usually do not touch each other, but are several cm apart. The distribution of these accumulations shows no obvious pattern. However, the specimens are usually fully grown and thus these accumulations are interpreted as small populations which achieved the adult stage. Catastrophic collapses of multi-generation populations, including juveniles, are completely missing in these layers.

5.2. Mytilopsis spathulata – monospecific patchy assemblage

*Mytilopsis spathulata*, a medium-sized, elongated bivalve (Fig. 6) was a byssally attached epibiont which, in contrast to *Congeria subglobosa*, was unable to adapt to soft bottom conditions throughout its life. It thus depended on hard bottom elements on the muddy substratum, specifically the valves of *Congeria subglobosa*. In the lowermost part of the investigated section, valves of the large *Congeria* in convex-side-down position are often settled by clumps of 7–35 *Mytilopsis spathulata*. The densely stacked pattern of the colony is still preserved in situ (Fig. 6, 3–5). The attachment is restricted to the inner side of the shell.

5.3. Sinucongeria primiformis – monospecific gregarious assemblage

This assemblage type (Fig. 7) is typical in the monotonous pelitic unit above the He 4 layer and developed at least 18 times within a 6-m-thick unit. The small-sized, elongated *Sinucongeria primiformis* forms a moderately dense pavement of only partly contacting individuals (Figs. 8 and 13a). Most specimens are articulated; fragmenta-
tion is low. Only few other mollusc species co-
occurs in this assemblage, such as Lymnocardium
schedelianum and Lymnocardium brunnense.

5.4. Congeria zsigmondyi/Mytilopsis czjzeki—
mixed gregarious assemblage

This assemblage (Fig. 9) is restricted at Hen-
nersdorf to a single, widespread and very charac-
teristic layer (He 4 in Fig. 3). It forms a con-
spicuous boundary in the pelitic sediment and is
therefore often outcropped despite the highly in-
dustrialised exploitation method. In detail this
only 4-cm-thick layer reveals a multi-phase histo-
ry (Fig. 10). It overlies monotonous darkgreen-
grey clay with the already described Congeria sub-
globosa clusters. The lower boundary is indicated
by an indistinct relief formed by a coquina of few-
mm-broad fragments of thin-shelled bivalves.
Lymnocardiid fragments and unidentifiable thin-
shelled dreissenids constitute this shell bed. The
underlying 3–5 cm clay displays distinct bioturba-
tion of shell hash-filled burrows. Towards the top
this dense, component-supported coquina be-
comes slightly looser and also bears well-pre-
served but disarticulated shells of Mytilopsis czje-
iki floating within the shell hash. The approxi-
mately 1-cm-thick uppermost part is char-
acterised by the occurrence of numerous disarticu-
lated, unfractured shells of Congeria zsigmondyi.
Congeria firmocarinata is also common but less
frequent; subordinate Mytilopsis czjzeki co-oc-
curs. This coquina ceases abruptly and is overlain
by 8 cm of darkgreen clay with few scattered
specimens of Congeria firmocarinata and Congeria
zsigmondyi floating in the pelitic sediment. These
specimens are usually almost articulated (both
valves are found connected or very close to each
other) but are never in life position. Upsection
follows the first layer of Sinucongeria primiformis,
indicating the beginning of another cycle.

6. Discussion

6.1. Strategies of settlement

6.1.1. Congeria subglobosa—the advantage of the
‘H₂S pump’

The mode of life of Congeria subglobosa has
Fig. 9. Representatives of the ‘Mytilopsis czjzeki/Congeria zsigmondyi’ gregarious assemblage from the Middle Pannonian (‘Zone E’) of the southern Vienna Basin. (1) C. zsigmondyi accumulation from Mannersdorf a.d. Leitha; l.a. = 57 mm, orthogonal view. (2) Right valve of C. zsigmondyi from Regelsbrunn a.d. Donau; l.a. = 32.5 mm; (a) exterior view; (b) interior view; (c) ventral view; (d) dorsal view. (3) Right valve of M. czjzeki from Regelsbrunn a.d. Donau; l.a. = 19 mm; (a) exterior view; (b) interior view; (c) detail of the septal area showing the spoon-like apophysis beneath the septum; (d) dorsal view; (e) anterior view; (f) ventral view.

Fig. 10. Detail of layer He 4 documenting a multi-phased origin of the coquina. See text for discussion.
been interpreted quite differently in the literature. Morton (1970) suggested a byssally attached, infaunal mode of life. Papp (1985) illustrated Congeria subglobosa as a byssally attached epifaunal species lying on the sediment surface. Finally, Nuttall (1990) reconstructed a byssally attached semi-infaunal mode of life, with short exhalant and inhalant siphons positioned on the posterodorsal shell margin. However, considering the soft body morphology of modern dreissenids and the position of posterior muscle and mantle catchments in Congeria subglobosa, a much more reliable interpretation is a position of the inhalant siphon along the posteroventral margin and a position of the exhalant siphon at the most posterior part of the posterodorsal margin (Fig. 11). Such siphonal positions exclude an infaunal way of life. The byssal/pedal gap is well developed, thus the shell was always open toward the bottom sediment, forming a considerable loop of up to 22 mm length and up to 11 mm width. Such a huge ‘pseudo-bysal gap’ would have meant excessive byssal attachment and is in harsh contrast to a muddy sediment without pebbles, sand grains or secondary hardgrounds. This discrepancy clearly indicates that this derived byssal gap has to be put in the perspective of another functional morphology.

The anterodorsal shell area in Congeria subglobosa is distinctly broadened and slightly concave, with its maximum concavity culminating in the byssal gap. This area of the shell is commonly extremely thickened in adult individuals, reminiscent of some kind of ‘anchor mechanism’ providing the animal with stability by the low position of the balance point. This enhanced the weight, and the enlarged surface area of the shell part in contact with the sediment surface significantly improved the stable position. The species was obviously excellently adapted for sediment reclining. Thus, after the initial byssally attached juvenile stage, the attachment became inconsequential for the large, heavy adults. A semi-infaunal mode of life might have arisen due to sedimentation. This resulted in a partly buried stage by passive coverage with suspended material and could have been promoted by passive sinking of heavy shells into the water-saturated bottom sediment. Both mechanisms would also explain the typical, articulated preservation of many Congeria subglobosa nests.

The preservation mode and the pelitic sediment suggest very calm conditions on the lake bottom during formation of Congeria clusters. Rarely, infaunal lymnocardiids co-occur, but all other epifaunal elements are absent. Note that the Mytilopsis spathulata colonies in Congeria subglobosa shells, as described below, are absent in the layers with in situ Congeria subglobosa. Moreover, the shells are often enclosed by pyrite concretions, indicating oxygen-depleted environments, which favoured the accumulation of sulphides in the sediment. Despite this rather unfriendly environment, the high number of heavy, full-grown individuals shows that Congeria subglobosa flourished and was optimally adapted to this kind of habitat. The hypertrophied shell points to an adequate amount of available energy that was used for mineralisation. Moreover, it appears paradoxical that the development of hypertrophied, heavy shells disagrees with ‘the light-weight paradigm of a mud floater that faces the danger of sinking into a soupy sediment’ (Savazzi, 1985; Seilacher, 1990). Ancestors of the species within the ‘subglobosae lineage’ sensu Papp (1985) display prerequisites concerning the overall shape but are distinctly more fragile. Therefore, the increase in shell thickness seems to be an adaptive feature of Congeria subglobosa coinciding with a switch.

Fig. 11. Reconstruction of the anatomy and mode of life of Congeria subglobosa. The internal organisation is modified after Yonge and Campbell (1968) for the Recent Dreissena polymorpha.
Hypertrophied bivalve shells are commonly explained as a result of symbiotic interaction with chemosynthetic micro-organisms (Seilacher, 1990). Since photosynthetic zooxanthellate algae have been discovered in the mantle margin of the giant tridacnids, similar processes have also been suspected for hypertrophied Mesozoic shallow-water bivalves like rudists and megalodonts. *Congeria* highly coincides with the shell form of some megalodonts, but this homeomorphy can be better explained by their adaptions to sediment reclining than by the same environmental requirements. Indeed, based on the sediment and biofacies analysis at Hennersdorf, *Congeria* was habituated to environments with low light content. A symbiosis with photosynthetic organisms is therefore unlikely. In contrast, by utilising reduced sulphur as an energy source the chemosynthetic symbiotic bacteria present in the tissue of many bivalve groups highly benefit from reduced, sulphide-rich sediment and dissolved sulphide from interstitial water (Taylor and Glover, 2000). Such symbiosis can distinctly influence bivalve growth, as shown by growth experiments with lucinids (Taylor and Glover, 2000) or by examples of the giant deep-sea representatives *Calyptogena* and *Bathymodiolus* (Gage and Tyler, 1991). Evidence is also available that extinct inoceramids – representing the largest bivalves ever known, with a maximal shell-length of 178 cm – harboured chemosynthetic symbionts (MacLeod and Hoppe, 1992, 1993).

The conspicuous interior morphology of *Congeria subglobosa* could be a result of body reorganisation characteristic of chemosymbiotic bivalves (Taylor and Glover, 2000). The most important problem in such groups is to separate the sulphide-rich water infiltrating from the sediment from the oxygen-bearing water inhaled by the siphon which is used for normal respiration (Reid, 1998). Hence, the anteroventral thickened portion of the shell, which coincides with the position of the hypothetically thickened, symbiont-bearing ctenidia, is clearly separated from the posterodorsal shell region bearing the inhalant siphon. A distinct antimarginal ridge marks their boundary. Moreover, as the anteroventral gap can hardly be explained by the presence of a thick byssus bunch, a more reliable explanation would be its function for accessing the sulphide-rich interstitial water from the bottom sediment. The apparent load of the heavy, widened anteroventral shell part onto the sediment could effect the isostatic rise of such water into the shell cavity. The foot might have served as a regulator for the contact with the sulfidic water, which would have been harmful if admitted into the shell interior in uncontrolled amounts. A corresponding process has been termed by Seilacher (1990) the ‘H$_2$S pump’ model.

Savazzi (2001) has emphasised the difficulties of recognising chemosymbiosis in fossil bivalves. He concluded that no evidence for chemosymbiosis is available except for a specific ichnofossil, produced by the probing bivalve foot (e.g. Zuschin et al., 2001). Nevertheless, Savazzi (2001) predicted that careful analysis might reveal instances of chemosymbiosis among fossil bivalves. Indeed, a more or less synchronous study by Taylor and Glover (2000) presented such data. The latter authors investigated Recent and fossil lucinids and concluded that ‘the most convincing evidence for the presence of chemosymbiosis may come from the morphology of the shell and preserved life positions...’. The chemosymbiont-bearing lucinids possess a so-called mantle gill organ, that is a pallial blood vessel, impressed into the shell interior and striking along the interior side of the mantle impression. A corresponding line of claw-like impressions is also visible in the investigated specimens of *Congeria subglobosa*. Note, however, that in contrast to lucinids the inhalant siphon in Recent dreissenids is placed posteriorly. Therefore, among other discussed morphological features especially the large size suspects an additional source of energy aside from suspension feeding enabling such massive shells mineralisation.

In conclusion, *Congeria subglobosa* – in contrast to other herein described dreissenids – shows all features of a typical, highly adapted K-strategist which managed to settle otherwise poorly inhabited lake environments. A hypothetical but unproven explanation for the success of *Congeria*
subglobosa in settling muddy and oxygen-depleted bottoms of Lake Pannon might be found in chemosymbiosis.

6.1.2. Mytilopsis spathulata – a ‘legacy hunter’ profiting from the deceased

Within each Mytilopsis spathulata clump, adult and subadult specimens co-occur, although also colonies of more or less equal-sized specimens may occur. The settlement was thus multi-phased rather than a single event. Rarely, juveniles are found in these clumps within the gaping valves of adult Mytilopsis spathulata. This late stage of colonisation documents the decline of settlement space and indicates the final phase before the breakdown of the spatially restricted colony. Colonisation was clearly limited only by space, whilst food resources and sedimentation were not the controlling factors. Mytilopsis spathulata is never found attached to the external surface of Congeria subglobosa or any other molluscs. This might be explained by the preference of the juveniles to settle in protected cavities as offered by the shells of Congeria subglobosa and rarely by apertures of the gastropod Melanopsis.

Although this type of colonisation is confined to occurrences of valves of Congeria subglobosa, there is no interference of competition between these species. Other shells, e.g. lymnocardiids or conspecific specimens, probably did not offer the stability of the heavy and deeply concave Congeria subglobosa shells. Nonetheless, Mytilopsis spathulata is never associated with in situ Congeria subglobosa nests and seems to have avoided this slightly deeper, less agitated and oxygen-depleted habitat. The ecological range of Congeria subglobosa was clearly broader than that of Mytilopsis spathulata, which did not penetrate as far offshore as C. subglobosa. This settlement of Mytilopsis spathulata is unknown from Congeria zsigmondyi and Congeria firmocarianta shells. Overall, Congeria species, in contrast to Mytilopsis, seem to have been adapted to rather low oxygenation and thus flourished during the rapid transgression documented in the lower part of the TST of the section Hennersdorf. During the probably even less aerated conditions of the early HST at the top of the section, Congeria subglobosa is the only species which is rarely found in life position above the He 1 layer.

6.1.3. Sinucongeria primiformis – boom and bust

The analysis of the size distribution within the shell pavements strongly suggests that most individuals represent fully grown specimens, whereas juveniles are very rare (Fig. 12). This fact and the negligible thickness indicate that the shell beds document single populations which reached the adult stage before their final collapse. This interpretation predicts only sporadically suitable conditions for settlement, because longer periods of favourable conditions would result in the formation of thick shell beds contributed by several populations. Therefore, the pavements are considered to represent more or less census assemblages as defined by Kidwell and Bosence (1991). Census assemblages, however, might be expected to produce polymodal size frequency curves due to the mixture of two or more age groups if more than one population is represented (Tanabe and Arimura, 1987). The unimodal size distribution observed in the described assemblage seems to contradict this prediction. An explanation of this discrepancy might be that these dreissenids were extreme r-strategists – ‘exploitive opportunists’ sensu Levinton (1970) – which formed boom-and-bust populations (Kidwell, 1991) with low juvenile mortality.

Sinucongeria primiformis and Mytilopsis czjzeki most likely fed on planktonic algae and zooplankton. The breakdown of populations after the sudden blooms might also be related to declining

Fig. 12. Size distribution of Sinucongeria primiformis. The shells display a unimodal size distribution which ranges around the usual adult size of the species.
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**Phase of frequent settlement by** *Strucongeria primiformis* or *Mytilopsis sathulata* discrete pavesments

<table>
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<th>Cycles and Number of Pavements</th>
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**Phase of frequent settlement by** *Strucongeria primiformis* or *Mytilopsis sathulata* discrete pavesments

**Within habitat time-averaged assemblage Condensed Shellbed**

**Phase of** *Congeria subglobosa* settlement in situ nests; no discrete layers

**Not outcropped**

**Multi habitat mixed assemblage nearshore environment**

*Mytilopsis sathulata* nests in *Congeria subglobosa*
food resources. The excess of adults within the pavements might thus be explained by competition of already established animals with their larvae, hindering larval settlement on living colonies. As reported by Strayer et al. (1996), adult *Dreissena polymorpha* populations can outcompete their planktonic larvae for limited food resources. The lack of population refreshment by juveniles would ultimately result in a population decline. There is no sedimentological feedback within these pavements which points to accelerations or slowing of the sedimentation rates. Therefore, the preservation of the articulated shells is hardly explained by rapid burial but might rather be correlated with low oxygenation and low energy conditions in the hypolimnion of Lake Pannon. Indeed, shell cavities are commonly incrusted with pyrite or marcasite, pointing to anoxia as a reliable cause both for their sudden death as well as for the missing displacement through bioturbation.

6.1.4. *Congeria zsigmondyi/Mytilopsis czjzeki – shell hash as lucky chance*

The sedimentary succession reveals that the two dreissenid species did not initially settle the muddy substrate but attached to already deposited, densely packed shell fragments. These might either result from a thin-shelled, more or less autochthonous dreissenid pioneer species or might have been transported to the basin by wave energy and currents. The latter interpretation seems unlikely based on the taxonomic composition of the coquina. Generally, all transported, allochthonous dreissenid pioneer species or might have been transported to the basin by wave energy and currents. The latter interpretation seems unlikely based on the taxonomic composition of the coquina. Generally, all transported, allochthonous dreissenid pioneer species or might have been transported to the basin by wave energy and currents. The latter interpretation seems unlikely based on the taxonomic composition of the coquina. 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6.2. Sequence stratigraphy and dreissenid settlement

Another close-by, equivalent development is known from Hodonín (Czech Republic) in the northern Vienna Basin. Jiricek (1985) describes a threefold succession: the lower unit (‘E1’) comprises thin lignites in the base, followed by 11 m clay with *Lymnocardium schedelianum* and 5 m blue-green marl. The second unit (‘E2’) consists of 3.5 m yellowish marl and is poor in macrofossils. The top of the succession is formed by sand with coquinas consisting of *Mytilopsis spathulata*, *Congeria subglobosa* and *Unio atavus*. Kováč et al. (1998) include these units in their reconstruction of the Pannonian sequence stratigraphy of the Vienna Basin. According to that study, the basal part of the succession represents a transgressive systems tract (TST) which passes into the low aerated conditions of a highstand systems tract (HST).
(HST) within the second unit. In basinal deposits, this sea-level rise during ‘Zone E’ culminates in dinoflagellate blooms and the deposition of clays enriched in *Spiniferites* close to the maximum flooding surface. Finally, the top unit of Hodonín (‘E3’) is correlated with a lowstand systems tract (LST).

The section Hennersdorf may best be correlated with the two basal units of Hodonín. The occurrence of the *Melanopsis–Congeria* shell bed in the very top of the section, followed by macrofossil-poor clay, agrees well with the basal HST of the second unit at Hodonín. In contrast, the sandy top unit of Hodonín (‘E3’; correlated with a LST) could not be detected in the current outcrop, which is truncated by Pleistocene gravel.

The remarkable distribution pattern of dreissenid bivalves on the muddy bottom of Lake Pannon during the Late Miocene is obviously triggered by the repeated but short-lived establishment of conditions favouring the sometimes even gregarious settlement by larvae. Nevertheless, the presented settlement types hardly co-occur, but rather seem to prove the ability of each species to settle very distinct habitats that are otherwise avoided by most other taxa. A rough succession of the *Mytilopsis spathulata > Congeria subglobosa > Mytilopsis czjzeki > Congeria zsigmondyi > Sinucongeria primiformis* assemblages can be documented as illustrated in Fig. 13. This succession is clearly linked to the rise of the lake level during a TST.

The initial transgressive impulse, documented in the basal-most part of the succession, led to the formation of thick coquinas and lignites in sandy sediment. The subsequent rapid transgression caused poorly oxidised conditions on the lake bottom coinciding with the sedimentation of dark clay. Most probably a well-developed hypolimnion established at that time. This nutrient- and oxygen-poor, barely agitated environment was successfully settled by very few lymnocardiids and by *Congeria subglobosa*, which probably utilised energy by chemosymbiosis.

A decrease in sediment input could account for the development of the shell hash in the basal part of the marker layer He 4 (Fig. 13c). This process might be quite similar to that described by Abbott (1997) as ‘Mid-Cycle Condensed Shellbed’ (MCS). These shell beds represent parautochthonous concentrations of shells and fragments during phases of reduced rates of terrigenous sediment accumulation; articulated bivalves are common, most taxa are preserved in a mud-rich matrix. Abbott (1997) recorded such MCS, which do not correspond to the maximum flooding surface, from upper transgressive systems tracts. Consequently, the following unit of clay with the typical *Sinucongeria primiformis* pavements is correlated with the upper TST. The spatial distribution of those pavements reveals a conspicuous pattern which seems to comprise four cycles of ‘pavement gathering’. Each cycle starts with a comparatively narrow-spaced succession of 2–3 pavements and displays a decrease in abundance towards the top. The next cycle is indicated with the onset of the next group of pavements. The four cycles bear 7, 5, 5, and 3 pavements (Fig. 13) and thus show a slight decrease in number upwards. These settlement phases seem to be linked to fluctuations in productivity and short-termed mixing of the hypolimnion. Sedimentation, however, did not significantly change during these episodes.

The top of the fourth cycle is poorly defined; the change of sediment colour from green-grey towards yellow-grey might indicate a boundary but could also result from post-Miocene oxidation of the sediment. The top unit, however, differs markedly in being nearly fossil free. Only few *Congeria subglobosa* settled the lower part of this unit. Oxygen-depleted bottom waters might have hampered any settlement by molluscs during the deposition of the pelite – an interpretation which fits well to the description of Kovác et al. (1998) concerning the low-aerated conditions during the HST at Hodonín. Hence, the thick shellbed (He 1) in the base of that unit at Hennersdorf might be a proper candidate for the maximum flooding surface (MFS).

6.3. Orbital forcing as a trigger for dreissenid settlement?

This sequence stratigraphical approach allows a very careful estimation of the absolute duration of the formation of the various units and cycles. The
duration of the *Lymnocardium schedelianum* Sub-zone is estimated to span approximately 1 my by Magyar et al., 1999b. About 0.8 my contribute to the more or less equivalent ‘zone E’ according to Kováč et al. (1998). As discussed above, the para-sequences preserved along the western margin of the Vienna Basin do not span the whole sequence, but represent the TST and only a part of the HST. Taking into account the asymmetry between the TST and the HST as indicated by Kováč et al. (1998), less than half of the time of the sequence can be attributed to the preserved units. Hence, a very rough estimation predicts a sediment accumulation of approximately 0.05 mm/yr for the 20-m-thick unit of Hennersdorf and Vösendorf during 0.4 my (for the compacted sediment!). This average sedimentation rate is quite reasonable compared to data from Lake Baikal, from where Colman et al. (1995) estimated $V = 5.1$ cm/ka.

Consequently, the duration for cycles b and c of the *Sinucongeria* pavement-bearing unit (Fig. 13) ranges about 28 ka and ca. 38 ka for cycle a. Despite the cautious nature of this estimation, the cycles could well be linked to high-frequency orbital forcing such as precession (21 kyr) or obliquity (41 kyr). Actually, the sedimentary cycles of the Late Miocene of the Pannonian Basin have already been linked to climatically driven relative lake-level changes in the Milankovitch frequency band by Juhász et al. (1997, 1999). Based on numerical cycle analysis and magnetostratigraphy of numerous boreholes of the Pannonian Basin in Hungary, Juhász et al. (1997) deduced three types of cycles in Pannonian sediments, i.e. $\sim 19$-ka, $\sim 50$-ka and $\sim 400$-ka cycles. Later, Juhász et al. (1999) refined the data and predicted 19-ka, 71-ka and 370-ka cycles which they related to precession, obliquity, and the longer period of eccentricity, respectively.

Thus, the settlement of the lake bottom by *Sinucongeria primiformis* did not occur randomly but followed periodic modifications that allowed the establishment of short-lived populations. Slight climatic changes related with these cycles might have caused cooler and/or more humid phases which favoured a repeated mixing of the hypolimnion with the epilimnion. The gradual decrease of humidity and/or the slight increase in surface water temperature during each cycle led to the re-establishment of rather stable, low-aerated or even oxygen-depleted hypolimnic conditions reflected in the scarceness of dreissenid pavements.

### 7. Conclusions

The described dreissenid palaeocommunities formed during the Pannonian ‘Zone E’ sensu Papp (1951a) or the *Spiniferites paradoxus* Biochron sensu Magyar et al. (1999a). At that time Lake Pannon attained its maximum areal extent, which can be roughly estimated at about 280 000 km$^2$. The rapid transgression seems to coincide with the establishment of oxygen-deficient muddy bottoms which provoked the development of especially adapted settlement strategies.

The family Dreissenidae successfully met the challenge by quite different modes, which all resulted in the massive distribution throughout Lake Pannon. The genera *Mytilopsis* and *Sinucongeria* turned out to be typical r-strategists which managed to settle even rather harsh habitats during short-lived events of improved ecological conditions. Thin shellbeds of *Sinucongeria* can be traced in contemporaneous outcrops across more than 800 m distance and seem to have covered enormous areas of the Vienna Basin, revealing them to be even more gregarious than most extant aquatic pest species such as *Dreissena polymorpha* or *Dreissena bugensis*.

The succession pattern of these boom-and-bust occurrences within the section Hennersdorf indicates that their formation was triggered by some kind of cyclicity. This cyclicity may be correlated best with low-frequency orbital forcing, which caused periodic changes in the epilimnion/hypolimnion relation in the offshore zone of the Vienna Basin. The climatic back-lash within each cycle was answered by the formation of a more stable hypolimnion with oxygen-depleted bottom conditions, which hindered *Mytilopsis* and *Sinucongeria* from settlement.

The second, more sophisticated, strategy is represented by *Congeria subglobosa* – the largest mollusc of Lake Pannon at that time. Both morphol-

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ology and environmental parameters strongly suggest that this strange bivalve utilised energy from chemosymbiosis. Its extreme byssal gap morphology and the interior shell morphology point to a highly adapted mode of life as a biological ‘H₂S pump’. This made the animal less dependent on environmental shifts than other dreissenids and would explain its wider spatial distribution.

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