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Late Pannonian Wetland Ecology of the Vienna Basin based on Molluscs and Lower Vertebrate Assemblages (Late Miocene, MN 9, Austria)

With 9 figs

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Abstract

With the beginning of the Late Pannonian, the long-lived Lake Pannon retreated from the Vienna Basin. A fluvial system, which already developed during the Early Pannonian in the Molasse Basin followed the receding shore. It crossed the basin from the NW towards the SE and established a vast floodplain within the flat basin. The deposits of its southern part are preserved as lignites, pelites and silty sand of the Neufeld Formation, outcropping at the Section Götzendorf/Sandberg. Mollusc assemblages and the herpetofauna allow the reconstruction of a floodplain structured by swift, oligotrophic rivulets accompanying the main channel. The giant salamander *Andrias*, the olm *Mioproteus* and the fresh water pearl mussel *Margaritifer*a inhabited these environments. Stagnant lakes and swamp forests developed on the interdistributary areas and were settled by newts, lake frogs, softshell turtles and a manifold planorbid, lymnaeid and rissooid gastropod fauna.

The wetlands, indicated by the marly deposits of the section Richardhof, differ in their more distal position along the slopes of the Alps. Their water supply is provided by drainage from the adjacent mountains. The closeness to the mountainous slopes is reflected in the occurrence of xerophile and/or calciphile gastropods and reptiles. In contrast, indices of fast-flowing lentic environments, such as typified by the Götzendorf fauna, are nearly absent.

The chosen time-slice comprises only faunas of the *Mytilopsis neumayri/Mytilopsis zahalkai* Zone and the upper part of the mammal zone MN 9, respectively. The slight stratigraphic difference of the faunas as indicted by the evolutionary levels of the smaller mammals probably reflects a diachronous development of wetlands in the Vienna Basin. Along the western basin margin, wetlands might have developed earlier than in the more central parts of the Vienna Basin.

Key words: Pannonian, *Mytilopsis neumayri/Mytilopsis zahalkai* Zone, paleoecology, fresh water, floodplain, Vienna Basin

Zusammenfassung

An der Wende zum späten Pannonium begann sich der Pannon See aus dem Wiener Becken zurückzuziehen. Ein Flusssystem dessen Bildung sich bereits im frühen Pannonium nachweisen lässt, folgte der zurückweichenden Uferzone aus dem Molasse Becken kommend. Der Fluss passierte das Wiener Becken in einer NW-SE-orientierten Linie und verließ das Becken über die Brucker Pforte in Richtung Pannonisches Becken. Im Wiener Becken bildeten sich ausgedehnte Feuchtgebiete. An der Lokalität Götzendorf/Sandberg repräsentieren Lignite, Pelite und siltige Sande der Neufeld Formation mit einer reichen Mollusken und Herpetofauna die Lebensräume dieser Flusslandschaften im südlichen Wiener Becken. Seitenarme des Hauptstroms mit rasch fließendem, oligotrophen Wasser erlaubten die Bildung großer Populationen der Flussperlmuschel *Margaritifera* und die Besiedelung durch den Riesensalamander *Andrias*. Stehende Gewässer in Altarmen und kleinen Seegebieten lassen sich durch Vergesellschaftungen aus Planorbiden, Lymnaeiden, Rissooiden, Molchen, Salamandern, Fröschen und Weichschildkröten nachweisen.

In etwas mehr distaler Position bildeten sich die Feuchtgebiete der Lokalität Richardhof. Ihre geographische Lage am Rand des Wiener Beckens lässt vermuten, dass die Ökosysteme durch Gewässer aus den angrenzenden Kalkalpen gespeist wurden, während der Einfluss vom Hauptstrom gering war. Aufgrund des Einzuggebietes und eventuell durch die Aktivität von Characeen war das Wasser deutlich kalkreicher und ermöglichte die Sedimentation von Mergeln. Die Nähe zu den Hängen der Alpen im Nordwesten drückt sich auch im Vorhandensein von xerophilen und/oder calciphilen Elementen in den Gastropoden- und Reptilienvergesellschaftungen aus.

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Die gewählte Zeitscheibe umfasst nur Fundstellen der *Mytilopsis neumayri/Mytilopsis zahalkai* Zone beziehungsweise der höheren Säugetierzone MN9. Geringe stratigraphische Unterschiede zwischen den Faunen vom Richardhof (älter) und Götzendorf (jünger), wie sie durch die unterschiedlichen Evolutionsniveaus der Säugetiervergesellschaftungen angedeutet werden, könnten auf eine leicht diachrone Entwicklung der Feuchtgebiete im Wiener Becken hinweisen. Entlang des Beckenrandes nahe der Alpen entstand ein Saum aus Feuchtgebieten ehe sich die Flusslandschaften im zentralen Teil des Beckens etablierten.

Schlüsselworte: Pannonium, *Mytilopsis neumayri/Mytilopsis zahalkai* Zone, Paläontologie, Flusssystem, Wiener Becken

Introduction

The final disruption of marine connections and the disintegration of the Eurasian Paratethys Sea into several repeatedly isolated basins led to the formation of Lake Pannon during the Late Miocene (Magyar et al. 1999a). Extensive fresh-water discharge into the Pannonian basins altered the composition of the water-body from a Late Sarmatian "mature", maybe hypersaline and calcium-oversaturated sea into a hyposaline brackish water environment. The endemic mollusc fauna of that lake is extraordinarily well documented by numerous systematic papers (e.g. Müller et al. 1999 and references therein), yielding an elaborated biostratigraphic concept (Magyar et al. 1999b; fig. 1).

Hence, geologists often associate the term Pannonian solely with the deposits of the vast European lake system that originated at the Middle Miocene/Late Miocene boundary from the land-locked Sarmatian Sea. This paper focuses on the wetlands which developed in the foreland of that lake in the area of the Vienna Basin.

Miocene Wetlands of the Vienna Basin

The Vienna Basin area experienced several episodes of wetland formation. The first one occurred during the Early Miocene Karpatian age prior to the tectonically driven development of the basin. At that time, a huge deltaic system which was fed from the south-west became established in the southern Vienna Basin. This system was bordered in the north by the Paratethys Sea. A marine ingression during the early Middle Miocene (Badenian), coinciding with the onset of the subsidence of the basin, drastically reduced most wetland environments. The sea covered large parts of the basin, and the few documented wetlands are confined to tectonically defined valleys along the Alpine shore (e.g. St. Veit/Tristing).

During the subsequent Sarmatian age, wetlands developed in the Molasse Basin, where the Paratethys Sea formed a narrow lough, and in the Eisenstadt Basin, where a deltaplain prograded from the southeast (Harzhauser & Kowalke 2002).

In the Vienna Basin, the cover by the Paratethys Sea prevented the formation of larger wetland-areas. Only during the sea level fall during the latest Sarmatian did the Vienna Basin become covered for the second time by a fluvial system along with its associated wetland habitats. According to unpublished 3D-seismic data of the OMV, meanders of a large river are still traceable in the deposits of the Upper Sarmatian in the Matzen area.

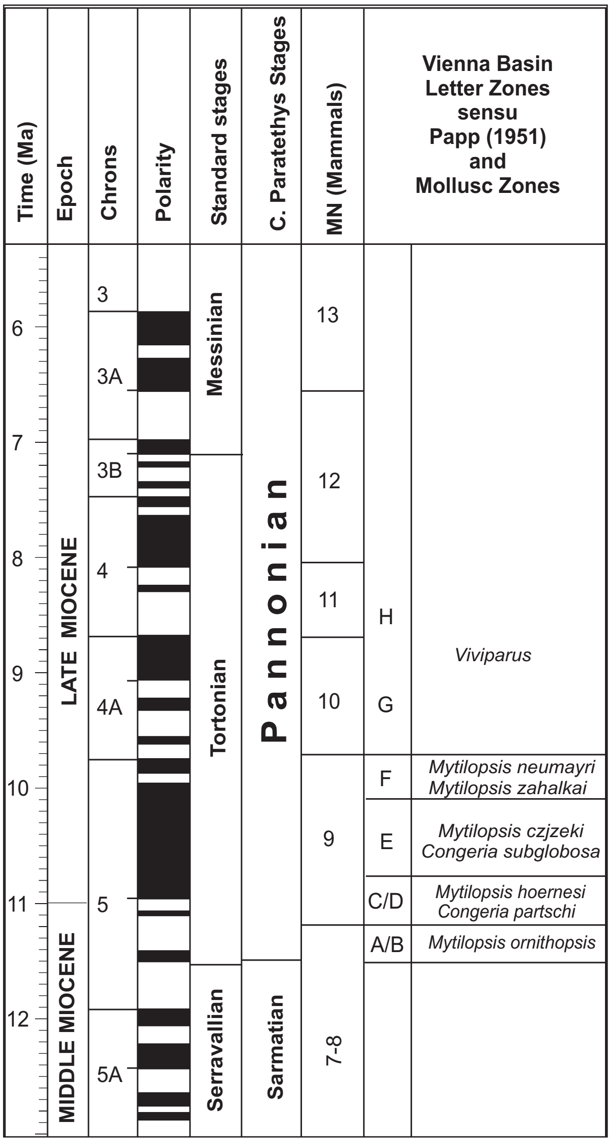

Fig. 1: Lake Pannon stratigraphy; modified after Magyar et al. (1999b) and Daxner-Höck (2001).

A major regression at the Sarmatian/Pannonian boundary triggered the progradation of several deltaic bodies along the entire margin of the Alps. The Vienna and the Styrian Basins became fringed by ecologically manifold wetlands. Plentiful data on the flora characterizing these Early Pannonian wetlands of Austria are provided by KOVAR-EDER (1988), KOVAR-EDER & KRAINER (1988, 1990), GROSS (1998), HARZHAUSER et al. 2003, KOVER-EDER et al. (2003) and others. The aquatic fauna of the rivers and streams, however, is poorly known even from the Early Pannonian. LUEGER (1980) reported on a *Psilunio atavus* assemblage from fluvial gravel in the Eisenstadt-Sopron Basin; HARZHAUSER et al. (2001) document an out-of-habitat assemblage consisting of various theodoxids, *Psilunio atavus* and *Tinnyea escheri vasarhelyii* which was shed into offshore environments of Lake Pannon. Finally, a similar assemblage comprising *Psilunio atavus, Tinnyea escheri* and *Melanopsis bouei* was reported by HARZHAUSER et al. (2003) from delta-plain deposits in the northern Vienna Basin.

The lake level rise during the late Early Pannonian (letter Zones D-E of PAPP 1951) mostly destroyed these wetlands, and Lake Pannon settings with the characteristic endemic mollusc fauna conquered the basin.

It took another 0.5 ma until the final retreat of Lake Pannon from the Vienna Basin allowed the last Miocene heyday of wetland formation. This phase, starting in the *Mytilopsis neumayri/Mytilopsis zahalkai* Zone (= letter Zone F of PAPP 1951), is reflected by the deposition of up to 90 m of lignites, pelites and sand united in the lower Neufeld Formation (BRIX 1989, ZORN 2000). Equivalent deposits are represented in the northern Vienna Basin by lignites and siliciclastics of the Cáry Formation (KOVAC et al. 1998) and the up to 300 m thick “Blaue Serie” (RÖGL & SUMMESBERGER 1978).

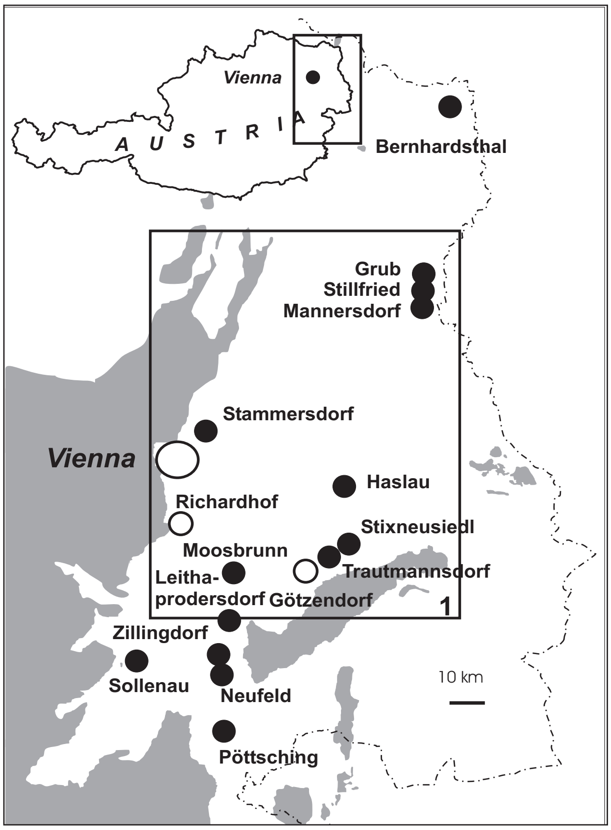

Fig. 2: Distribution of deposits of the Upper Pannonian *Mytilopsis neumayri/Mytilopsis zahalkai* Zone (= letter Zone F of PAPP 1951) in the southern Vienna Basin (based on surface outcrops, minings and wells).
[Insert 1 represents the sector illustrated in figure 9]

Although the sediments of the “post-lake-stage” cover considerable parts of the Vienna Basin and the Eisenstadt Sopron Basin (fig. 2), little information is available on the associated ecosystems. Data on Late Pannonian wetlands are usually “hidden” in papers focussing on taxonomy or stratigraphy (e.g. LUEGER 1981, RÖGL et al. 1993).

Two sections have been chosen to discuss the various Late Pannonian wetland habitats of the Vienna Basin. These are Götzendorf/Sandberg and Richardhof, both situated in the southern Vienna Basin. The geographic situation suggests that the fauna of Götzendorf reflects habitats close to the main channel of the river that crossed the basin. In contrast, the assemblages of the section Richardhof formed at the basins’ margin along the slopes of the Eastern Alps.

Götzendorf/Sandberg

E 016° 34’ 55”, N 48° 00’ 26”

Geological setting

The locality Sandberg near Götzendorf an der Leitha (in the vicinity of Mannersdorf am Leithagebirge) is an important geological site due to the occurrence of Miocene primates. It is positioned at the eastern margin of the southern Vienna Basin on top of a SW-NE trending block; this block is bordered by the Engelhartstetten fault system in the SE and towards the Vienna Basin by the Kopfstetten/Maria Ellend fault system in the NW. The deposits are part of the lower sequence of the Upper Pannonian Neufeld Formation, which is characterized by the occurrence of thick lignites (BRIX 1989, RÖGL et al. 1993, ZORN 2000).

The outcrop starts with a basal unit of silty clay with scattered lignites. It is overlain by about 5 m bedded clay, silt and fine sand with intercalations of cross-bedded silt. Upsection, an up to 100 cm thick layer of badly sorted sand, gravel and mud clasts follows, containing the studied mollusc and vertebrate fauna (fig. 3).

Laterally, the mollusc shells form loose coquinas as well as patches of densely stacked valves (fig. 4). The top of the Pannonian part of the section is formed by 7 m cross-bedded fine to medium sand with rare shells of *Mytilopsis neumayri*.

A more detailed introduction into the geology and paleontology of the section Götzendorf/Sandberg was given by RÖGL et al. (1993). PAPP (1951, 1953), SAUERZOPF (1953),

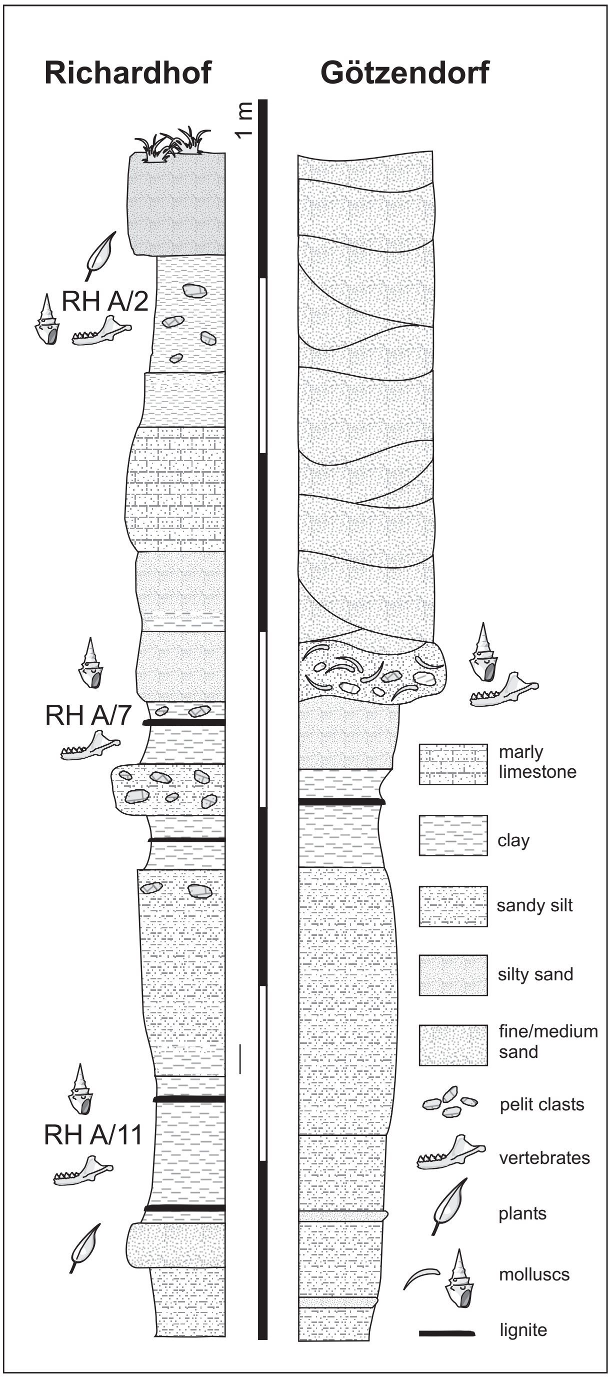

Fig. 3: Logs of the sections Richardhof and Götzendorf/Sandberg.

LUEGER (1981) and SCHULTZ in RÖGL et al. (1993) dealt with various systematic aspects of the mollusc fauna. The vertebrates of Götzendorf/Sandberg have been considered by BACHMAYER and MLYNARSKY (1977), BACHMAYER and WILSON (1984), BERNOR et al. (1993), M. BÖHME (2002), BRZOBOHATY (1992), DAXNER-HÖCK (1993, 1996), MIKLAS (2002), MLIKOVSKY (1991) and ZAPFE (1988a, 1988b, 1989, 1993).

Fig. 4: Excavated quadrant at the section Götzendorf/Sandberg exposing a *Margaritifera*-coquina.

Biostratigraphy

The mollusc fauna indicates a correlation with the *Mytilopsis neumayri/Mytilopsis zahalkai* Zone (= letter Zone F of PAPP 1951). This dating agrees fully with the mammal fauna, allowing a correlation with the upper part of the mammal zone MN9 (DAXNER-HÖCK 1993, DAXNER-HÖCK 1996). According to DAXNER-HÖCK (2001) the clay underlying the fossiliferous sand can be correlated with Chron C5n1r, pointing to an absolute age between 9.7 and 10 ma.

The fauna and its paleoecological feedback

The herein (re)studied material, stored in the collection of the NHMW, was collected during two excavation campaigns under the leadership of F. Bachmayer and H. Zapfe (1988–1990) and G. Daxner-Höck (1992). These excavations focused on the occurrence of the primate *Anapithecus hernyaki* and on biostratigraphically indicative smaller mammals. Thus, aside from the solely systematic papers, most studies were devoted to solving stratigraphical problems rather than discussing paleoecological aspects.

Molluscs: About 27 mollusc species were recorded at the locality Götzendorf/Sandberg. Five of these are bivalves, but only the fresh water pearl mussel *Margaritifera flabellatiformis* and the zebra mussel *Mytilopsis neumayri* dominate the spectrum (fig. 5). Gastropods are represented by 8 aquatic species and 13 terrestrial taxa. The latter, however, are subordinate in number. Several species are only recorded by very few specimens, despite the extraordinary intense collecting. The terrestrial assemblage displays a striking trend towards gigantism, with the giant clausiliid door snail *Milneedwardsia schultzi* and the bulbous helicids *Galactochilus leobersdorfensis* and *Cepaea bulla*. *Theodoxus postcrenulatus*, *Bithynia jurinaci* and *Melanopsis bouei sturii* are the most frequent aquatic gastropods in the sieve samples.

The preservation of the aquatic taxa is good; fragmentation occurred mainly secondarily during the washing procedure. In contrast, the terrestrial shells are often slightly damaged (e.g. apical whorls of *Milneedwardsia* are truncated); leaching of shells, however, is absent.

By contrast, the overlying up to 100 cm thick layer of badly sorted siliciclastics and mud clasts lacks any evidence of a limnic origination. This layer yields a conspicuous coquina dominated by large- sized valves of the unionid *Margaritifera flabellatiformis*. The bivalve, along-side disarticulated *Mytilopsis neumayri*, *Pisidium amnicum* and *Dreissena minima,* is frequently represented by articulated but gaping specimens. Nesting of isolated valves is also typical; no preference for a convex-side up position can be stated. The unit was interpreted by RÖGL et al. 1993 to be related to a single flooding. Using a stricter terminology, we interpret the layer as crevasse splay. During that event, fluvial elements such as *Margaritifera flabellatiformis* and *Theodoxus postcrenulatus* were mixed with shells, bones and clay clasts from the flooded marshland. Especially *Margaritifera flabellatiformis* seems to be highly significant for paleoecological interpretations. Its modern congener is the freshwater pearl mussel *Margaritifera margaritifera.* This species burrows into sandy substrates, often between boulders and pebbles. It is indicative for fast-flowing, oligotrophic, calcium-deficient rivers and streams. *Margaritifera margaritifera* requires cool, well-oxygenated water and shuns turbidity and hard water. Its glochidial stage attaches to the gills of salmonid fishes. Later, the juvenile mussel drops off and settles in the riverbed gravel. Highest mussel densities – with sometimes even piling specimens – are associated with shaded channels and low channel depths between 1–3 m (all data from BAUER 1988, GITTINGS et al. 1998, VALOVIRTA 1995, ZIUGANOV et al. 1994, HARSÁNYI 1999).

Fig. 5: Characteristic molluscs from Götzendorf/Sandberg (not to scale). 1 *Margaritifera flabellatiformis*, 2 *Theodoxus postcrenulatus*, 3 *Planorbarius grandis*, 4 *Stagnicola bouilleti*, 5 *Mytilopsis neumayri*, 6 *Milneedwardsia schultzi*

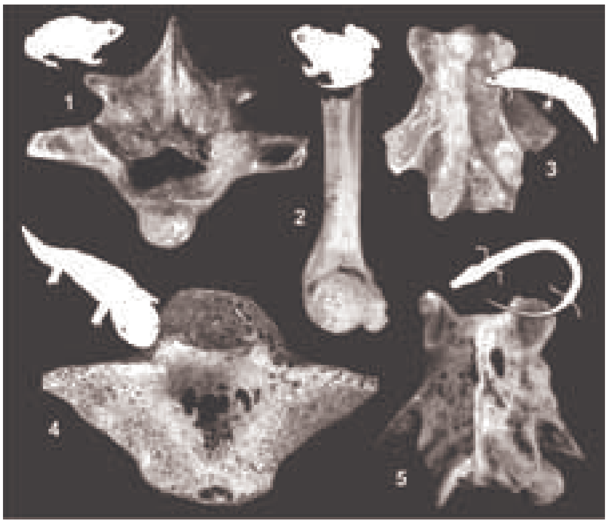

Fig. 6: Important taxa of the herpetofauna at Götzendorf/Sandberg (not to scale). 1 *Latonia gigantea* (trunk vertebra, dorsocranially), 2 *Rana* cf. *ridibunda* (right humerus, ventrally), 3 *Triturus roehrsi* (trunk vertebra, dorsally), 4 *Andrias scheuchzeri* (atlas, ventrally), 5 *Mioproteus caucasicus* (trunk vertebra, dorsally) [see MIKLAS (2002) for details]

Herpetofauna: Relating to the minimum number of individuals (MNI), amphibians represent the main part of the herpetofauna, which comprises only 6% Reptilia. Three species of Anura (56%) are mixed with the 4 species of Caudata (38%) (MIKLAS 2002). The giant discoglossid *Latonia gigantea* (MNI = 44%) is most frequent, followed by the proteid olm *Mioproteus caucasicus* (MNI = 31%). The Lake Frog *Rana* cf. *ridibunda* (MNI = 9%), the giant salamander *Andrias scheuchzeri* (MNI = 4%), the palaeobatrachid *Pliobatrachus* cf. *langhae* (MN I = 3%), and the newts *Chelotriton paradoxus* (MNI = 2%, related to the living *Tylototriton*) and *Triturus roehrsi* (MNI = 1%) are distinctly less abundant. Among the rather rare reptiles, only the Glass Lizard *Pseudopus pannonicus* (MNI = 2%) is slightly more frequent, whereas the terrapin *Trionyx* sp. (MN = 1%), the turtle *Testudo* sp. (MNI = 1%), an unidentified scleroglossid (MNI = 1%) and a colubrid snake (MNI = 1%) are subordinate within the assemblage.

All taxa are documented by disarticulated elements only.

Interpretation: RÖGL et al. (1993) reconstructed a limnic paleoenvironment for the clayey basal part, underlying the coquina-bearing layer. Intercalations of cross-bedded silt point to occasional fluvial ingressions by rivulets, introducing scattered shells of *Theodoxus postcrenulatus* and *Mytilopsis neumayri*.

Theodoxus postcrenulatus is the most abundant species among the gastropods, being documented by thousands of specimens. It was probably also a rather rheophilic species, based on the ecological requirements of modern European theodoxids such as *Theodoxus fluviatilis* or *Theodoxus danubialis*. These prefer agitated fluvial environments, where they cling to rocks and pebbles or settle higher energy shores of lakes (Lozek 1964, Wiese 1991, Ejka & Horsák 2002).

Among the amphibians, the olm *Mioproteus caucasicus* and the giant salamander *Andrias scheuchzeri* require similar lotic conditions. The frequent *Mioproteus caucasicus* indicates a well-flowing river (Dehm 1961). As emphasized by Estes & Darevsky (1977) this fossil species is associated with newts and frogs, pointing to aerial habitats as living space, whilst its blind, modern relative *Proteus anguineus* lives subterraneously. Correspondingly, larvae of *Andrias* need well-flowing, oxygenated water. Modern relatives of *Andrias scheuchzeri*, such as the Chinese *Andrias davidianus*, inhabit mountainous rivers with swift current, clear water and bottoms with rocky crevices (Westphal 1958). These requirements agree well with the fish fauna, which is interpreted by Böhme (2002) as a lotic fish assemblage with a high percentage of bottom dwellers such as catfishes.

Thus, the two predominant mollusc species and the most frequent amphibian species indicate a fast-flowing lotic environment with well-oxygenated and probably "soft" water. This evidence is strongly contrasted by several other taxa, which preferred lentic habitats. Among these, especially the giant *Planorbarius grandis*, the small-sized planorbids *Segmentina loczyi* and *Gyraulus goetzendorfensis* and the rare lymnaeid *Stagnicola bouilleti* point to swampy stagnant lakes. As stated by Lueger (1981), the terrestrial gastropods represent an assemblage of damp woods and lack species of dry and open habitats.

The herpetofauna, too, displays several taxa which shun swift riverine environments. The recent *Rana ridibunda* is frequently found in water meadows and prefers oxbow lakes for hibernation and reproduction (Günther 1990). The newt *Triturus roehrsi* also probably needed standing or slowly flowing water for reproduction during its aquatic stage. Pintar and Spolwind (1998), who studied coenoses of fishes and amphibians in Danubian water-meadows, reported *Triturus vulgaris* and *Rana ridibunda* as most frequent in oxbow lakes. Correspondingly, terrapins of the genus *Trionyx* occur in lentic environments or flowing, shallow freshwaters with sandy bottoms for burrowing.

Terrestrial wetlands are well documented by the occurrence of *Pliobatrachus, Chelotriton* and *Pseudopus. Pliobatrachus* is described by Hodrová (1982) associated with newts, frogs, and terrapins indicating damp environments. *Chelotriton paradoxus* is related to the Crocodile Newt *Tylototriton*, which inhabits mountainous, damp areas with dense vegetation (Estes 1981). The rare remains of snakes determined as Colubridae indet. might either represent the predominantly aquatic Natricinae or the terrestrial Colubrinae.

Only the herpetofauna, with fragments of turtles, yields elements of the hinterland, since Testudinidae prefer dry habitats (Deckert et al. 1991).

Therefore, the discrepancy expressed in a "solely" synoptic faunal list results from the mixing of faunas of at least two quite different paleoenvironments. Whilst the fluvial unionids and theodoxids are found in the splay deposit, most taxa preferring lentic environments derive from mud clasts, which are floating in the sandy sediment. Samples from isolated mud clasts comprise high numbers of *Bithynia jurinaci, Valvata obtusaeformis*, scattered *Emmericia canaliculata* and numerous small-sized planorbids and lymnaeids. A reworking of more or less synchronous limnic clay during the flooding is obvious.

There is also a striking disproportion within the small-sized mollusc fauna between aquatic and terrestrial taxa. Most of the microshells represent aquatic taxa such as *Bithynia jurinaci* and derive from the reworked clasts. In contrast, the composition of the terrestrial gastropod fauna is predominated by large-sized and rather thick-shelled taxa such as *Cepaea etelkae, Galactochilus leobersdorfensis, Tropidomphalus (Pseudochlorites) depressus* and *Milneedwardsia schultzi*. Small-sized vertiginids, gastrocoptids or carychiids are almost lacking and are negligible in numbers. This was already mentioned by Lueger (1981), who stressed some kind of taphonomic loss. A leaching of small shells, however, seems to be unlikely since none of the larger shells display traces of dissolution.

The overlying topunit of cross-bedded sand indicates the establishment of a well-agitated riverine system, partly eroding the basal overbank deposits.

The following list summarizes the molluscan, amphibian and reptile fauna from the section Götzendorf. Amphibians and their specific aquatic ecosystems are documented by Miklas (2002). Molluscs are listed according to the collection of the NHMW and data presented by Schultz in Rögl et al. (1993). A tentative affiliation with preferred environments is indicated for the molluscs, based on ecological requirements of modern relatives.

Mollusca

aquatic species

lotic environments

Margaritifera flabellatiformis (Grigorovits-Beresovski)
Mytilopsis neumayri (Andrusov)
[= *Congeria neumayri* in Rögl et al. 1993]
Mytilopsis zahalkai (Spalek)
[= *Congeria zahalkai* in Rögl et al. 1993]
Dreissena minima Lörenthey
Theodoxus postcrenulatus Papp
Melanopsis bouei sturii Fuchs

lentic environments
(mainly deriving from mud clasts)

Pisidium amnicum (Müller)
Valvata obtusaeformis Lörenthey
Bithynia jurinaci (Brusina)
Emmericia canaliculata Brusina
Stagnicola bouilleti (Michaud)
[=*Lymnaea* sp. in Rögl et al. 1993]
Gyraulus goetzendorfensis (Sauerzopf)
Segmentina loczyi (Lörenthey)
Planorbarius grandis (Halavats)

terrestrial species

wetlands and woodland

Milneedwardsia schultzi (Lueger)
Limax sp.
Archaeozonites (Pontaegopis) laticostatus Sandberger
Aegopinella reussi (Hörnes)
[=*Aegopinella orbicularis* in Rögl et al. 1993]
Leucochroopsis kleini (Klein)
Heilcigona wenzi (Klein)
Klikia (Apula) planispira Lueger
Klikia (Steklovia) magna Lueger
Cepaea bulla Lueger

taxa preferring open and
less moist terrestrial environments

Gastrocopta (Sinalbinula) ferdinandi (Andreae)
Galactochilus leobersdorfensis (Troll)
Tropidomphalus (Pseudochlorites) depressus Wenz
Cepaea etelkae (Halavats)

Amphibia

Caudata

Cryptobranchidae: *Andrias scheuchzeri* Holl
Proteidae: *Mioproteus caucasicus* Estes & Darevsky
Salamandridae: *Chelotriton paradoxus* Pomel
Triturus roehrsi Herre

Anura

Discoglossidae: *Latonia gigantea* (Lartet)
Palaeobatrachidae: *Pliobatrachus* cf. *langhae* Fejérváry
Ranidae: *Rana* cf. *ridibunda* (Pallas)

Reptilia

Testudines
Trionychidae: *Trionyx* sp.
Testudinidae: *Testudo* sp.
Scleroglossa: Scleroglossa indet.
Anguidae: *Pseudopus pannonicus* (Kormos)
Serpentes: Colubridae indet.

Discussion

The depositional area is interpreted to represent a Late Pannonian floodplain with floodplain lakes. A crevasse through the channel banks allowed a sand-laden splay to spread sheets of rapidly depositing sand across the flooded areas. Depending on current velocity, the intermixed shells formed densely stacked nests or loose coquinas. Limnic clay with abundant gastropods indicating a stagnant, swampy lake became reworked and re-deposited within the crevasse splay. In the same way, terrestrial gastropods, which inhabited the wetlands of the interdistributary area, became admixed in the overbank deposits. In terms of taphonomy, the coquina is therefore a multi-habitat, environmentally condensed assemblage (Kidwell & Bosence, 1991) yielding elements of various lentic, lotic and terrestrial wetland habitats. The crevasse splay deposit might indicate beginning shifts of a larger distributary channel, which finally established its course in the study area.

The palynological study by Draxler and Zetter (1993) fits well to these data. According to the pollen assemblage, the swampy lake was settled by floating leaved, rooted water chestnut *Trapa* and the submerged pond weed *Potamogeton.* The frequent remains of castorids identified by Daxner-Höck (1993) derive from the same setting. Water willows *(Decodon)* and the saw grass *Cladium* characterized the lakeside areas. These habitats have been settled by the darter *Anhinga* – described by Mlikovsky (1991) from Götzendorf – a piscivorous bird that prefers marshy sloughs of saw grass with clumps of willows. *Glyptostrobus*, *Nyssa* and *Taxodium* contributed the swamp forest flora. *Betula*, *Salix* and *Alnus* are documented from the adjacent bog wood associations.

Richardhof-Golfplatz

E 016° 16’ 08”, N 48° 03’ 23”

Geological setting

A thorough review of the geological literature of the section Richardhof is given by Harzhauser and Binder (in press). The section is positioned close to the western margin of the southern Vienna Basin on the Mödling block (Hamilton et al. 1990). There, Pannonian deposits occur along small fault zones as erosional relics lying already on Alpine units. Section Richardhof was logged during excavations by the Museum of Natural History Vienna in 2002. The artificial outcrop – now covered by a golf course – comprises an about 7 m thick section of clay, silty sand and marly limestone (fig. 3). The studied assemblages derive from 3 bulk samples taken in pelitic sediment; no distinct layers or accumulations of molluscs or vertebrate remains were observed.

Biostratigraphy

According to Gudrun Daxner-Höck (pers. comm.), the mammal assemblage of the samples Richardhof RH A/2 and RH A/7 allow a clear dating as mammal zone MN 9 (note that there are also slightly younger deposits containing faunas of the MN 10 at the section Richardhof-Wald mentioned by Daxner-Höck 1996). The evolutionary level of the mammal assemblages points to a stratigraphical position below the fauna from Götzendorf. Among the mollusc fauna, only the gastropod *Prososthenia sepulcralis*, is of biostratigraphic significance. It is known in the Vienna Basin only from the ecostratigraphic letter "zone" F corresponding to the *Mytilopsis neumayri/Mytilopsis zahalkai* Zone.

Fig. 7: Characteristic molluscs from Richardhof (not to scale). 1 Operculum of *Bithynia jurinaci*, 2 *Emmericia canaliculata,* 3 *Valvata helicoides*, 4 *Anisus krambergeri*, 5 *Vertigo callosa,* 6 *Carychium sandbergeri,* 7 *Acicula edlaueri,* 8 *Discus pleuradrus,* 9 *Acanthinula trochulus,* 10 *Truncatellina suprapontica* [see Harzhauser and Binder (in press) for details]

The fauna and its paleoecological feedback

Molluscs: Harzhauser and Binder (in press) describe 59 mollusc taxa from the section Richardhof. Hence, the fauna is the most diverse mollusc fauna known from zone MN 9 in the hinterland of Lake Pannon. The aquatic fauna (17 gastropods, 1 bivalve) predominates, whereas the more manifold terrestrial fauna with 41 taxa is poor in specimens. Only the herald snail *Carychium sandbergeri,* the land winkle *Pomatias conicum* and the helicids *Tropidomphalus (Pseudochlorites) richarzi* and *Cepaea etelkae* are quite abundant. Among the aquatic gastropods *Valvata helicoides* and the rissooids *Bithynia jurinaci* and *Emmericia canaliculata* are most important in numbers, followed by *Hydrobia pseudocornea.*

The preservation of the small-sized taxa is excellent (fig. 7); no leaching or abrasion was observed. In contrast, the large-sized, frequent helicids are usually found as fragments. This is partly related to sediment compaction, but usually the fragments are found isolated and the shells seem to have been broken prior to deposition.

Herpetofauna: The total fauna comprises 54% Anura, 33% Reptilia and 13% Allocaudata and Caudata. The high percentage of reptiles is a remarkable feature of the assemblage.

According to the minimum number of individuals (MNI), the discoglossid *Latonia gigantea* (MNI = 25%) predominates the spectrum, followed by the lizard *Lacerta* sp. (MNI = 19%) and the Real Frog *Rana* sp. (MNI = 17%). Other taxa (fig. 8) such as the Tree Frog *Hyla* cf. *arborea* (MNI = 8%), the Glass Lizard *Pseudopus pannonicus* (MNI = 6%), *Albanerpeton inexpectatum* (MNI = 6%) as a member of the fossil order Allocaudata, the proteid olm *Mioproteus caucasicus* (MNI = 4%), the spadefoot *Pelobates* sp. (MNI = 4%), and the newt *Triturus* sp. (MNI = 3%) are distinctly less frequent. Snakes are documented by Natricinae (MNI = 5%) and Colubrinae (MNI = 3%).

All vertebrate remains are disarticulated.

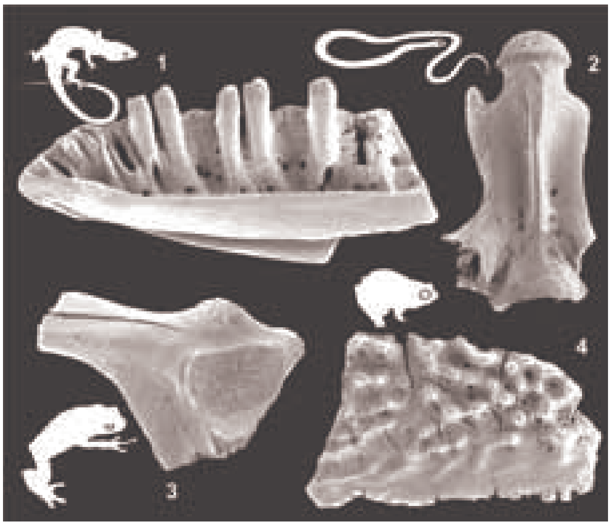

Fig. 8: Important taxa of the herpetofauna from the section Richardhof (not to scale). 1 *Lacerta* sp. (right dentary fragment, lingually), 2 *Natricinae* indet. (trunk vertebra, ventrally), 3 *Hyla* cf. *arborea* (left ilium, laterally), 4 *Pelobates* sp. (right maxillary, labially)

Interpretation: The fauna breaks down into three groups with quite different habitat requirements. The first, most frequent group, represented by aquatic taxa points to a predominantly lentic freshwater habitat with a well-developed phytal zone. Modern relatives of the common *Bithynia jurinaci* such as *Bithynia leachii* prefer vegetated lentic fresh water or may also settle slowly flowing water like *Bithynia tentaculata* (Fechter & Falkner 1989, Gittenberger et al. 1998). Furthermore, the dense populations of *Bithynia* offered a surplus supply of spawn that might have served as nourishment for various lymnaeids (Richter & Wächter 1999). The Recent counterpart of *Emmericia canaliculata* is *Emmericia patula*, which appears in carbonatic waters of wells in the northern Adriatic region (Fechter & Falkner 1989). Late Miocene and Pliocene representatives of *Emmericia* have been described by Esu et al. (2001) from lacustrine clays. Ambrosetti et al. (1995) report on a similar fauna from the Pliocene fossil forest Dunarobba in Umbria. Corresponding to the Richardhof assemblage, *Emmericia* is an associated element at the Italian section which is interpreted as a lacustrine environment with slowly moving or stagnant water containing *Prososthenia, Bithynia, Valvata, Pisidium* and *Melanopsis.* A poorly agitated, lentic environment with rich vegetation is also indicated by the diverse lymnaeid and planorbid fauna. *Aplexa hypnorum* is restricted to lakes and ponds; *Planorbarius corneus*, which is closely related to *Planorbarius mantelli*, prefers vegetated, lentic environments, and *Anisus septemgyratus*, which is highly reminiscent of *Anisus krambergeri*, settles ponds and swamps (Lozek 1964, Fechter & Falkner 1989). The modern analogue of *Valvata helicoides* seems to be represented by *Valvata cristata*, which inhabits vegetated ponds and lakes but appears also in temporarily drying wetlands (Lozek 1964, Gittenberger et al. 1998).

Among the documented reptiles, only the Natricinae are aquatic snakes; they swim and hunt mainly in standing but also in slowly flowing water.

The second group comprises terrestrial gastropods with preference for humid lakesides, other wetland habitats such as water meadows and woodland. These are represented in high numbers by *Carychium sandbergeri*, *Carychium berthae*, *Vertigo callosa*, *Zonitoides schaireri* and *Succinea* sp. among others. The adjacent woodland fauna is also well established with *Acicula edlaueri*, *Argna oppoliensis, Pseudoleacina eburnean, Acanthinula trochulus, Punctum propygmaeum, Discus pleuradrus, Semilimax intermedius, Tropidomphalus (Pseudochlorites) richarzi, Archaeozonites (Pontaegopis) laticostatus, Aegopinella reussi* and *Nesovitrea disciformis* (estimated from ecological requirements of modern congeners described by Lozek 1964, Fechter & Falkner 1989, Kerney et al. 1979). These habitats were settled by the anurans *Hyla* cf. *arborea* and *Pelobates* sp. The Common Tree Frog *Hyla arborea* lives climbing on bushes and trees near water bodies, and *Pelobates* burrows itself into sand along lakesides (Diesener & Reichholf 1996). Newts such as *Triturus* sp. were also bound to the lake and the adjacent wetland because they require standing or more rarely slowly flowing waters for reproduction.

The discoglossid *Latonia gigantea* is documented from various sections representing a broad range of paleohabitats. This frequent species is therefore classified as a ubiquist with minor habitat restrictions; its abundance, however, points to an occurrence close to the lake.

Finally, a smaller group of gastropod species suggests the existence of distinctly less damp and rather open areas such as rocks and dry meadows. Among this group, *Truncatellina suprapontica, Granaria schlosseri,* and *Vallonia subpulchella* are typical. The subterraneous *Cecilioides (Cecilioides) aciculella* and *Helicodiscus roemeri*, too, derive from the hinterland, where they avoided a high ground-water level. Among the herpetofauna, especially the abundant lizard *Lacerta* sp. correlates with this third group. Recent species of *Lacerta* can be found in very dry sun-exposed areas but shun environments completely devoid of vegetation (Arnold & Burton 1978). The Glass Lizard *Pseudopus pannonicus* prefers dense vegetation in dry environments but uses damp crevices to hide (Petzold 1971). Colubrinae snakes also prefer dry, vegetated settings, where they climb and hunt in trees and bushes. This group of snakes is rather independent from access to wetlands (Böhme 1993).

The following list summarizes the molluscan fauna identified by Harzhauser and Binder (in press). The herpetofauna was identified during the current study by the second author.

Mollusca

aquatic species

littoral aquatic species with unknown requirements or supposedly rather broad ecological range

Hydrobia pseudocornea (Brusina)
Melanopsis fuchsi Handmann
Melanopsis bouei sturii Fuchs
Prososthenia sepulcralis (Neumayr & Paul)

lentic environments

Pisidium personatum Malm
Bithynia jurinaci (Brusina)
Pseudamnicola nov. sp.
Emmericia canaliculata Brusina
Valvata helicoides Stolicka
Stagnicola bouilleti (Michaud)
Radix aff. *cucuronensis* (Fontannes)
Galba halavatsi Wenz
Aplexa cf. *subhypnorum* Gottschick
Planorbarius mantelli (Dunker)

Planorbarius thiollierei (Michaud)
Anisus krambergeri (Halaváts)
Anisus confusus Soós
Armiger subptychophorus (Halaváts)

terrestrial species

wetlands and woodland

Pomatias conicum (Klein)
Acicula edlaueri (Schlickum)
Carychium sandbergeri Handmann
Carychium berthae (Halaváts)
Argna oppoliensis (Andreae)
Succinea sp.
Acanthinula trochulus (Sandberger)
Vertigo(Vertigo) callosa Reuss
Vertigo (Vertilla) oecsensis (Halaváts)
Pseudoleacina eburnea (Klein)
Discus pleuradrus (Bourguignat)
Zonitoides schaireri Schlickum
Nesovitrea disciformis (Lueger)
Aegopinella reussi (HÖRNES)
Punctum propygmaeum (Andreae)
Milax sp.
Archaeozonites (Pontaegopis) laticostatus Sandberger
Vitrea procrystallina steinheimensis Gottschick
Semilimax intermedius (Reuss)
Limax spp.
Tropidomphalus (Pseudochlorites) richarzi (Schlosser)
Klikia (Klikia) trolli Lueger
Klikia (Apula) nov. sp.
Klikia (Apula) goniostoma (Sandberger)

taxa preferring open and dry terrestrial environments

Strobilops (Strobilops) pappi Schlickum
Strobilops (Strobilops) pachychila Soós
Vallonia subpulchella (Sandberger)
Granaria nov. sp.
Granaria schlosseri (COSSMANN).
Truncatellina suprapontica Wenz & Edlauer
Cecilioides (Cecilioides) aciculella (Sandberger)
Helicodiscus roemeri (Andreae)
Cepaea etelkae (Halaváts)

terrestrial species with unknown requirements

Negulus gracilis Gottschick & Wenz
Gastrocopta (Albinula) edlaueri WENZ
Gastrocopta (Albinula) acuminata (Klein)
Nordsieckia pontica Lueger
Macrogastra nov. sp.
Triptychia sp.
Janulus nov. sp.
Leiostyla (Leiostyla) austriaca (Wenz)

Amphibia

Allocaudata
Albanerpetontidae:
Albanerpeton inexpectatum Estes & Hoffstetter

Caudata
Proteidae: *Mioproteus caucasicus* Estes & Darevsky
Salamandridae: *Triturus* sp.

Anura
Discoglossidae: *Latonia gigantea* (Lartet)
Pelobatidae: *Pelobates* sp.
Hylidae: *Hyla* cf. *arborea* (Linné)
Ranidae: *Rana* sp.

Reptilia

Scleroglossa
Lacertidae: *Lacerta* sp.
Anguidae: *Pseudopus pannonicus* (Kormos)

Serpentes
Colubridae: Colubrinae indet.
Colubridae: Natricinae indet.

Discussion

Pure freshwater settings of a riparian lake with dense vegetation are reconstructed based on the diverse planorbid, lymnaeid, and rissooid gastropod fauna. The mollusc fauna and amphibians point to a well-developed zone of wetlands with water meadows and riparian woodland. Nevertheless, the rather xerophilic elements among the reptiles and gastropods also indicate close-by areas with dry and sunny conditions. This rapid facies succession is explained by the position of the riparian lake along the slopes of the Calcareous Alps. The limestones and dolostones of the Alpine units outcropping close to the lake offered optimal habitats for the calciphile gastropod *Granaria* and might have been populated by the lizard *Lacerta*. Finger (1998) discusses a similar setting for the fauna of the *Gyraulus kleini* Zone of the Steinheim Basin. She interpreted the assemblage comprising both humidity-indicators and species of rather dry environments to result from habitat mixing of species from the lakeside together with elements from the exposed slope of the Steinheim crater.

The absence of any riverine taxa such as *Psilunio atavus, Margaritifera flabellatiformis, Mytilopsis, Dreissena, Tinnyea* or theodoxids indicates very low influx from lotic environments. Furthermore, the absence of any typical Lake Pannon molluscs, adapted to the aberrant water chemistry of the long-lived lake, furnishes evidence that the wetlands along the margin of the Vienna Basin were already completely disconnected from Lake Pannon. The absence of a faunistic influence from Lake Pannon is also indicated by the brachyuran fauna. Dense populations of *Potamon (Pontipotamon) ibericum* settled the marginal freshwater lake – a species that is unknown from Lake Pannon.

No sedimentological analysis is available for the section Richardhof and therefore the origin of the freshwater marls is unclear. However, the water of the lentic environment seems to have had a high base content, which supported the development of calcareous marls. The $CaCO_3$ content could have derived from the adjoining and underlying limestone substrate provided by the Alpine units. Additionally, the recorded charophytes could have removed seston from the water and subsequently caused the marl formation that typically encrusts the stoneworts (OTSUKI & WETZEL 1972, TUCKER & WRIGHT 1992). Thus, calcium carbonate precipitation by characeans might have formed a shallow bench along the lake. Additionally, thermal springs, which are frequent in that area even today, could have influenced the water chemistry (F. RÖGL & G. WESSELY pers. comm.).

Conclusions

Lake Pannon experienced its maximum extension during the *Mytilopsis czjzeki* Zone (letter Zone E of PAPP 1951) correlating with chron C5n2n (MAGYAR et al. 1999b). The corresponding sedimentary sequence is characterised throughout the Vienna Basin by predominantly pelitic deposits yielding a diverse endemic mollusc fauna. This phase is indicated by the formation of the maximum flooding surface in seismic logs of the Vienna Basin and seems to correlate with algal blooms (KOVAC et al. 1998).

In the southern Vienna Basin, clay and silty sand with *Congeria subglobosa*, *Mytilopsis spathulata*, *Melanopsis vindobonensis* and other Lake Pannon taxa occur even along the lower slopes of the Eastern Alps. Thus, the shores of the long-lived lake reached up to the topographic margin of the basin in the area of the section Richardhof. At the locality Götzendorf, too, a covering by Lake Pannon during the *Mytilopsis czjzeki* Zone is reflected by pelitic deposits (RÖGL et al. 1993). Consequently, wetland settings are rarely recorded from that biozone throughout the Vienna Basin. The few reports on fresh-water mollusc faunas such as *Psilunio atavus* and *Tinnyea escheri* in Vösendorf and the Eisenstadt Basin (LUEGER 1980) derive only from lotic environments or are deposited out-of-habitat.

The highstand systems tract that became installed during the upper part of the zone (KOVAC et al. 1998) triggered a beginning backstepping of the shoreline towards the basin. Thus, a fringe of freshwater lakes could establish along the margin of the Eastern Alps, probably already during the latest *Mytilopsis czjzeki* Zone, whilst the floodplains of the basin could not develop before the final withdrawal of Lake Pannon. The slight differences in the evolutionary levels of the smaller mammal assemblages between the ”marginal” Richardhof and those of the ”basinal” Götzendorf observed by G. DAXNER-HÖCK (pers. comm.) might be explained by this diachronous establishment of freshwater settings in the Vienna Basin.

With the dawn of the Late Pannonian (*Mytilopsis neumayri/Mytilopsis zahalkai* Zone), the lake retreated from the Vienna Basin and established its north-western coast in the Hungarian basins (MAGYAR et al. 1999a). Consequently, the drainage systems from the Alps and the Molasse Basin entered the Vienna Basin and formed extended floodplains (fig. 9). The course of the main river anastomosed roughly from NW towards SE across the Vienna Basin. It left the Vienna Basin through the Bruck Gate between the Leitha Mountains and the Hainburg Mountains and continued into the Pannonian Basin (ZAPFE 1989, RÖGL & STEININGER 1990).

Fig. 9: Hypothetic course of the fluvial system that dominated the landscape of the Vienna Basin during the Late Pannonian. The river crosses the basin from the north, passes the Bruck Gate between the Leitha Mountains and the Hainburg Mountains and enters the Pannonian Basin system. Abandoned meanders and oxbow lakes are reconstructed for the Götzendorf area. The southern-most part of the basin, where up to 90 m of lignites of the Neufeld Formation formed, might be provided by drainage from the adjacent Alps. Note that the dating of the gravels on which the paleogeography of the river is based span a stratigraphic range covering the entire Late Pannonian. [The sector corresponds to insert 1 in figure 2]

The precursor of that river can be traced back at least to the Early Pannonian, when a major drainage system, passing the Molasse Basin, entered the Vienna Basin near Mistelbach (Lower Austria), shedding a huge deltaic body into Lake Pannon (Harzhauser et al. 2003).

The river divided the Vienna Basin into a northern and southern part. Its gravel load of the main channels is hardly preserved in surface outcrops (e.g. Prottes, Lower Austria) and a precise correlation with the ecozones is difficult. By contrast, the associated floodplain deposits are well preserved in the southern and northern part of the Vienna Basin. Small tributaries, rivulets and floodplain lakes, as suggested for Götzendorf, structured the wetland of the southern region. The swift rivulets carried oligotrophic, probably calcium-deficient water. Large stocks of *Margaritifera flabellatiformis* and the giant salamander *Andrias scheuchzeri* populated the bottom of the rivulets; the pebbles of the banks gave shelter to masses of *Theodoxus postcrenulatus*. Floodplain lakes and oxbow lakes settled by water chestnuts, pond weeds, numerous planorbids and newts passed into swamp forest and water meadows covering the interdistributary areas.

In the northern Vienna Basin, similar swamp vegetation with *Nyssa* and *Glyptostrobus* is documented from the Čáry Formation (Knobloch 1963).

Along the slope of the Alps, the influence of the main channel declined distinctly. The lakes and swamps, indicated by the fauna of the section Richardhof, were probably provided with drainage from the adjacent Calcareous Alps. Stagnant lakes with dense vegetation and a manifold herbivorous gastropod fauna developed. A supply of hard water from the Alps and the activity of characeans allowed the formation of marly deposits. Lotic environments are less important in this marginal setting. Consequently, rheophilic species such as the olm *Mioproteus caucasicus* or the gastropod *Theodoxus postcrenulatus* are distinctly less frequent or even absent. Instead, xerophilic taxa such as the lizard *Lacerta* and the gastropods *Granaria* and *Truncatellina* are frequent constituents of these assemblages, because of the proximity of the sunny and dry slopes of the Alps.

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