Molluscs from the Badenian (Middle Miocene) of the Gaindorf Formation (Alpine Molasse Basin, NE Austria) – Taxonomy, Paleoecology and Biostratigraphy

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(with 4 textfigures and 8 plates)

Abstract

The taxonomy, paleoecology, taphonomy and biostratigraphy of a remarkable mollusc fauna deriving from Middle Miocene sediments of the Alpine Molasse Basin have been investigated. Those sediments, termed the Gaindorf Formation paleogeographically represent the western margin of the Paratethys Sea, an epicontinental sea extending since Early Oligocene on the northern margin of the Mediterranean and the Indian Ocean. The section at Mühlbach (NE Austria) exposed a fully marine fining-upward sandy to muddy sequence transgressively overlying the Early Miocene offshore mud. The two samples were taken 60 cm from the transgression base and represent a muddy silt horizon characterised by conspicuously rich terrestrial vertebrate remains. The samples were washed and sieved. The extracted molluscs, numbering more than 500 individuals, were investigated by quantitative and qualitative methods. Bivalves dominated the taxonomic structure with 15 (species-level) taxa, followed by gastropods (7 taxa) and scaphopods (1 taxon). The quantitative data showed the good correlation of species frequency distribution in the two samples. The taxonomic structure as well as taphonomic features, e.g. left/right valve ratio, pointed to an intensive inter-habitat mixing. Four distinct habitats could be interpreted as sources for the represented taphocenosis: (1) muddy, moderately deep sublittoral characterised by a Corbula (Varicorbula) gibba-community and representing the actual depositional environment, (2) rocky sublittoral representing the firm ground colonised by attached pectinids and anomiids, in addition to an anemone-wentletrap gastropod community, (3) wave-exposed rocky coastal zone marked by an oyster community and (4) terrestrial zone with a rich terrestrial gastropod fauna. As no riverine habitat is indicated, the terrestrial elements may well have simply been washed down from the shore cliffs by rain. The source habitat distribution can be best explained by a coast morphology in which the rocky littoral and sublittoral pass abruptly to the moderately deep sublittoral sea bottom. Such a geomorphology would facilitate the upwelling and the presumed algal blooms, resulting in unstable bottom conditions, as evidenced by the Corbula (Varicorbula) gibba-community at the place of deposition. Biostratigraphically the studied fauna correlates well with the molluscs of the NE Austrian Grund Formation and can be thus dated as Early Badenian (early Middle Miocene, Langhian). The absolute age is interpreted by RÖGL & SPEZZAFERRI (2003, this volume) to range around 15.1 my.

Keywords: Bivalvia, Gastropoda, Paratethys, Middle Miocene, Badenian, Paleoecology, Corbula, Epitonium

1. Introduction

The described mollusc fauna derives from Mühlbach am Manhartsberg, 15 km NE of Krems in Lower Austria. There, about 100 m E of the local church, a small, short-lived,
artificial outcrop existed during excavations for a well. Large bulk samples for micro-
mammal studies were taken by Gudrun DAXNER-HÖCK (Museum of Natural History,
Vienna). Thus, aside from numerous vertebrate remains, several mollusc shells were
detected in the residue.

The unusual composition of the small fauna differs remarkably from synchronous
assemblages from the Molasse Basin and the Vienna Basin, which are usually predomi-
nated by diverse, sublittoral mollusc faunas. The misfit of a thanotocoenosis composed
of terrestrial gastropods, a nearly monospecific marine gastropod fauna, lacking nears-
hore taxa and a small-sized bivalve fauna with a striking left/right-valve discrepancy
within the epifaunal oysters is a challenge for paleoecological interpretations.

2. Geological setting and the history of investigation

The pelitic to sandy sediment is part of the Gaindorf Formation (ROETZEL & al. 1999),
which is dated to the Lower Badenian based on the ostracod and foraminifera fauna
(ZORN 1999, ROGL & al. 2002). The Gaindorf Formation is characterised by a manifold
lithology ranging from clay to gravel. It represents the western counterpart of the more
uniform Grund Formation (ROETZEL & al. 1999), with its remarkable mollusc fauna (Fig. 1).
The latter fauna was already extensively studied in the monographs of HÖRNES (1856,
1870) and HÖRNES & AUINGER (1879-91). Later, SIEBER (1935, 1947a, 1947b, 1949)
presented species lists of several localities of the Grund Formation, documenting more
than 300 mollusc species. Recently, HARZHAUSER & al. (1999) and ZUSCHIN & al. (2001) interpreted the assemblage of the classical site as a result of strong faunal mixing of littoral and sublittoral species that were deposited in a moderately deep sublittoral setting under at least partly dysaerobic conditions.

By contrast, the Gaindorf Formation is considerably poorer in macrofauna, although the closeness to the Grund Formation suggests that a similar faunistic spectrum might be expected. The presence of pectinid bivalves at Gaindorf is noted by KAUTSKY (1928) and SCHULTZ (2001).

Paleogeographically the sediments belong to the Paratethys Sea, extending during the early Middle Miocene time on the northern margin of the Proto-Mediterranean and the Indian Ocean Regions from Austria to Kazachstan (RÖGL 1998; Fig. 1).

3. Material and methods

The section is described in detail by ROETZEL (2003, this volume). About 2 m of artificially exposed Gaindorf Formation overlay discordantly a muddy sequence containing the characteristic foraminifera assemblage of the Early Miocene (Ottnangian) Zellendorf Formation (RÖGL & SPEZZAFERRI 2003, this volume; compare Fig. 2 and 3).
The fining upward sequence of the Gaindorf Formation begins with about 50 cm of muddy sand passing continuously into monotonous silt-mud within the upper part of the section. The initial horizon characterises a mytilid bivalve coquina embedded in a pelitic sandy matrix. The sandy component diminishes upwards from almost 50 % in the base of the horizon to less than 20 % within the following horizon. The studied samples, positioned about 60 cm above the base of the sequence, were taken in that overlying sandy to silty mud horizon, bearing scattered vertebrate (this volume) and mollusc remains. Labelled as Mühlbach (Mü1) and Mühlbach (Mü2), they originate from opposing walls of the well.

The sieving residues of those samples, carefully examined for all fossils, yielded a small mollusc fauna. Bivalves are mostly whole; in some cases only proximal thickened shell parts are available. Gastropods, by contrast, are nearly exclusively fragmented; especially the apertures of most specimens are lacking.

The mollusc remains have been counted; in bivalves the left and right valves were counted separately, providing detailed information on their taphonomy and the community structure.

4. Results and Discussion

4.1. Faunal composition

Despite the large quantity of sieved material, the detected mollusc fauna is poor. Hence only 23 species-level taxa were determined in two investigated samples. The bivalves apparently dominate the assemblage composition.

A total of 336 identifiable bivalve specimens were counted from the two investigated samples (Tab. 1) - 199 stem from the sample Mühlbach (Mü1) and 137 from the sample Mühlbach (Mü2). Despite such high individual numbers, only 15 species level bivalve taxa were represented within those samples.

Fig. 3: Section Mühlbach am Manhartsberg with indicated position of studied samples (after Roetz 2003, this volume).
Tab. 1: Distribution of bivalves within the samples. Numbers correspond with the number of specimens in the respective sample.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Mühlbach (Mü1)</th>
<th>Mühlbach (Mü2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yoldiidae</td>
<td>Yoldia (Yoldia) reussi (HÖRNES)</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Mytilidae</td>
<td>Mytilus (Crenomytilus) aquitanicus (MAYER)</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Arcidae</td>
<td>Anadara diluvii (LAMARCK)</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Ostreidae</td>
<td>Ostrea (Ostrea) digitalina (EICHWALD)</td>
<td>46</td>
<td>13</td>
</tr>
<tr>
<td>Pectinidae</td>
<td>&quot;Chlamys&quot; trilirata (ALMERA &amp; BOFILL)</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Crassadoma multistriata (POLI)</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Aequipecten macrotis (SOWERBY)</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>Anomiidae</td>
<td>Anomia ephippium Brocchi in BRONN</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Lucinidae</td>
<td>Lopites (Microloripes) dentatus (DEFRANCE)</td>
<td>15</td>
<td>7</td>
</tr>
<tr>
<td>Corbulidae</td>
<td>Corbula (Varicorbula) gibba (OLIVI)</td>
<td>90</td>
<td>17</td>
</tr>
<tr>
<td>Cardiidae</td>
<td>Parvicardium minimum (PHILIPPI)</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Mactridae</td>
<td>Spisula (Spisula) subtruncata (DA COSTA)</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Veneridae</td>
<td>Gouldia (Gouldia) minima (MONTAGU)</td>
<td>31</td>
<td>11</td>
</tr>
<tr>
<td>Teredinidae</td>
<td>indet.</td>
<td>5</td>
<td>88</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>199</td>
<td>137</td>
</tr>
</tbody>
</table>

Gastropods, in contrast, are represented by few species and few specimens. The "mixed character" of this gastropod assemblage is obvious in both Mühlbach samples. The fauna contains only two marine taxa but a large number of terrestrial gastropods. Among the marine species, a single species of the family Epitoniidae predominates, whilst Turritella is documented by a single specimen. Scaphopods are equally scarce, being recorded by only a single fragment. The very poor preservation of the two most frequent terrestrial gastropod taxa prevents from any identification, and thus only the rather unsatisfactory determination "terrestrial gastropod" is possible.

Tab. 2: List of gastropods and scaphopods found in the samples. Numbers correspond with the number of specimens in listed sample.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Mühlbach (Mü1)</th>
<th>Mühlbach (Mü2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pomatiidae</td>
<td>Pomatias sp.</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Turritellidae</td>
<td>Turritella badensis SACCO</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Epitoniidae</td>
<td>Epitonium miofrondiculoides (SACCO)</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Gastrocoptidae</td>
<td>Gastrocopta (Albinula) cf. cuminata (KLEIN)</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Valloniidae</td>
<td>Vallonia subcyclophorella (GOTTSCHICK)</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Clausiliidae</td>
<td>indet.</td>
<td>4</td>
<td>26</td>
</tr>
<tr>
<td>Helicidae</td>
<td>indet. cf. Cepaea</td>
<td>19</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>terrestrial gastropod indet.</td>
<td>24</td>
<td>116</td>
</tr>
</tbody>
</table>

SCAPHOPODA

Dentaliidae | Antalis quindeciesstriata (EICHWALD) | 1              | -              |

The more detailed taxonomic data are provided in the systematic part that follows in the final part of the presented study.
4.2. Analysis of the fossil record

In the following the paleoecological significance of the qualitative and quantitative taxonomic data will be analysed in detail. Quantitatively, only bivalves provided a sound record, whereas based on the qualitative data the gastropods also yielded valuable information. The bivalve record not only clearly points to the presence of faunal and environmental mixing, but moreover also enables a very reliable inference of the original, autochthonous community. The gastropod taxonomic distribution underlines the interpretation of a faunal mixing because terrestrial gastropods occur together with the fully marine ones. A very striking feature both in gastropods and bivalves is the absence of brackish and estuarine elements (e.g. Congeria, Melanopsis, Crassostrea, Granulolabium, Potamides). Hence, the mechanism behind the mixing was obviously not bounded to a riverine influx.

Autecological data with literature sources are given in the systematic part that follows in the final part of this study.

4.2.1. Qualitative data

The bivalves from Mühlbach (Tab. 1) represent various paleoecological requirements, so it can be excluded that they lived within one and the same environment. Hence, *Mytilus* (*Crenomytilus*) *aquitanicus* is typical for intertidal mudflats, whereas the presence of *Yoldia* (*Yoldia*) *reussi* points to at least a moderately deep muddy sublittoral. At such depths, *Ostrea* (*O*) *digitalina* also certainly could not flourish because it is typical for the energy-rich rocky sublittoral environments down to 10 m water depths. Remarkable is also the presence of *Anomia ephippium*, “*Chlamys*” *trilirata*, *Crassadoma multistriata* and young *Aequipecten macrotis* shells: all of them are epibionts dependent on the presence of secondary and primary hard substrata such as rock surfaces, plants or sessile animals to attach their shells. Based on the pelitic sediment and the absence of pebbles or larger biogenetic components, in combination with the middle sublittoral depth (at the shallowest) indicated by the presence of *Yoldia*, the sedimentary environment apparently could not provide abundant attachment opportunities. In consequence, all those faunal elements must be suspected to be allochthonous. The supplying environments were, in addition to the muddy intertidal (*Mytilus*), mainly the wave-dominated, exposed fully marine rocky intertidal to shallow subtidal (*Ostrea*). The influence of the less exposed, probably lower shallow subtidal zone on the firm substrata with plant or animal epibenthos is indicated (*Anomia*, pectinids).

Specialities of the bivalve record are the teredinids, which are particularly common in Mühlbach. These deadwood borers feed on celluloses, and also filtered food from the water column (WILLMANN 1989). These bivalves may have profited from chemosynthesis involved symbiotic bacteria in their tissues (SEILACHER 1990). This makes them independent from the environment, i.e. they occur the moment wood is available. The presence of teredinids therefore confirms the presence of a sunken piece of wood at the sediment bottom. As teredinids build extremely dense colonies (BOSCH 1995) and the volume of the sample from Mühlbach fills only a small laboratory glass, a very small piece of wood is indicated.
The remaining, unmentioned taxa are infaunal elements, all shallow burrowers except for *Loripes dentatus*. All these bivalves show wide depth ranges, so that depth does not seem to be a principal factor influencing their environmental distribution. Also *Spisula (S.) subtruncata*, known for its dense colonies in modern, shallow-water environments, shows the normal depth range down to 200 m (Poppe & Goto 1993). Hence, those taxa, but especially *Corbula (Varicorbula) gibba*, are opportunists that are well adapted to habitats under unstable environmental conditions.

The striking gastropod composition indicates rather unsuitable bottom conditions; these are no doubt responsible for the absence of most benthic forms. Despite the proximity to the coast – as can be assumed based on the accumulation of terrestrial elements such as small mammals, reptiles and gastropods – no littoral gastropods were detected in the assemblage. Potamidids, batillariids, theodoxids and melanopsids which are frequent components in the assemblages of the Grund Formation, are absent from the samples. In addition, typical representatives of the shallow sublittoral are absent.

### 4.2.2. Quantitative data

The individual richnesses of the bivalve fauna are analysed for sample correlation and to define the community structure. Subsequently, the left/right valve distribution pattern helps filter out the distortions due to inter-habitat transportation (Fig. 4).

The distribution of individual richnesses of the Mühlbach (Mü1) and Mühlbach (Mü2) samples apparently correlate. All taxa represented in the poorer Mühlbach (Mü2) sample are represented in the Mühlbach (Mü1) sample as well. Their dominance hierarchies show the same regression pattern, with one exception. The distortion of the regression pattern is created by teredinids. The nature of the Teredinidae record hinders a quantitative comparison with other bivalves: teredinids are represented by calcareous siphonal tubes and not by shells as other bivalves. Those tubes are fragmented so that one individual is represented by several counted tubes. As already discussed, their distribution within one sedimentary environment is defined by the presence of sunken wood and is therefore highly incidental. The presence of such colonised wood in the sample Mühlbach (Mü2) consequently led to an explosion of the recorded teredinid number.

With the exception of teredinids, the thanotocoenosis is clearly dominated by 4 taxa – 3 infaunal (*Corbula, Gouldia* and *Loripes*) and 1 epifaunal cementing species (*Ostrea*), all exceeding the 7% contribution to individual richness of the sample Mühlbach (Mü1). Thereby, the left/right valve distribution points to the autochthonous presence of all three infaunal taxa (Fig. 4). For *Ostrea digitalina* in contrast the minority of cementing right valve indicates that the free left valves reached their burial site by some kind of transport. This inference coincides with the above-discussed depositional depth, which is certainly unfavourable for this shallow-water *Ostrea*. The absence of deeper-water epibionts such as *Pycnodonta cochlear* (comp. Studencka 1986), on the other hand, points to the absence of firm substrates in that sedimentary environment.

In conclusion, the autochthonous paleocommunity is dominated mainly by *Corbula (Varicorbula) gibba* (66% in Mü1), followed by *Gouldia minima* (23% in Mü1) and *Loripes (Microloripes) dentatus* (11% in Mü1). The paleoecological significance of that opportunists community (comp. text above) will be discussed in the following chapter.
4.3. Paleoecological inferences – bringing the allochthonous elements home

The mollusc analysis enables a more clear distinction between the contribution of allochthonous and autochthonous elements to the Mühlbach samples. Moreover, the filtering of the ecological niches characterised by the represented taxa allowed more than merely the interpretation of the paleoenvironment at the site of sample sedimentation. More importantly, this approach has shed light on interactions between single, neighbouring environments that make up the overall ecosystem.
4.3.1. Muddy sublittoral – The basket-shell paleo-community

The muddy sublittoral was the studied thanotoenosis’ burial site. As the previous analysis shows (Fig. 4), the main members of the autochthonous community in this particular depositional environment were *Corbula (Varicorbula) gibba* (basket-shell), followed by *Gouldia minima* and *Loripes (Microloripes) dentatus*.

The striking dominance of corbulids is significant for unstable environmental conditions (WELLE 1998). These bivalves apparently tolerate environmental deterioration or degradation (LAMPRELL & al. 1998). Hence, they are among the few species that survive exterminations of the benthic fauna by oxygen depletion or chemical pollutants in Recent seas. After reduction of accompanying organisms, *Corbula* - as a typical opportunist and r-strategist - conquers (within a pioneer-phase of bottom re-colonisation) the whole devastated area. Series of such catastrophic events then lead to its dominance also within the time-averaged assemblages. Such Recent *Corbula (Varicorbula) gibba* communities are characteristic for the northern Adriatic Sea, which has been affected over the last decades by events of algal blooms resulting in sea bottom hypoxia, anoxia and coverage by mucus aggregates (ALEFFI & al. 1996). *Gouldia minima* is commonly present in the Recent Black Sea - apparently also in regions affected by oxygen crises (POVCHUN & SUBBOTIN 1991). Modern *Loripes* is reported to be capable bacterial chemosymbiosis, enhancing its competitiveness in dysoxic environments (TAYLOR & GLOVER 2000).

A corresponding fossil *Corbula (Varicorbula) gibba*-community is known from the Early Badenian Korytnica Clays in Central Poland; it is interpreted as a pioneer stage community typically re-colonising, barren, aphytal muddy grounds (HOFFMAN 1977, 1979).

In conclusion, the presented data indicate the presence of an unstable environment during the deposition. The most likely stress factor is interpreted to be repetitive algal blooms causing sea bottom oxygen depletions. This interpretation coincides with the inference of upwelling conditions for the Mühlbach section based on the foraminifera data (RÖGL & SPEZZAFERRI 2003, this volume).

4.3.2. Rocky sublittoral – a wentletrap-sea anemone paleo-community

This zone of somewhat deeper rocky sublittoral less exposed to wave action is indicated not only by thin-shelled, byssate pectinids and anomiids. Indirect evidence is also given by the presence of *Epitonium*, a gastropod specialised on cnidarian predation. As such cnidarians are dependant on firm substrates, which were apparently absent within the depositionary environment, this is the most probable zone from which those organisms originated.

The rather frequent *Epitonium miofrondiculoides* (SACCO) does not allow a straightforward interpretation of the paleo-waterdepth. Extant wentletraps range from intertidal habitats to abyssal depths (BEESLEY & al. 1998). It does, however, provide clear evidence for an otherwise unpreserved organism. Epitonids are well documented to depend on cnidarians – especially on sea anemones – on which they feed in a commensal or ectoparasitic manner (ROBERTSON 1963, 1970, 1980, 1983a, 1983b). Most inve-
stigated species have been observed to feed on various cnidarians, but usually they display a preference to a single host species (PERRON 1978). *Epitonium greenlandicum* (PERRY) was observed to prey on at least 6 different actinarians by PERRON (1978), but showed a distinct preference for *Metridium senile* LINNÉ. *Epitonium albidum* (D’ORBIGNY) lives with the sea anemone *Stichodactyla helianthus* (ELLIS), feeding on tentacles as well as on parts of the column (ROBERTSON 1983b). A single anemone may give shelter to up to 39 specimens of that wentletrap. Other wentletrap-anemone relationships are reported for *Epitonium echinaticostatum* (D’ORBIGNY), feeding on tentacles of *Bunodeopsis globulifera* (DUCHASSAING) (ROBERTSON 1983a), for *Epitonium millecostatum* (PEASE), taking tissue and mucus of the anemone *Palythoa* (ROBERTSON 1980), and for *Epitonium rupicola* (KURTZ), feeding on *Paranthus rapiformis* (LESUEUR) and *Haliplanella luciae* (VERRILL) (ROBERTSON 1963).

Parasitism on scleractinians seems to be relatively less common. The dendrophyllid corals *Tubastrea tenuilamellosa* and *Tubastrea coccinea* are the hosts of *Epitonium billeeana* (DUSHANE & BRATCHER) (DEBELIUS 1997, ROBERTSON 1970), whilst *Epitonium costulatum* (KIENER) and *Epitonium ulu* PILSBRY are associated with *Fungia* (ROBERTSON 1970). Therefore, a priori, corals cannot be excluded as hosts for *Epitonium miofrondiculoides*. Dendrophyllid corals, for example, are reported from the Badenian of the Vienna Basin (REUSS, 1871, SCHULTZ 1998). However, no scleractinians were detected in the samples from Mühlbach. Thus, the presence of an actinarian host species seems to be more likely. These cnidarians lack hardparts and are therefore hardly documented in the fossil record.

4.3.3. Rocky coastline – The oyster paleo-community

Evidence for a wave-exposed rocky coastline is provided by abundant *Ostrea (Ostrea) digitalina*. Its Recent relatives are typical for the corresponding zone down to the 10 m water depth (MILISIC 1991). As already discussed, the Mühlbach samples are characterized by the dominance of the free left valves. The cementing right valves obviously remained fixed to the substrate, whereas their left counterparts floated away as result of the action of the turbulent water.

4.3.4. The hinterland – The terrestrial gastropods

The small assemblage of terrestrial gastropods does not allow a detailed paleoecologic interpretation. Based on the absence of taxa instead of relying on "hard" data, it seems to indicate a moderately dry and open habitat in the adjacent hinterland rather than moist, dense woodland. Recent representatives of *Vallonia* prefer open habitats such as grassland (LUEGER 1981).

Typical inhabitants of moist habitats such as carychiids are missing. Furthermore, limnic-fluvial gastropods such as planorbids, lymnaeids, or valvatids are absent.
4.3. Biostratigraphy

The stratigraphic significance of the mollusc assemblage is somewhat restricted by the low number of documented taxa. Nevertheless, the Mühlbach bivalves show a striking similarity with the fauna from Grund. Hence, the Mühlbach bivalves are 100% represented in Grund. Note also that characteristic morphotypes in variable species (e.g. *Crassadoma multistriata*) are identical with those represented in Grund. Also, the species typical for the Grund Formation, such as *Yoldia (Y.) reussi*, or for the Gaindorf Formation, such as “*Chlamys*” *trilirata*, are now found occurring in both localities.

Among the gastropods and scaphopods, only *Turritella badensis* is restricted to the Badenian, whilst *Epitonium miofrondiculoides* and *Antalis quindeciesstriata* appear already during the Karpatian (late Early Miocene).

In conclusion, despite the restricted number of taxa found in Mühlbach, its biostratigraphic correlation with Grund is strongly supported by molluscs, in particular bivalves.

5. Conclusions

The quantitative and qualitative analysis of molluscs from two samples of the Middle Miocene Mühlbach section (Gaindorf Formation) pointed to an intensive inter-habitat mixing. At least four distinct zones could be clearly separated as the most important habitats from which the taxa represented in the studied samples originated: (1) the muddy sublittoral, (2) rocky sublittoral, (3) rocky coastal zone and (4) the hinterland.

1. The muddy sublittoral coincides with the depository environment. Based mainly on the occurrence of *Yoldia (Y.) reussi*, the depositional depth is inferred to be at least a moderately deep sublittoral zone. This zone was populated by a mollusc community dominated by *Corbula (Varicorbula) gibba*, indicating a habitat influenced by frequent environmental crises. Corbulids represent the pioneers that first, re-colonise the sea bottom when environmental conditions become more stable. As this community is typical for Recent regions suffering from algal blooms, a similar process is proposed also for the studied samples.

2. The rocky sublittoral supplied the depositional environment with epibiont bivalve remains of thin pectinids and anomiids. Among the scarce marine gastropods, *Epitonium miofrondiculoides* appears in relatively high numbers and presumably represents this zone. Modern counterparts of this species display an obligatory relationship with cnidarians. The absence of scleratinians in the investigated samples point to the presence of actinarians as the preferred resource for the abundant wentletraps. As actinarians depend on firm substrata, which are absent within the depositional environment, this is the closest zone where they could be present. This would be a first but indirect hint to the presence of Middle Miocene sea anemones in the Central Paratethys.

3. The oyster community is inferred to stem from a rocky coastal zone. The common left oyster valves in the studied samples are interpreted as having become disarticulated from their cemented right counterparts within turbulent water and then transported into
the depositional environment. The gastropod assemblage lacks littoral and shallow sublittoral elements despite of the proximity of the coastline. This points to a shoreline which was hardly settled by gastropods, probably due to harsh environmental conditions.

(4) Finally, although the influence of the hinterland is apparently strong (Tab. 2), it does not seem to be characterised by a riverine system. The terrestrial gastropods apparently derive from the bordering coastland and do not support any interpretation of fluvial transport. Freshwater or typical estuarine mollusc taxa appear to be missing. In consequence, some other mechanism must be considered as having transported those elements to the place of deposition. The terrestrial elements may have simply been washed down from the shore cliffs by rain. There is sound faunal evidence for the rocky littoral and sublittoral passing abruptly to the moderately deep sublittoral sea bottom. Such a geomorphology could also facilitate upwelling events, resulting in the indicated algal blooms.

Biostratigraphically, the studied fauna correlates with the molluscs of the Grund Formation and can therefore be dated as Early Badenian (early Middle Miocene).

6. Systematic part

Classis Gastropoda Cuvier, 1795
Subclassis Orthogastropoda Ponder & Lindberg, 1995
Superordo Caenogastropoda Cox, 1960
Ordo Sorbeoconcha Ponder & Lindberg, 1997
Superfamilia Littorinoidea Children, 1834
Familia Pomatiidae Newton, 1891
Genus Pomatias Studer, 1789

Pomatias sp. (Pl. 1, Fig. 4)

Material: 1 operculum from Mühlbach (Mü2).

The genus is a common element in the Karpatian, Sarmatian and Pannonian faunas of the Vienna Basins complex (Binder 2002, Harzhauser & Kowalke 2002, Lueger 1981) and is thus of little stratigraphic significance.

The extant Pomatias elegans (Müller) is a xerothermophilic species which prefers woodland habitats but appears also along rivers and lake sides (Crispino & Esu 1995). The extraordinary abundance of Pomatias conicus (Klein) in Sarmatian and Pannonian swampy deposits might point to a preference for moist habitats by the fossil species. However, the single occurrence of a very robust and stable operculum is a poor basis for any paleecological interpretation.
**Turritella badensis SACCO, 1895** (Pl. 1, Fig. 1)

1975 *Turritella (Haustator) badensis* (Sacco, 1895) – Baluk, p. 105, pl. 12, figs. 22-27, cum syn.

**Material:** 1 fragment from Mühlbach (Mü1).

A single fragment consisting of 5 early whorls was detected in the samples. Its sculpture fits well to that of better-preserved specimens of *Turritella badensis* SACCO from the Grund Formation as described by Sieber (1958). This species appears in the Vienna Basin and adjacent areas during the Early Badenian and is one of the most common turritellid gastropods throughout the Badenian.

Suborder: Ptenoglossa Gray, 1853  
Superfamily: Janthinoidea Lamarck, 1810  
Family: Epitoniidae Berry, 1910  
Genus: *Epitonium* Röding, 1789

**Epitonium miofrondiculoides** (SACCO, 1891) (Pl. 1, Figs. 2-3)

2002a *Epitonium spinosum* (Bonelli, 1826) – Harzhauser, p. 93, cum syn.

**Material:** 4 fragments from Mühlbach (Mü2) and 1 from Mühlbach (Mü1).

Surprisingly, the otherwise rare *Epitonium miofrondiculoides* is one of the most frequent marine gastropod species at the locality Mühlbach. As already discussed in Harzhauser (2002a) this species was traditionally lumped with the mainly Pliocene *Epitonium spinosum* (Bonelli).

In the Central Paratethys the species appears already during the Karpatian. During the Badenian it displays a wide distribution in the Central Paratethys, from the Carpathian Foredeep in the north to the Transylvanian Basin in the south. From the synchronous Grund formation it was mentioned by Hörnes (1856).

**Gastrocopta (Albinula) cf. acuminata** (Klein, 1846) (Pl. 1, Figs. 5-6)

2000 *Gastrocopta (Albinula) acuminata* (Klein) – Manganelli & Giusti, p. 60, pl. 1, figs. 1-6, pl. 2, figs. 1-7.

**Material:** 1 shell from Mühlbach (Mü2).

The specimen agrees well with typical representatives of *Gastrocopta (Albinula) acuminata* concerning shape, the faint axial ornamentation, and the general apertural fea-
tures. Differences are the small, secondary palatal plications between the two prominent palatal teeth and the almost absent basal plica.

*Gastrocopta acuminata* is reported by *Lueger* (1981) from the Badenian, Sarmatian and Pannonian of the Vienna Basin. Recently, it was described by *Manganelli & Giusti* (2000) from the Pliocene of Italy.

Familia Valloniidae Morse, 1864
Genus *Vallonia* Riss, 1826

*Vallonia subcyclophorella* (Gottschi, 1911) (Pl. 1, Figs. 7-8)


**Material:** 2 shells from Mühlbach (Mü2).

This species is rarely reported from the Austrian Miocene. *Gottschick* (1911) and *Finger* (1998) mention *Vallonia subcyclophorella* from the slightly younger Steinheim Basin (Germany). An occurrence from the Lower Sarmatian deposits of Hollabrunn (Lower Austria) was reported by *Schütt* (1967). The species displays a range spanning the Badenian and Sarmatian but it is absent in the Pannonian faunas of the Vienna Basin described by *Lueger* (1981).

Classis Scaphopoda Bronn, 1862
Ordo Dentaliida Starobogatov, 1974
Familia Dentaliidae Gray, 1834
Genus *Antalis* H. & A. Adams, 1854

*Antalis quindeciesstriata* (Eichwald, 1853)

**Material:** One small fragment of 4.9 mm length was found in sample Mühlbach (Mü1).

The sculpture of this specimen is highly reminiscent of that of *Antalis quindeciesstriata* (Eichwald, 1853), which was described as Dentalium (Antalis) fossile var. raricostata Sacco by *Sieber* (1949) from the synchronous Grund formation. For a detailed discussion on the complex synonymy of this species see *Harzhauser* (2002b).

The stratigraphic resolution of *Antalis quindeciesstriata* is rather low; it appears in the Central Paratethys already during the Karpatian and persists throughout the Badenian from the Lower Badenian Grund formation to the Late Badenian of Pötzleinsdorf/Vienna.

Classis Bivalvia Linne, 1758

Subclassis Palaeotaxodonta Korobkov, 1954
Ordo Nuculoida Dall, 1889
Familia Yoldiidae Allen, 1985
Genus Yoldia Møller, 1842
Subgenus Yoldia Møller, 1842

Yoldia (Yoldia) reussi (Hörnes, 1865) (Pl. 2, Fig. 1)

2001 Yoldia (Yoldia) reussi (Hörnes, 1865) – Schultz, p. 28, pl. 2, fig. 7.

Material: Mühlbach (Mü1) – fragment of the right posterior hinge region; the original shell length was 5 to 8 mm.

The fragment correlates perfectly with the corresponding portion of one complete right valve in the authors’ collection from the locality Grund. The identification therefore follows the review of the Austrian Nuculoidea by Schultz (2001). Its shell is not nacreous, excluding its relationship with Nuculidae. The exterior sculpture consists of very fine concentric lines, distinguishing it from coarsely sculptured Badenian Nuculana representatives. The position and depth of the resilifer, the long and very fine hinge teeth, in distance from the exterior valve margin, and a thin fragile and shiny shell are typical features of Yoldia (Yoldia) reussi.

This species is originally described from the locality Grund. Apart from the Grund Formation it was formerly known only from the Baden Formation of the southern Vienna Basin (Schultz 2001). The muddy sediments of the latter formation represent medium to deep sublittoral offshore conditions (Piller & Vavra, 1991).

Subclassis Isofilibranchia Iredale, 1939
Ordo Mytiloida Féruussac, 1822
Familia Mytilidae Rafinesque, 1815
Genus Mytilus Linné, 1758
Subgenus Crenomytilus Soot-Ryen, 1955

Mytilus (Crenomytilus) aquitanicus (Mayer-Eymar, 1858) (Pl. 2, Fig. 2)

2001 Mytilus (Crenomytilus) aquitanicus (Mayer-Eymar, 1858) – Harzhauser & Mandic, p. 719, pl. 3, fig. 2

Material: Mühlbach (Mül) – one fragment of the right anterior shell region.

The hinge fragment points to a very thickened, foliated mytilid shell composed of thick nacreous layers; this is a feature combination that is uniquely present in Mytilus (Crenomytilus) aquitanicus. Hörnes (1870) already described such fragments as typical remains of the latter species. As discussed by Harzhauser & Mandic (2001), it is synonymous with Mytilus haidingeri Hörnes, although Schultz (2001) presented a different point of view. The subgeneric classification follows Studencka & al. (1998).
*Mytilus (Crenomytilus) aquitanicus* is typical for intertidal to shallow subtidal mudflats in estuaries and lagoons; under optimal ecological conditions it forms densely packed shell beds (Harzhauser & al. 2002). It is a typical species of ecologically similar deposits of the Late Oligocene to Early Miocene in the entire Paratethys. Its latest occurrence is recorded from the Grund Formation, where it is suspected of being possibly re-deposited and from the Early Badenian of Styria (Schultz 2001).

**Anadara diluvii (Lamarck, 1805)** (Pl. 2, Fig. 3)

Material: Mühlbach (Mü1) – one badly abraded, fragmented right valve of a young individual; its inferred shell height is of about 5 mm.

Shell is centrally convex, with a broadly inflated, dorsally incurved, opistogyrate umbo. It has 29 ribs, each marked only by radial ridge pair that remained after exterior surface abrasion.

The earliest certain record of *Anadara (A.) diluvii* is from the Late Oligocene of the Central Paratethys (Baldi 1973). This (semi)infaunal, byssate species is still present in the Mediterranean on sandy and muddy bottoms from 5 to 500 m depth (Milisic 1991, Poppe & Goto 1993)

**Ostrea (Ostrea) digitalina (Dubois, 1831)** (Pl. 2, Figs. 4-7)

Material: Mühlbach (Mü1) – 46 specimens, Mühlbach (Mü2) – 13 specimens; maximal shell length 67 mm.

This common Miocene *Ostrea* has a small to medium-sized, more or less posteriorly bent shell, which is usually higher than long, being oval to subquadrate in outline. The cementing left valve is more convex that the right valve, exposing commonly a steeply elevated marginal area. In contrast to the smooth right valve, its exterior shows coarse radial ribs.

The species is known throughout the Miocene in the Mediterranean and in the Paratethys. According to Studencka (1986) it is possibly synonymous with the Atlantic and
Mediterranean *Ostrea frondosa* DE SERRES. In contrast to *Crassostrea* this is a fully marine oyster, cementing on different kinds of hard substrata. It is closely related with the Recent Mediterranean *Ostrea edulis* (SCHULTZ 2001), which forms scattered colonies in shallow coastal waters, not deeper than 10 m (MILISIC 1991).

**Family** Pectinidae WILKES, 1810 [emend. WALLER, 1978]
**Subfamily** Chlamydinae TEPNTER, 1922
**Tribe** Chlamydini TEPNTER, 1922 [emend. WALLER, 1993]
**Genus** indet. *"Chlamys" trilirata* (ALMERA & BOFILL, 1897) (Pl. 2, Fig. 8; Pl. 3, Fig. 1-3)

2001 Aequipecten bryozodermis (ALMERA & BOFILL, 1897) - SCHULTZ, p. 187, pl. 17, fig. 8.

**Material:** Material: Mühlbach (Mü1) – morph 1 (Pl. 2, Fig. 8; Pl. 3, Fig. 1-2): two fragmented specimens: one posterior part of the left valve and one posteroventral part of a right valve; the original height of the larger, right valve did not exceed 20 mm. Morph 2 (Pl. 3, Fig. 3): one somewhat distally fragmented left valve; original disc height was about 10 mm.

The available material includes two distinct morphs representing extremes in the variation of that conspicuous but still insufficiently known species. The morph 1 is characterised by a fragile, small sized shell, having both valves convex. The ribs of the slightly (secondarily?) flattened left valve are proximally sharp, whereas the ribs are distally weakly convex in the larger specimen. The rib ordination is regular, except for the very proximal shell region showing non-synchronous rib origination. The exterior surface, at least up to a disc height of 10 mm, is completely covered by a shagreen microsculpture. Distally this sculpture abruptly smooths and passes into the Camptonectes-type microsculpture. Within the marginal area several additional ribs are irregularly intercalated on the ribs and within the interspaces. Left posterior ear shows 4 radial riblets. Interior valve surface is characterised by the absence of internal rib carinae on the disc and by a posterior left hinge without teeth structures. The morph 2 resembles morph 1 in its small fragile shell, the disc convexity, the shell outline and the proximal initiation of the disc ribs. Yet the ribs, 21 in number, are apparently stronger and more densely arranged, with narrower interspaces. In contrast to morph 1, the ribs are ornamented by regularly and densely arranged, sub-orthogonal, commarginal lamellae. The shagreen microsculpture reduced to the anterior ear exterior surface is absent from the disc, showing a well developed Camptonectes-type microsculpture.

In the present study "Chlamys" bryozodermis (ALMERA & BOFILL) is included into the synonymy of "Chlamys" trilirata. This revision is based on the authors' investigations of the ALMERA & BOFILL (1897) and ROGER (1939) type material from the type collection of the Department of Earth Sciences, Claude Bernard University Lyon. Except for this revision, the applied species concept follows SCHULTZ (2001). The generic classification follows, in contrast, the phylogenetic pectinid taxonomy introduced by WALLER (1991, 1993). Among other typical features like hinge and commarginal lamellae shape, especially the presence of a shagreen microsculpture does not allow a identification as
Aequipecten. The shagreen microsculpture is a feature unique for the Chlamydini tribe. Yet, as being probably unrelated with *Chlamys* s.s. of Waller (1993), the genus is referred to as "Chlamys".

"Chlamys" *trilirata* is originally described from the Miocene sediments of Catalonia. In the Paratethys, apart from the Gaindorf Formation, it has been recorded also from the Early Badenian of the Styrian Basin (Schultz 2001). Both morphs found at Mühlbach are present also in authors' collection from the Early Badenian of Grund.

**Tribe** Crassadomini Waller, 1993  
**Genus** Crassadoma Bernard, 1986 [emend. Waller, 1993]

**Crassadoma multistriata** (Poli, 1795) (Pl. 4, Fig. 1)

1993 *Crassadoma multistriata* (Poli, 1795) - Waller, p. 212, figs. 5a, d, g; 6c-j.

**Material**: Mühlbach (Mü1) – one fragment of the proximal shell region with exceptionally well-preserved microsculptural elements; original disc height was about 10 mm.

Shell convex, with about 25 narrow ribs, introduced non-synchronously; at lateral marginal areas the ribs are ornamented by prominent scales. The proximal exterior area is ornamented by prominent commarginal lirae that form a typical net pattern together with the ribs. The preradial stage of the dissoconch is coarsely, irregularly punctate. Laterally, continuing to disc flanks, the antimarginal microstriation develops.

As a consequence of the exceptional preservation, for the first time (according to authors’ knowledge) the early prodissoconch microsculpture of a fossil *Crassadoma* could be documented. The latter apparently correlate well with that in Recent specimens illustrated by Waller (1993).

*Crassadoma multistriata* is common in the Mediterranean, Paratethys, Atlantic and Indian Oceans at least since the Early Miocene, although its oldest reference is dated as Late Eocene. The modern representatives live in the Mediterranean and E Atlantic waters. They attach themselves with their byssus on hard substrates from shallow to deep subtidal depths (Poppe & Goto 1993).

**Tribe** Aequipectinini Waller, 1993  
**Genus** Aequipecten Fischer, 1886

**Aequipecten macrotis** (Sowerby, 1847) (Pl. 5, Fig. 2, Pl. 6, Fig. 1)

2001 *Aequipecten macrotis macrotis* (Sowerby, 1847) – Schultz, p. 192, pl. 18, fig. 2.

**Material**: Mühlbach (Mü1) – one distally fragmented right valve and one fragment of the posterodorsal region of one left valve; the original height of the left valve did not exceed 15 mm.

Shell biconvex, with 18 regularly arranged, prominent, highly convex ribs, which initiate synchronously. The ribs of the central region are smooth (abraded?); the ribs on the
Lateral region bear scales on the tops. The interspaces are somewhat narrower than the ribs, weakly concave, ornamented by projecting, commarginal lamellae and an antimarginal microsculpture. The lamellae climb up the ribs, especially in the lateral regions. The right anterior ear is pointed anteriorly; the active ctenolium is well developed with 4 strong denticles; the ears bear scaly riblets and projecting commarginal lirae. The left posterior ear is large with a concave posterior margin. Interior shell side develops interior rib carinae; the right hinge has pronounced resilial teeth and thin dorsal teeth.

The ctenolium development of the right valve indicates a byssate mode of life. Usually the young *Aequipecten* preferably live fixed to substrate, whereas the large adult specimens recline on the sediment (WALLER 1991).

*Aequipecten macrotis* is typically represented in the Early Badenian Sediments of Grund and Niederleis (MANDIC & al. 2002). In the latter locality it is characteristically found is a maerl facies. In the Paratethys it is present since the Ottnangian. In the Mediterranean and Atlantic it seems to be represented throughout the Miocene (SCHULTZ 2001).

**Anomia ephippium** LINNÉ, 1758 (Pl. 6, Fig. 2-3)

2001 *Anomia ephippium* LINNÉ, 1758 – HARZHAUSER & MANDIC, p. 732, pl. 6, fig. 7.

Material: Mühlbach (Mü1) – two left valves, Mühlbach (Mü2) – one left valve; maximal height 37 mm.

The left valve is weakly convex in the proximal region, flattening distally. The shell outline is irregular with straight, thickened dorsal margin and more or less rounded rest. The exterior surface is proximally more or less smooth, but develops an irregular sculpture towards the distal part. Laterally, a radial rib-like and antimarginal striae-like sculpture may appear.

The modern representatives live in the Mediterranean and NE Atlantic. They colonise all types of hard substrates from intertidal to deep subtidal depths (POPPE & GOTO 1993). This species originated in the Early Oligocene of the Paratethys and North Sea Basin (HARZHAUSER & MANDIC 2001)

**Loripes (Microloripes) dentatus** (DEFRANCE, 1823) (Pl. 7, Fig. 1-3)

1986 Parvilucina (*Microloripes*) *dentata* (DEFRANCE, 1823) – STUDENCKA, p. 50, pl. 8, fig. 2, 3, 5, 6.

Material: Mühlbach (Mü1) – 15 specimens, Mühlbach (Mü2) – 7 specimens; maximal height is 2.5 mm.

Shells small, convex, suborbicular; beaks strongly prosogyrate; lunular region concave, exterior smooth with fine commarginal lirae passing partly to fine projecting lamellae; interior shell margin crenulated; hinge teeth prominent.

*Loripes* (*Microloripes*) *dentatus* ranges from the Early Miocene to the Late Pliocene of the Mediterranean and Atlantic region (STUDENCKA 1986). It is frequent in the Badenian of the Paratethys (KOJUMGIEVA & STRACHIMIROV 1960), occurring as a marine relict even in Sarmatian sediments (PAPP, MARINESCU & SENES 1974). The modern *Loripes* is reported to be capable of bacterial chemosymbiosis (TAYLOR & GLOVER 2000).

Subclassis *Heteroconchia* HERTWIG, 1895
Ordo *Veneroida* ADAMS & ADAMS, 1856
Familia *Corbulidae* LAMARCK, 1818
Genus *Corbula* BRUGUIÈRE, 1797
Subgenus *Varicorbula* GRANT & GALE, 1931

*Corbula* (*Varicorbula*) *gibba* (OLIVI, 1792) (Pl. 7, Fig. 4-14)

1986 *Corbula* (*Varicorbula*) *gibba* (OLIVI, 1792) – STUDENCKA, p. 103, pl. 16, figs. 13-15, pl. 18, figs. 2, 3, 6, 8, 10.
2001 *Corbula* (*Varicorbula*) *gibba* (OLIVI, 1792) – HARZHAUSER & MANDIC, p. 744, pl. 9, fig. 2.

Material: Mühlbach (Mü1) – 90 specimens, Mühlbach (Mü2) – 17 specimens; the largest specimen is a right valve with a height of 5.4 mm (pl. 7, fig. 4).

Shells small, biconvex, inequivalve with a larger and thicker right valve. The morphologic variation is pronounced - the young individuals (pl. 7, fig. 11, 13) are typically strongly elongated posteriorly, flattened and thinner, whereas larger adults (pl. 7, fig. 4, 10) are typically thick shelled, oval and highly convex. The exterior shell surface is ornamented with concentric ridges or lamellae. The dorsoventral keel is prominent; the posterior margin is more or less truncated.

The modern representatives of this opportunistic species are very common on mud bottoms, where they live infaunally, anchored by a byssus to the sediment particles (WILLMANN 1989). They seem to be a good indicator for the presence of organic matter on the sea bottom. Moreover, they easily switch from suspension to deposit feeding and back, which is an optimal adaptation for living on unstable substrate types (WELLE 1998).

*Corbula* (*Varicorbula*) *gibba* occurs in the Mediterranean and NE Atlantic waters from the low intertidal to the bathyal (POPPE & GOTO 1993). The fossil record begins with the Early Oligocene North Sea Basin and Paratethys representatives (HARZHAUSER & MANDIC 2001). It remains common in Recent environments.

Familia *Cardiidae* LAMARCK, 1809
Genus *Parvicardium* MONTEROSATO, 1884
Parvicardium minimum (Philippi, 1836) (Pl. 8, Fig. 1)

Material: Mühlbach ( Mü1) – one left valve; reconstructed height 2.5 mm.
The shell is minute, thin, convex, orbicular, with a small prosogyrate beak, ornamented by 27 broad, flattened ribs bounded by narrow interspaces. The ribs bear minute pustulae anteriorly, the interspaces are ornamented by extremely fine concentric lamellae.

Our specimen is identical with specimens from the Badenian of Southern Poland described by Studencka (1986). See also there for a more detailed description. The similar Papillicardium papillosum (Poli) has rounded and not flattened ribs. Parvicardium minimum is recorded from the Middle Miocene to the Recent (Malatesta 1974). The modern representatives live in the Mediterranean and NE Atlantic, from the shallow- to the deep subtidal zones (Poppe & Goto 1993).

Familia Mactridae Lamarck, 1809
Genus Spisula Gray, 1837

Spicula (Spisula) subtruncata (Da Costa, 1778) (Pl. 8, Fig. 2)

Material: Sample M1 - One fragment of the left valve proximal region including the complete hinge.

As indicated in the bivalve Treatise (Moore 1969-1971), the subgenus Spisula is characterised by striate lateral teeth. This feature, displayed by our fragment, enables its accurate generic classification within the Paratethyan Mactridae. Accordingly, the hinge type and morphology of the proximal shell area is identical with numerous specimens of Spicula (Spisula) subtruncata from the locality Grund. As indicated by Studencka (1998), other Spisula species are not known from the Badenian of the Paratethys.

The modern Spicula (Spisula) subtruncata lives in the Mediterranean and NE Atlantic. It is a typical shallow subtidal, shallow infaunal, gregarious bivalve (Milicic 1991, Poppe & Goto 1993). In the Paratethys it is known from the Late Oligocene to the Badenian (Teikal & al. 1967).

Familia Veneridae Rafinesque, 1815
Genus Gouldia Adams, 1847
Subgenus Gouldia Adams, 1847

Gouldia (Gouldia) minima (Montagu, 1803) (Pl. 8, Figs. 3-8)

1986 Gouldia (Gouldia) minima (Montagu, 1803) – Studencka, p. 96, pl. 14, fig. 7.
Material: Mühlbach (Mü1) – 31 specimens, Mühlbach (Mü2) – 11 specimens; the largest specimen is 5.5 mm high (pl. 8, fig. 4).

Shells small, convex, subrounded, with umbo pointed anteriorly and rounded ventral margin. The lunula is large, elongated anteriorly, well separated and convexly elevated. The exterior shell is ornamented by fine concentric lirae or projecting lamellae; the interior edge is smooth, the pallial sinus shallow.

The modern representatives live in the Mediterranean and NE Atlantic, from the shallow subtidal to the bathyal (POPPE & GOTO 1993). The fossil record begins with the late Early Miocene to early Middle Miocene in the North Sea Basin, Atlantic, Mediterranean, Central and Eastern Paratethys and maybe also Indian Ocean (KAUTSKY 1936-1937, JANSSEN 1984, NEVESSKAJA & al. 1993).

Subclassis: Anomalodesmata DALL, 1889
Ordo: Myoida STOLICZKA, 1870
Familia: Teredinidae RAFINESQUE, 1815
Genus: indet.

**Teredinidae indet.** (Pl. 8, Figs. 9-10)

Material: Mühlbach (Mü1) – 5 calcareous tubes, Mühlbach (Mü2) - 88 calcareous tubes; maximal tube diameter 5.5 mm

Despite numerous calcareous siphonal tubes, no pallets or shells are available, hindering a more detailed taxonomic classification. Except for *Kuphus*, characterised by distinctly stronger calcified and larger tubes, Teredinidae are typical wood borers (MOORE 1969-1971).

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Plates

All specimens are stored in the collection of the NHMW
Plate 1

Fig. 1: *Turritella badensis* SACCO, 1895, height: 5.6 mm, fragment of the early teleoconch, Mü1
Fig. 2: *Epitonium miofrondiculoides* (SACCO, 1891), height: 2.3 mm, fragment, Mü2
Fig. 3: *Epitonium miofrondiculoides* (SACCO, 1891), height: 2.4 mm, fragment, Mü2
Fig. 4: *Pomatias* sp., maximum diameter: 4.8 mm, operculum, Mü2
Figs. 5-6: *Gastrocopta (Albinula)* cf. *acuminata* (KLEIN, 1846), height: 3 mm, Mü2
Figs. 7-8: *Vallonia subcyclophorella* (GOTTSCHECK, 1911), diameter: 2.2 mm, Mü2
Plate 2

Fig. 1: *Yoldia (Yoldia) reussi* (HÖRNES), right valve (RV), fragment of the hinge region, the arrow shows position of the resilifer, length part.: 3 mm, Mü1; a: dorsal view, b: ventral view, c: interior view.

Fig. 2: *Mytilus (Crenomytilus) haidingeri* HÖRNES, RV, fragment of the umbonal region, the arrow shows pit-row tracing the ligament area, length part.: 6.8 mm, Mü1; a: exterior view, b: interior view.

Fig. 3: *Anadara diluvii* (LAMARCK), RV, fragmented, height part.: 4.5 mm, Mü1; a: exterior view, b: dorsal view, c: anterior view, d: interior view.

Fig. 4: *Ostrea (Ostrea) digitalina* (EICHWALD), left valve (LV), young specimen, height: 13.5 mm, Mü1; a: exterior view, b: interior view.

Fig. 5: *Ostrea (Ostrea) digitalina* (EICHWALD), LV, adult specimen, height: 67 mm, Mü2; a: anterior view, b: interior view, c: exterior view.

Fig. 6: *Ostrea (Ostrea) digitalina* (EICHWALD), RV, young specimen showing one successful and two unsuccessful predatory gastropod borings, height: 6.5 mm, Mü1; a: exterior view, b: interior view, c: dorsal view.

Fig. 7: *Ostrea (Ostrea) digitalina* (EICHWALD), RV, young specimen, height: 12.2 mm, Mü1; a: exterior view, b: anterior view, c: interior view.

Fig. 8: “*Chlamys* trillirata” (ALMERA & BOFILL), morph 1, LV, fragmented, height: 9.6 mm, Mü1; a: interior view, b: posterior view, c: exterior view; exterior of the specimen coated with gold layer.
Plate 3

Fig. 1: "Chlamys" trilirata (ALMERA & BOFILL), morph 1, specimen of pl. 2, fig. 8; detail of the posterior ear and the proximal exterior disk region; exterior of the specimen coated with gold layer.

Fig. 2: "Chlamys" trilirata (ALMERA & BOFILL), morph 1, RV, fragment of the anteroventral disk portion, height part.: 16.1 mm, Mü1; a: exterior view, b: interior view, c: detail of the central exterior disc showing ontogenetic transition from shagreen into Camptonectes-type microsculpture; exterior of the specimen coated with gold layer.

Fig. 3: "Chlamys" trilirata (ALMERA & BOFILL), morph 2, fragmented, height part.: 9 mm, Mü1; a: exterior view, b: interior view, c: detail of the anterodorsal exterior region showing antimarginal striae on disk and shagreen microsculpture on ear, d: detail showing proximal exterior region and the non-synchronous initiation of disk ribs; exterior of the specimen coated with gold layer.
Plate 4

Fig. 1: *Crassadoma multistriata* (Pol.), LV, fragmented but with excellently preserved sculpture elements, height part.: 6.4 mm, Mü1; a: exterior view, b: interior view, c: dorsal view, d: detail of the posterodorsal exterior region, e: detail of the anterodorsal exterior region, f: detail of the proximal exterior region, g: Scanning electron micrograph of early dissoconch (pre-radial stage of the postlarval shell) showing coarsely punctate sculpture and the preserved prodissococonch (larval shell), h: detail of the central proximal exterior dissoconch showing typical net pattern; exterior of the specimen coated with gold layer.
Plate 5

Fig. 1: *Aequipecten macrotis* (Sowerby), LV, fragment of the posterodorsal region, height part.: 8.1 mm, Mü1; a: exterior view, b: dorsal view, c: interior view, d: orthogonal view of the posterodorsal exterior region, e: detail of the disk flank showing antimal marginal striation, f: detail of the distal portion of the fragment showing the typical *Camptonectes*-type microsculpture; exterior of the specimen coated with gold layer.

Fig. 2: *Aequipecten macrotis* (Sowerby), RV, fragmented, height part.: 11.2 mm, Mü1; a: exterior view, b: detail showing proximal exterior disk region and ears, c: dorsal view, d: posterior view; exterior of the specimen coated with gold layer.
Plate 6

Fig. 1: *Aequipecten macrotis* (Sowerby), as in pl. 5, fig. 2, Mü1; a: interior view, b: detail of the hinge, ctenolium and adductor scar, c: detail showing the prodissoconch (damaged), d: detail showing the ctenolium; exterior of the specimen coated with gold layer.

Fig. 2: *Anomia* (*Anomia*) *ephippium* Brocchi in Bronn, LV, adult specimen, fragmented, height: 15.2 mm, Mü1; a: exterior view, b: posterior view, c: dorsal view, d: interior view.

Fig. 3: *Anomia* (*Anomia*) *ephippium* Brocchi in Bronn, LV, young specimen, fragmented, height: 37 mm, Mü1; a: interior view, b: exterior view.
Plate 7

Fig. 1: *Loripes (Micoloripes) dentatus* (DEFRANCE), LV, adult specimen, height: 1.5 mm, Mü1; a: exterior view, b: dorsal view, c: interior view, d: posterior view.

Fig. 2: *Loripes (Micoloripes) dentatus* (DEFRANCE), RV, adult specimen with the naticid? gastropod boring, height: 1.9 mm, Mü1; a: exterior view, b: dorsal view, c: interior view.

Fig. 3: *Loripes (Micoloripes) dentatus* (DEFRANCE), RV, adult specimen with the naticid? boring at similar position as in Fig. 6, but distinctly larger in diameter, height: 2.3 mm, Mü1; a: exterior view, b: interior view.

Fig. 4: *Corbula (Varicorbula) gibba* (OLIVI), RV with peeled proximal part, height: 5.4 mm, Mü1; a: exterior view, b: interior view, c: posterior view, d: dorsal view.

Fig. 5: *Corbula (Varicorbula) gibba* (OLIVI), LV, height: 4 mm, Mü1; a: posterior view, b: exterior view, c: interior view, d: dorsal view.

Fig. 6: *Corbula (Varicorbula) gibba* (OLIVI), RV, height: 4 mm, Mü1; a: dorsal view, b: exterior view, c: interior view, d: posterior view.

Fig. 7: *Corbula (Varicorbula) gibba* (OLIVI), RV, fragmented, juvenile specimen showing larval shell, height: 0.9 mm, Mü1; exterior view.

Fig. 8: *Corbula (Varicorbula) gibba* (OLIVI), RV, height: 3 mm, Mü1; a: exterior view, b: interior view.

Fig. 9: *Corbula (Varicorbula) gibba* (OLIVI), RV, apparently elongated juvenile specimen died as a naticid prey, height: 3.1 mm, Mü1; a: exterior view, b: posterior view, c: dorsal view, d: interior view.

Fig. 10: *Corbula (Varicorbula) gibba* (OLIVI), LV, height: 3.1 mm, Mü1; a: interior view, b: exterior view.

Fig. 11: *Corbula (Varicorbula) gibba* (OLIVI), RV, juvenile specimen, height: 2.1 mm, Mü1; a: exterior view, b: interior view.

Fig. 12: *Corbula (Varicorbula) gibba* (OLIVI), LV, height: 3.6 mm, Mü1; exterior view showing the naticid boring at similar position as in Fig. 6.

Fig. 13: *Corbula (Varicorbula) gibba* (OLIVI), LV, juvenile specimen, height: 1.7 mm, Mü1; a: interior view, b: exterior view.

Fig. 14: *Corbula (Varicorbula) gibba* (OLIVI), LV, height: 2.5 mm, Mü1; a: exterior view, b: posterior view, c: interior view.
Plate 8

Fig. 1: *Parvicardium minimum* (Philippi), LV, fragmented, adult specimen, height part.: 2.3 mm, Mü1; a: interior view, b: dorsal view, c: exterior view, d: anterior view.

Fig. 2: *Spisula (Spisula) subtruncata* (Da Costa), RV, fragment of the proximal shell region, height part.: 2.6 mm, Mü1; a: dorsal view, b: exterior view, c: interior view.

Fig. 3: *Gouldia minima* (Montagu), RV; height: 2 mm, Mü1; a: exterior view, b: interior view.

Fig. 4: *Gouldia minima* (Montagu), LV, height: 5.5 mm, Mü1; a: interior view, smaller picture with light directed to enhance the hinge relief, b: dorsal view, c: exterior view, d: posterior view.

Fig. 5: *Gouldia minima* (Montagu), RV, fragmented specimen; height: 6 mm, Mü1; a: interior view, b: posterior view.

Fig. 6: *Gouldia minima* (Montagu), RV, height: 2.5 mm, Mü1; a: interior view, b: posterior view, c: dorsal view, d: exterior view.

Fig. 7: *Gouldia minima* (Montagu), LV, specimen shows one successful and one unsuccessful naticid? gastropod boring, height: 3 mm, Mü1; a: exterior view, b: interior view.

Fig. 8: *Gouldia minima* (Montagu), RV, height: 2.2 mm, Mü1; a: interior view, smaller picture with light directed to enhance the hinge relief, b: exterior view.

Fig. 9: Teredinidae indet., calcareous siphonal tube, length: 3 mm, Mü2.

Fig. 10: Teredinidae indet., calcareous siphonal tube, length: 5.5 mm, Mü2.