

PECTINID BIVALVES FROM THE GRUND FORMATION (LOWER BADENIAN, MIDDLE MIOCENE, ALPINE-CARPATHIAN FOREDEEP) — TAXONOMIC REVISION AND STRATIGRAPHIC SIGNIFICANCE

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Abstract: The present study investigates the pectinid bivalve record characterizing the Middle Miocene Grund Formation from the Lower Austrian part of the Alpine-Carpathian Foredeep. The results provide the first comprehensive compilation of that pectinid assemblage, based on the recent excavation material and historic collections. Updating and revision of genus and species level taxa excluded polyphyletic taxa and allowed a more accurate correlation with occurrences from adjacent regions distributed across the NE Atlantic, Mediterranean, Paratethys and Indian Ocean. Hence 10 species level taxa — “*Chlamys*” *trilirata*, *Hinnites crispus*, *Crassadoma multistriata*, *Aequipecten malvinae*, *Ae. macrotis*, *Costellamussiopecten cristatus badense*, *Oopecten solarium*, *Macrochlamis nodosiformis*, *M. tournali* and *Pecten subarcuatus styriacus* — were identified. Thereby the subgenus *Costellamussiopecten* was separated from *Amussiopecten*, elevated to the genus level and applied to the lineage including the European “*Amusium*” — *C. cristatus*. *Macrochlamis* has been regarded as a valid name, and a senior synonym of *Gigantopecten*. “*Chlamys*” represents a still unavailable genus-name closely related to the *Chlamys* group. The species level revisions include discovery of *H. crispus* based on previously erroneously identified specimens. Moreover the new material brought the first evidence of the presence of *Ae. malvinae* and “*Ch.*” *trilirata* in the Grund Formation. The latter three taxa greatly enhanced the stratigraphic signature of this pectinid assemblage allowing an accurate inference of the Early to Middle Badenian (regional Central Paratethys geochronological unit isochronous with the Langhian, that is early Middle Miocene) age and a regional correlation with the Lower Lagenidae Zone for the NE Austrian Neogene basins.

Key words: Middle Miocene, Lower Badenian, Central Paratethys, Alpine-Carpathian Foredeep, biostratigraphy, taxonomic revision, pectinid bivalves.

Introduction

The pectinid bivalves are substantial contributors to the Grund Formation molluscan fauna (e.g. Kautsky 1928), representing the oldest Middle Miocene molluscan assemblage of the Alpine Molasse Zone in Lower Austria. Those characteristic inhabitants of the past and recent marine shelf regions went through a massive radiation event in the Lower Miocene and rose consequently to typical elements of the Neogene shallow benthic fauna (Ben Moussa & Demarcq 1992). Due to their abundance, intensive speciation, common short species duration but also due to enhanced preservation potential due to predominantly calcite shell mineralogy (e.g. Taylor et al. 1969; Carter et al. 1998), this group of bivalves represents an important biostratigraphic tools in shallow marine environments from Oligocene to recent times. Indeed the Paleogene-Neogene pectinid biozonations exist both for the Mediterranean (Demarcq 1990, 1992) as well as for the Paratethyan regions (Báldi & Seneš 1975; Bohn-Havas et al. 1987; Studencka 1999).

The aim of the present study is to provide the first comprehensive compilation of the pectinid bivalve record contributing the Grund Formation, based on the published material, historic collection of the Natural History Museum in Vienna and the University of Vienna — Department of Paleontology and on the recent excavation material. Updating and revision

of genus and species level taxa should exclude the polyphyletic taxa and allow accurate species level correlations with other well defined occurrences. This will enable the construction of a most accurate stratigraphic range chart for the assemblage providing finally a solid base for analysis of the faunal biostratigraphic signature.

Paleogeography, age and regional geological setting

The studied assemblage derives from the Alpine Molasse Zone situated in the western part of the Alpine-Carpathian Foredeep (Fig. 1). In the Middle Miocene the region belonged to the western part of the Paratethys Sea, termed also the Central Paratethys. The Western Paratethys Sea that occupied the Alpine Foredeep westwards from the Bohemian Massif terminated in the latest Oligocene. The regional geodynamic history influenced strongly the Central Paratethys deposition and environment resulting in difficulties in correlations with the standard stratigraphic divisions and development of the regional chronostratigraphic division. Hence the Grund Formation belongs to the regional Badenian Stage corresponding to the lower part of the Middle Miocene.

The fully marine deposits of the Grund Formation (Fig. 2) overlay similar deposits of the Karpatian Laa Formation complicating commonly their distinction in the field (Rögl et al.



Fig. 1. Regional geological and paleogeographical position of studied samples from the Lower Badenian Grund Formation (modified after Mandic et al. 2002). The Molasse Zone corresponds with the Alpine-Carpathian Foredeep, whereas the Vienna Basin is an intra mountainous strike-slip basin raised through extensional movements between the Alpidic and the Carpathian Units. In the Middle Miocene the region belonged to the western part of the Paratethys Sea, termed also the Central Paratethys. The Western Paratethys Sea that occupied the Alpine Foredeep westwards from the Bohemian Massif terminated in the latest Oligocene (cf. Fig. 3).

2002). The mollusc bearing outcrops of the Grund Formation are scattered in wine cellars, representing the upper part of the 250 m thick succession. This succession belongs to the NN5 Calcareous Nannoplankton Zone and bears foraminiferal assemblage with *Praeorbulina glomerosa circularis* and *Uvigerina macrocarinata* and in its upper part also *Orbulina suturalis* (Rögl et al. 2002; Ćorić et al. 2004). The site at Grund was artificially outcropped during the excavation seasons in 1998 and 1999 (Zuschin et al. 1999; Roetzel & Pervesler 2004). NN5 datum was inferred by Ćorić & Švábenická (2004) throughout the section, whereas the introduction of rare *P. glomerosa circularis* and *Uvigerina macrocarinata* was found by Rögl et al. (2002) in the upper part of the composite section, correlating with the paleoenvironmental deepening. Hence the FAD of the *P. glomerosa circularis* with 16.0 Ma precede distinctly the base of the NN5 Zone (Rögl et al. 2002). *Orbulina suturalis*, possibly requiring still deeper marine settings, was not found at Grund excavation sites 1998 and 1999. The paleomagnetic survey of the site proved, how-

ever, a normal polarity, corresponding with the Chron C5Bn.2n (Fig. 3; Ćorić et al. 2004) having the lower boundary at 15.1 Ma and correlating exactly with the base of the M6 Zone (defined indeed by the FAD of *Orbulina suturalis*) by Berggren et al. (1995). For the latter reasons the mollusc bearing horizons at latter site must succeed the base of the Middle Miocene by at least 1.3 Ma (cf. Rögl et al. 2002). This site along with other fossiliferous localities of the Grund Formation are all attributed previously by Grill (1968) into the Lower Lagenidae Zone. As argued by Rögl et al. (2002) the cooccurrence of *Praeorbulina glomerosa circularis* and *Orbulina suturalis* is typical for the upper part of the Lower Lagenidae Zone.

Material

The studied material derives from different sites in the Grund Formation (Figs. 1, 2). Except for a very fine surface abrasion the shells are exceptionally well preserved. The juvenile as well as adult specimens are abundantly present.

This study is based on the material sampled during the excavation 1998 at Grund (Fig. 2, point 1). The series of ditches exposed a predominantly silty and sandy siliciclastic succession including numerous specimen rich shell beds of tempestitic origin (Roetzel et al. 1999; Zuschin et al. 2001; Roetzel & Pervesler 2004). The complete shell material has apparently been transported from a shallower subtidal sea bottom area into a deeper marine environment inhabited mono-specifically by a chemosymbiont bearing bivalve *Thyasira michelottii* (Hoernes). The material is in the collection of the Department of Paleontology, University of Vienna (abbreviated in text as **DPUV1**).

The specimen richer material derives, however, from a field ditch E Grund (Fig. 2, point 2) in lateral eastward continuation to the former locality. Its sediment character — the yellowish, silty fine sand — and the taphonomic features of shells is identical to that of the Grund Excavation 1998 site. The site position is on the acre, about 100 m south-southwest wards from the railroad crossing between Grund and Wullersdorf (Fred Rögl, pers. com. 2003). Fritz Steininger (Senckenberg Museum Frankfurt) & Fred Rögl (Natural History Museum Vienna) took a large bulk sample there, that has been sorted out and stored in the Stratigraphic Collection of the Department of Paleontology, University of Vienna (abbreviated in text as **DPUV2**).

Additional studied material derives from the Locality and Systematic Collections of the Department of Geology and Paleontology at the Natural History Museum in Vienna. The locality specifications of investigated specimens are Grund, Immendorf, Gunterdsdorf and Windpassing (Fig. 2, underlined village names). The exact position of historic localities is unknown. The systematic collection (abbreviated in text as **NHM1s**) comprises specimens investigated and documented by Höernes (1867) and Kautsky (1928). The locality collection comprises the material studied by Sieber (1947, 1949) (abbreviated in text as **NHM1s**), but also the material derived from the Grund Excavation 1998 (abbreviated in text as **NHM1v**). The latter specimens derive from a large microvertebrate bulk sample collected by Gudrun Höck & Mathias Harzhauser (both



Fig. 2. Geographical and geological position of sites from which the studied pectinids come. The fully marine deposits of the Grund Formation overlay similar deposits of the Karpatian Laa Formation generally complicating their distinction in the field. Biogenic limestone of the Badenian Mailberg Formation intercalates with the topmost part of the Grund Formation. The Sarmatian sands in the marginal, restricted marine facies transgressively overlay later deposits and are exposed in the southeastern part of the region, around Hollabrunn. Conglomerates of the Pannonian Hollabrunn-Mistelbach Formation on the top of the succession represent an ancient E-W striking fluvial stream. The indicated sites are: (1) Excavation Grund 1998 and (2) Field ditch E Grund (cf. text). The underlined names of villages are site specifications of the studied material from the Natural History Museum Collections. The more precise positions of the historical sites are however unknown (illustration combines geology by Roetzel & Pervesler (2004) and geography by the Austrian Map 1:200,000, BEV, Vienna).

Natural History Museum Vienna). The sample derives from the basal bed of the section B1 of Zuschin et al. (2001) and corresponds to the sample specification GRU B1-1 of Roetzel & Pervesler (2004). It represents a composite shell bed with a silty matrix in the lower 20 cm and a coarse sandy matrix in the upper 10 cm. The base of the upper part is characterized by the occurrence of flattened mud clasts. Beside predominantly fully marine molluscs, also land gastropods, brackish bivalves and remains of marine and terrestrial vertebrates are present.

Results and discussions

Faunal composition and taxonomic revisions

The investigated samples documents ten different pectinid species contributing to the Grund Formation. These are:

1. "*Chlamys*" *trilirata*
2. *Hinnites crispus*
3. *Crassadoma multistriata*
4. *Aequipecten malvinae*
5. *Aequipecten macrotis*
6. *Costellamussiopecten cristatus badense*
7. *Oopecten solarium*
8. *Macrochlamis nodosiformis*
9. *Macrochlamis tournali*
10. *Pecten subarcuatus styriacus*

Three species among them can be considered new for the Grund Formation. This is an unexpected result as the taxonomic content of the famous assemblage was already the subject of numerous previous studies (e.g. Hörnes 1867; Kautsky 1928; Sieber 1947, 1949; Schultz 2001). In particular, whereas *Aequipecten malvinae* and *Hinnites cristatus* represent completely new records, a note on the presence of "*Chlamys*" *trilirata* was provided recently by Mandić & Harzhauser (2003). The specimens of the latter species were recently extracted from samples from the field ditch E Grund and from the Grund excavation 1998 material. Correspondingly *Aequipecten malvinae* derived also from the Grund excavation and from the field ditch E Grund. Both species were indeed absent from the historical collections. Hence only the specimens of *Hinnites cristatus* were found within the material already investigated by Hörnes (1867) and Schultz (2001). As discussed below these represent the erroneous identifications of *Hinnites brussoni leufroyi*.

Among the new Grund material however no traces of *Macrochlamis tournali*, *M. nodosiformis*, *Oopecten solarium*, *Costellamussiopecten cristatus badense* and *Hinnites crispus* were found. Thereby whereas *Pecten subarcuatus styriacus*, *Aequipecten macrotis* and *Crassadoma multistriata* are relatively common contributors, the two newly found species are rather rare. Finally, it can be stated that the new fauna includes many juveniles, but lacks the larger individuals, which is an apparent sorting effect (cf. Zuschin et al. submitted).

Two taxa mentioned by previous workers are not included in the present study. These are *Aequipecten scabrellus* and *Oppenheimopecten aduncus* (cf. Schultz 2001). The first species could not be traced within the investigated material and could possibly represent an erroneous identification of *Aequipecten macrotis*. A candidate for *Oppenheimopecten aduncus* is a small, abraded, single left valve found in the Sieber Collection. The identification of that specimen however on the species level appears not possible to the present author also because the shape of the right valve remained unknown.

Previous authors (Hörnes 1867; Kautsky 1928 and Schultz 2001) illustrated only five taxa of the Grund Formation. These are *Crassadoma multistriata*, *Aequipecten macrotis*, *Macrochlamis nodosiformis*, *Macrochlamis tournali* and *Pecten subarcuatus styriacus*. Hence the present study provides the most comprehensive documentation of the Grund Formation pectinids hitherto.

As mentioned above one of the most important species level revisions was made by regarding the specimens previously identified with *Hinnites brussoni leufroyi* as the typical *Hinnites crispus*. The former taxon, characterizing the Late Egg-

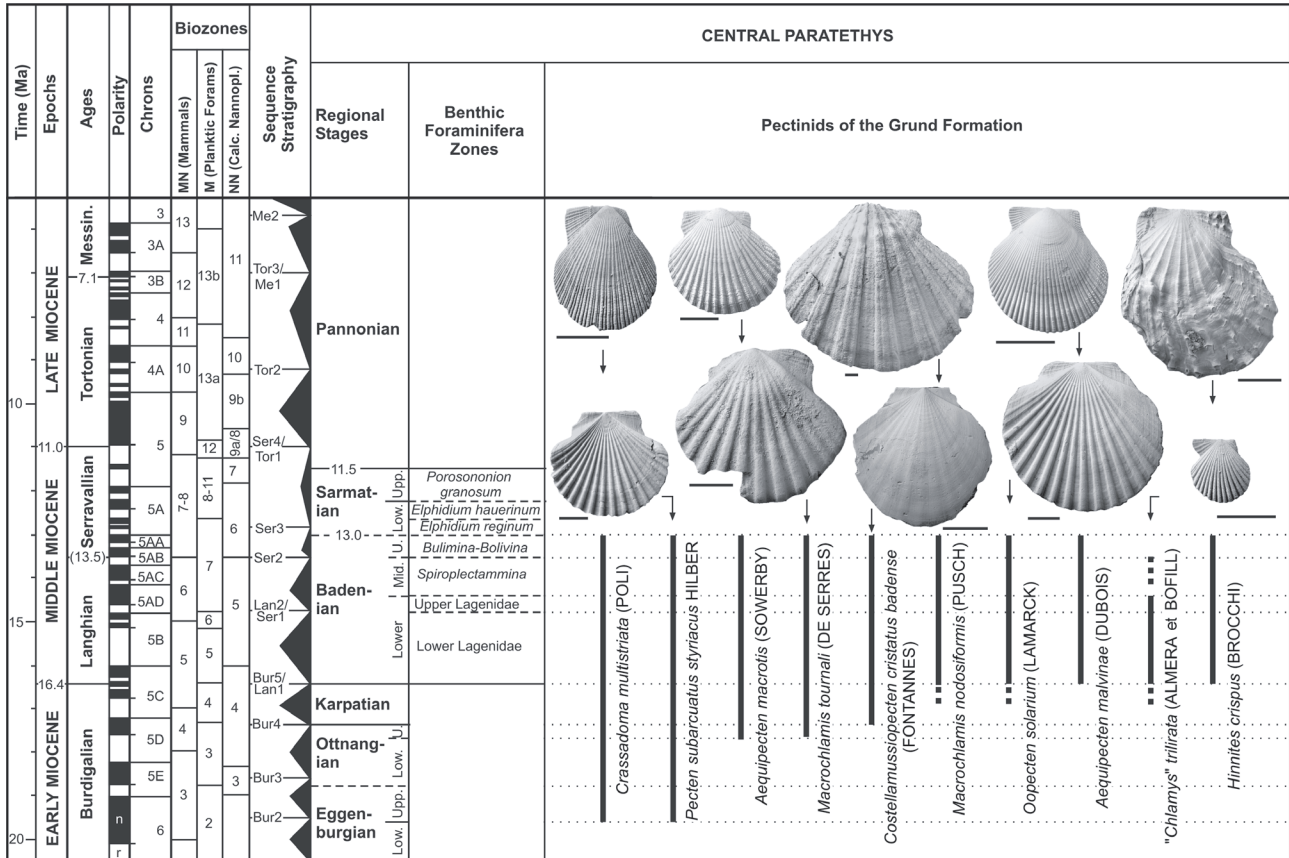


Fig. 3. Illustration shows the pectinid assemblage of the Grund Formation clearly demonstrating its Early Badenian age. The left side of the table provides a correlation of standard geochronology, magnetostratigraphy, biostratigraphy (European Mammal, (Sub)tropical Planktonic Foraminiferal and Calcareous Nannofossil — Faunal Zones) and sequence stratigraphy (European Basins) with the regional Central Paratethys chronostratigraphic and biostratigraphic divisions (modified after Mandic et al. 2002). The right side shows stratigraphic distributions of pectinid species documented by the present study from the Grund Formation. The dashed line points to an uncertain, insufficiently documented literature record. The photograph of a single left valve is provided for each species. Scale bars mark the 1 cm distances.

enburghian successions (cf. Mandic & Steininger 2003) is completely external covered with shagreen microsculpture. *Hinnites crispus* with macrosculpture almost identical with *Hinnites brussoni* lacks completely the shagreen microsculpture (cf. Roger 1939; Waller 1993). As even the most careful reinvestigation of the Grund specimens, could not prove any trace of that microsculpture on ears or disc exterior the previous identifications by Kautsky (1928), Sieber (1947, 1949) and Schultz (2001) were rejected and emended to *Hinnites crispus*.

Following the results of current reinvestigation of the type material of Roger (1939), Almera & Bofill (1897), Kittl (1887) and Schultz (2001) by the present author (see also Mandic & Harzhauser 2003) "*Chlamys*" *trilirata* replaces *Aequipecten bryozoderms* of Schultz (2001) as being found to represent its senior synonym. The latter author already recognized the Middle Miocene specimens from the Lower Badenian Gaindorf Formation (Lower Austria) and Florian Formation (Styria) as unrelated to the Eggenburgian "*Chlamys*" *jakloweciana* (Kittl). The species is now additionally documented from the Grund Formation as well.

Following detailed reinvestigations by Studencka (1986) the present study contradicts Schultz (2001) and reunites

Aequipecten flavus and *Aequipecten malvinae*. The former author showed clearly that those taxa represent only growth stages of one and the same taxon. This is underpinned by the fact that their type specimens (Dubois 1831) derived from one and the same locality. Indeed the findings from the Grund Formation representing the *Aequipecten flavus* morphology are all small and represent maximally young adult growth stages.

Beside species level revisions, the present study proposes several genus-level emendations (see Systematic paleontology chapter for details). Hence it neglects the phyletic relationship between *Costellamussiopecten* and *Amussiopecten* and elevates the former subgenus of Bongrain et al. (1994) to the genus level. Moreover the previous generic classification of *Amusium cristatum* (e.g. Freneix et al. 1982; Demarcq 1990; Studencka 1999; Schultz 2001) is rejected and its classification with *Costellamussiopecten* is proposed. This is based on phyletic as well as on morphological evidence. Thus *Amusium* with its type species *A. pleuronectes* inhabiting Pliocene to Recent Indo-Pacific (e.g. Eames & Cox 1956) do not possess the scaly ornament of the dorsal ears margin. In contrast the latter is not only typically developed in the European Pliocene

“*Amusium*” *cristatum*, but also in the whole Oligocene to Miocene lineage preceding the later species including the Grund Formation contributor “*Amusium*” *cristatum badense*. Their similarity in disc morphology is regarded as a consequence of a parallel evolution due to best possible shape adaptation to similarly preferred swimming behaviour and is categorized as a striking example of homeomorphy (cf. Waller 1991). Morphology with dorsal scaly ornament (“*crista*”) combined with a three tooth pair hinge, proved to be a feature typical for the *Costellamussiopecten* type species — *C. haueri* (Michelotti). Consequently the present author regards the European “*Amusium*” as a member of the genus *Costellamussiopecten*.

The usage of the generic designation *Macrochlamis* is explicitly favoured in the present study instead of the genus name *Gigantopecten*, which has found unfortunately common usage in the newer literature (e.g. Bongrain 1988, 1992; Studencka et al. 1998; Schultz 2001). The original spelling *Macrochlamis* by Sacco (1897a) is the correct original spelling sensu ICZN 1985 Art. 32b because no evidence for an incorrect spelling is provided in the original publication according to the same article, section c. Its emendation by Sacco (1897b) into *Macrochlamys* by means of different subsequent spelling without explanation in a following publication (Art. 33b (i)) must be discarded as being homonymic with the name already occupied by a gastropod (comp. Hertlein 1969). The substitution of the name *Macrochlamys* with the new name *Gigantopecten* by Rovereto (1899) is consequently also invalid because the next available name is already provided with *Macrochlamis*. The principle of one-letter difference in genus-group names (Art. 56b) provides the final argument for the validity of the latter name.

Oopecten solarium was currently classified with *Flabellipeecten* (e.g. Bongrain 1986; Schultz 2001), which contradicted the result of Roger (1939). The latter author investigated the complete European Neogene pectinid record and concluded its closest relationship with the *Oopecten rotundatus* (Lamarck) — the type species of *Oopecten* (Sacco 1897b). The present author follows the latter result and refers to the extremely laterally elongated ears, but also to the gigantic size that this species can attain (e.g. Kautsky 1928), a feature coinciding with other related taxa like for example the Early Eggenburgian *Oopecten gigas*.

The generic emendation for “*Chlamys*” *trilirata* was made by neglecting its classification with the *Aequipeecten* proposed by Schultz (2001). Thus Waller (1991, 1993) very clearly defined *Aequipeecten* using morphological as well as phylogenetical arguments. Beside the hinge shape with a prominent laterally elongated resiliar tooth pair in the right valve, the development of the commarginal sculpture with projecting lamellae forming an inner lobe on the rib flanks are also among the most striking features, definitely absent in “*Chlamys*” *trilirata*. In contrast the latter species bears well developed shagreen microsculpture unique for the group of taxa closely related to the genus *Chlamys* in the strict sense (cf. Waller 1993). As, however, another feature typical of *Chlamys* — the numerous thin radial ribs multiplying distally by intercalation or bifurcation — is absent, and another genus level designation including forms similar to “*Chlamys*” *trilirata* is not available the present study applies the provisional

taxonomic genus level designation. Hence the possible new genus represented by that unusual morphology also apparently includes “*Chlamys*” *jakloweciana*.

Biostratigraphic inferences

The recognition of three new species (*Aequipeecten malvinae*, *Hinnites cristatus*, “*Chlamys*” *trilirata*) in the Grund Formation apparently improved the biostratigraphic significance of the represented assemblage. Thus the FOD (First Occurrence Datum) of all three taxa is above the base of the Middle Miocene in the Paratethys, excluding unequivocally the speculated Lower Miocene age for Grund Formation deposits (Fig. 3). Moreover *Aequipeecten malvinae* with its form *Aequipeecten flavus* was regarded as having a high biostratigraphic significance in contributing the Badenian pectinid assemblage zone defined by Bohn-Havas et al. (1987). Its only older record deriving from a list by Kóky (1967), which provided the author’s identifications of the Karpatian molluscs collected at Várpalota in Central Hungary is classified as highly doubtful in the present study. No other Lower Miocene Paratethys record of that species is additionally available.

Oopecten solarium and *Macrochlamis nodosiformis* are principally unknown from the Early Miocene of the Central Paratethys, being otherwise common in the Middle Miocene reaching there huge dimensions (cf. Kautsky 1928). The only possible exception is their “Karpatian” record in the Várpalota Basin of Central Hungary (Kóky 1967 and 1991). Yet the biostratigraphic re-evaluation of the Várpalota Basin deposits formerly attributed to the Karpatian shows that at least their upper part (the series 4. and 5. of Kóky 1967, acc. to personal communication to author) exactly correlates with the “Grund Horizon”. Hence, as referred by Kóky (1991) they bear not only the Badenian benthic foraminifer *Borelis melo*, but also passes gradually toward the basin into pelitic-sandy sediments bearing the calcareous nannoplankton assemblage of the NN5 Zone. From these sediments indeed the local FOD of *Aequipeecten malvinae* is recorded. *Oopecten solarium* and *Macrochlamis nodosiformis* derive, however, from the underlying sediments belonging to the NN4 Zone (Kóky 1991). Their attribution to the Karpatian still remains questionable as NN4 datum has been likely recorded from the lower part of the Grund Formation (Ćorić & Rögl 2004) as well as from the Lower Badenian of the Styrian Basin (Rögl et al. 2002). Interestingly, as proved by the present author in the Kóky Collection (Budapest), the oldest Central Paratethys occurrence of “*Chlamys*” *trilirata* is also recorded from the latter horizon of the I-116 well.

Oopecten solarium, *Macrochlamis nodosiformis* along with *Aequipeecten malvinae* all seem to originate in the Early Miocene of the NE Atlantic and Mediterranean (cf. Roger 1939; Schultz 2001), migrating with the changing paleoclimate around the Early/Middle Miocene transition into the Central Paratethys (cf. Harzhauser et al. 2003). The Early Miocene record of “*Chlamys*” *trilirata* is possibly represented by specimens from the Algerian Burdigalian identified by Freneix et al. (1974) with *Chlamys jakloweciana*. In contrast *Hinnites crispus* is apparently absent in any Lower Miocene deposits according to the author’s knowledge (cf. Roger 1939; Waller

1993) implying unequivocally the Middle Miocene age for the Grund Formation.

Whereas all other species are transitional throughout the Badenian, the absence of "*Chlamys*" *trilirata* seems to be proven at least from the Upper Badenian. Its only Middle Badenian record was signaled to the author currently by Kókay (pers. comm.) by referring to findings from exploration wells for the new metroline of Budapest in Hungary. Its presence in the Lower Lagenidae Zone is recorded throughout Austria — in the Grund-, Gaiendorf- and Florian Formations. Yet from the Austrian Upper Lagenidae Zone no records are available. Yet, from the latter horizon of the Hungarian Várpalota Basin a well preserved right valve is illustrated by Keskemeti Körmeny (1962). Interestingly, Ben Moussa & Demarcq (1992) restricted their *Chlamys jakloweciana* from the Mediterranean and NE Atlantic (most probably corresponding) with "*Chlamys*" *trilirata* to the Langian and Serravallian. The type locality of "*Chlamys*" *trilirata* is dated to the Early Langhian (Freneix et al. 1982). The locality in the Boujan in Provence produced a specimen rich sample originally studied by Roger (1939) has been dated to the Helvetian and its actual position within the Middle Miocene could not be detected within the more modern literature.

The transitional Early to Middle Miocene character of the represented molluscs is underlined by the common occurrence of taxa like *Pecten subarcuatus styriacus*, *Crassadoma multistriata* and *Aequipecten macrotis*. Those species are known already from the Late Eggenburgian to Early Ottnangian deposits. The FOD of *Macrochlamis tournali* is recorded from the "Late Ottnangian" of the Várpalota Basin and from the Karpatian of other Central Paratethyan sites. The stratigraphically oldest record of *Costellamussiopecten cristatum badense* seems to be in the Karpatian (Csepregy-Meznerics 1960).

Whereas the pectinid assemblage of the Grund Formation accurately indicates its Badenian age as suggested at least by the occurrence of *Aequipecten malvinae* and *Hinnites crispus*, a more precise bistratigraphic resolution based on the stratigraphic ranges of recorded taxa is impoverished. Hence all species except for "*Chlamys*" *trilirata* seem to be present throughout the Badenian (Fig. 3). Nevertheless the above discussed range of "*Chlamys*" *trilirata* means that at least the Late Badenian age of the Grund Formation can be accurately excluded.

Despite that, the absence of some characteristic Badenian taxa, might be suspected as highly indicative for its lowermost Badenian position (cf. Kautsky 1928). Hence the species typically present in the younger sediments of the Vienna Basin — such as the Upper Lagenidae Zone Baden-Sooß and Vösendorf — like *Costellamussiopecten spinulosus* and *Aequipecten elegans* are definitely absent in the Grund Formation. Apparently they are also missing in the same level of the Niederleis Basin. Studencka (1999), however, argued that the introduction of the Badenian pectinids including *Aequipecten elegans* appears to be diachronous in the Central Paratethys. Hence whereas *Aequipecten elegans* is very common in the Lower Badenian of the Pannonian Basin System — allowing Bon Havas et al. (1987) to define there the regional "*Chlamys elegans*-*Pecten revolutus* Subzone" — it is absent in the same horizon of the Alpine-Carpathian Foredeep. For the Pannon-

ian basinal system, its record from the Lower Lagenidae Zone of Costei in Romania is referred by Nicorici (1977) and Studencka et al. (1998). From the same locality *Costellamussiopecten spinulosus attenuatus* — a form closely related with *C. spinulosus spinulosus* and likely absent from the Grund Formation — is also available. Therefore at least the absence of the former taxon might be controlled by the paleoenvironmental conditions.

Conclusions

An updating and revision of the genus and species level taxa discarded several polyphyletic taxa and allowed a more accurate stratigraphic and paleobiogeographical correlation with occurrences from the Paratethys, NE Atlantic, Mediterranean, and Indian Ocean. Taxonomic revision brought several important genus-level and species level emendations. Hence the European "*Amusium*" *cristatum* lineage is for the first time classified with *Costellamussiopecten*. This former subgenus of *Amussiopecten* has been regarded as phylogenetically unrelated to it and in consequence elevated to the genus level. *Macrochlamis* has been regarded as a valid name, the genus-level designation *Gigantopecten* was recognized as its senior synonym. Probably a still unavailable genus-name for a shagreen bearing "*Chlamys*" *trilirata* and probably also Early Miocene "*Chlamys*" *jakloweciana* species related with the *Chlamys* in the strict sense are provisionally termed as "*Chlamys*". The species level revisions include discovery of *Hinnites crispus* based on previously erroneously identified specimens. Moreover the new material brought the first evidence of the presence of *Ae. malvinae* and "*Ch.*" *trilirata* in the Grund Formation. *Ae. malvinae* is thereby considered to be the senior synonym and the adult growth stage of *Ae. flavus*.

Based on reviewed taxonomy, this study proves that the pectinid bivalves as an important tool in solving the regional biostratigraphical problems. Hence, at least for the taxonomically and stratigraphically secured record from Austria, a resolution corresponding to the regional foraminiferal ecozone system has been detected. Thus the 10 species from the Grund Formation allow an accurate regional correlation with the Lower Lagenidae Zone and the lower part of the Lower Badenian based on the absence of taxa such as *Aequipecten elegans* and *Costellamussiopecten spinulosus*, which are common and typical species of the Vienna Basin Upper Lagenidae Zone. The correlation on the Central Paratethys level approximates the resolution of the calcareous nannoplankton implying its Early Badenian and possible Middle Badenian age.

Systematic part

Class **Bivalvia** Linné, 1758

Order **Ostreoida** Férussac, 1822 [emend. Waller, 1978]

Family **Pectinidae** Wilkes, 1810 [emend. Waller, 1978]

Remark: The taxonomy of the suprageneric level is left out in consequence that the emendation of the subfamily level taxonomy by Waller (1993) did not achieve a clear monophyletic division on that taxonomic level (Beu 1996; Waller,

pers. com. 2001; the present author's unpublished results). The tribal division on the other hand, introduced by Waller (1991, 1993), for the main recent taxa is left out as being apparently still under construction.

Except for revisions, the species level taxonomy applied in the present study follows Schultz (2001). As the latter author provided extended synonymy lists for each of those taxa, the synonymy lists of the present study refer primarily to that source.

Genus *Chlamys* (Bolten) Röding, 1798
[emend. Waller, 1993]

Type species: By Herrmannsen (1846), *Pecten islandicus* Müller, 1776, Pleistocene to Recent, N-Atlantic, within the cold pulses also in the Mediterranean (Roger 1939; Waller 1991).

“Chlamys” trilirata (Almera et Bofill, 1897)
(Fig. 4.1,5)

- 1897 *Pecten triliratus* Almera et Bofill — Almera et Bofill, p. 401, pl. 4, Figs. 6 and 6a
1897 *Pecten bryozodermis* Almera et Bofill — Almera et Bofill, p. 403, pl. 4, Figs. 13, 13a and 13b
1900 *Pecten jaklowecianus* Kittl — Bauer, p. 46, pl. 2, Figs. 19–22
1928 *Chlamys jakloweciana* Kittl — Kautsky, p. 255 (pars)
1939 *Chlamys jakloweciana* Kittl — Roger, p. 163 (pars), pl. 22, Figs. 9–10 and 16–18, pl. 24, fig. 7, pl. 26, Figs. 18–19
1962 *Chlamys jakloweciana* Kittl — Kecskemeti Körmendy, p. 218, pl. 23, Figs. 12 and 17
2001 *Aequipecten bryozodermis* (Almera et Bofill, 1897) — Schultz, p. 187, pl. 17, Fig. 8
2003 *“Chlamys” trilirata* (Almera et Bofill, 1897) — Mandic et Harzhauser, p. 101, pl. 2, Fig. 8, pl. 3, Figs. 1–3

Type: Roger (1939) referred the single right valve, originally reproduced as a drawing by Almera & Bofill (1897), with the height of 26.0 mm and the anterodorsal part broken for the holotype. It is housed in the Type Collection of the Department of Earth Sciences, Claude Bernard University Lyon (Identification No.: 29.088). Roger (1939, Pl. 22, Fig. 16) provided its photograph. Type locality, according to Almera (1896) and the identification card of the holotype, are exposures along the railway trench from E Ermita de Bará to San Vicente (Vendrell) in Catalonia (Tarragona, NE Spain). The succession of marine marls, sands and detritic limestones according to planktonic foraminiferal data of Freneix et al. (1982) is Langhian (early Middle Miocene) in age.

Material: 2 right valves from Grund (Coll. NHMlv), 2 right and 3 left valves from E Grund (Coll. DPUV2). Additionally studied material is from the Lower Badenian of the Gaiendorf Formation (Alpine-Carpathian Foredeep in Lower Austria) from Mühlbach, investigated by Mandic & Harzhauser (2003), from Gaiendorf investigated and identified by Kautsky (1928) and Roger (1939) as *Chlamys jakloweciana* (Coll. NHMs and NHMls) and from Goggendorf (Coll. NHMls; cf. Mandic & Harzhauser 2003). The holotype and the type specimen of *Pecten bryozodermis* Almera et Bofill from the Langhian of the Bara region in NE Spain and numerous other specimens from the Middle Miocene of Boujan (NE Bezier in S France) housed in the Type Collection of the De-

partment of Earth Sciences, Claude Bernard University Lyon and originally classified with *Chlamys jakloweciana* (Kittl) were also investigated.

Dimensions: Right valve — disc height = 22 mm, disc convexity = 3.2 mm; left valve — disc height = 11.2 mm, disc length = 10.4 mm, disc convexity = 1.9 mm, umbonal angle = 89.5°, ears length = 8.3 mm, ears height = 3.1 mm.

Description: Chlamydoid shell is small (maximally 22 mm in length), higher than long with length/high-ratio ranging between 0.88 and 0.93, biconvex, moderately arched, valves are thin and outside the palial line translucent, discs both posteroventrally elongated with rounded posterior and ventral margins and pointed anterior and dorsal margins, umbonal angles ranging between 83 and 90°. The right valve with 18–19 ribs, the left one with 17 ribs; on both valves ribs moderately prominent, wider than interspaces convex to subtriangular, initiated non-synchronously (the subsequent ones by intercalation) between shell height of 0.7 and 2 mm. At shell height of about 10 mm a single riblet can intercalate the interspaces of the lateral region, at shell height of about 20 mm three riblets on rib tops and one in each interspace become initiated on the central disc region, the riblets can develop coarse scales on tops. Ears large, pointed and about two times longer anteriorly, truncated posteriorly, up to 5 riblets can sculpture each one. Active ctenolium with fine denticles, and deep byssal synus present. Exterior typically sculptured by shagreen microsculpture present on the whole shell or reduced to its parts as in morphs with transversal bars developed on rib tops. The smooth parts bear commonly *Camptonectes*-type microsculpture. Interior with internal ribs lining the interspaces and missing the rib carinae. Hinge region very narrow with reduced dentition and shallow, triangular resiliar pit.

Variation: The strong morphological variation typical for this species (cf. Mandic & Harzhauser 2003) is expressed in the prominence of ribs and riblets and in the development of the shagreen microsculpture that can be almost completely absent. The transversal bars on rib tops are also rarely present. Normally the weaker radial sculpture is followed by reduced shagreen microsculpture. The transitional character of this variation is documented by a sample from the Middle Miocene of Boujan in S-France including more than 40 specimens and housed in the Roger (1939) collection.

Remarks: As noted by Mandic & Harzhauser (2003) investigations of the type material housed at the Type Collection of the Department of Earth Sciences, Claude Bernard University Lyon proved types of *“Chlamys” triliratus* and *“Chlamys” bryozodermis* (Almera et Bofill) for the left and the right valve of the same species. Roger (1939) correctly classified the latter specimen together with the specimens from the Lower Badenian of the Gaiendorf Formation. Yet as he erroneously held them for the topotypes of *Chlamys jakloweciana* (Kittl) he applied the latter name to all those specimens. The mistake was detected and partly revised by Schultz (2001). Hence *Chlamys jakloweciana* is not only restricted to the Early Miocene, but also differs by distinctly larger size, more massive shell and less numerous but more prominent ribs with a different sculptural pattern. The large left valve from the Badenian of Sievring being a part of the *Chlamys jakloweciana* original type series also differs from the Eggenburgian representatives (cf. Schultz 2001). According to the

arrangement and trigonal shape of ribs it appears to be related to *Chlamys justiniana* (Fontannes).

Chlamys jakloweciana indicated by Kautsky (1928) from the Karpatian (Late Burdigalian, Early Miocene) of Stetten/Korneuburg (NE Austria) is an erroneous identification of *Aequipecten* fragments previously published by Glaessner (1926) as *Pecten* (*Chlamys*) sp. nova. The lot bearing an identical inscription written by Glaessner (pers. com. M. Harzhauser, Vienna), but also "*Chlamys jakloweciana* Kittl, Dr. Kautsky det." is housed in the Locality Collection of the Geological Department — Natural History Museum Vienna.

As pointed out by Waller (1993) the shagreen microsculpture is a feature unique to *Chlamys*-related pectinids. Thus among other typical features like hinge and commarginal lamellae shape, especially the presence of shagreen microsculpture do not allow classification of "*Chlamys*" *triliratus* with *Aequipecten* (cf. Waller 1991). However, its morphology also differs importantly from the representatives of *Chlamys* s.s. (cf. Waller 1993). Hence the genus is provisionally referred to as "*Chlamys*".

Stratigr./Geogr. range: Early (to Middle?) Badenian of the Central Paratethys and Middle (to Late?) Miocene of the Mediterranean to NE Atlantic.

Its proper Central Paratethys documentation is restricted to the Lower Lagenidae Zone of the Gaidorf Formation, Grund Formation and Florian Formation in Styria (Bauer 1900) and Upper Lagenidae Zone of the Várpalota Basin (Kecskeméti Körmendy 1962). Other records, referring to "*Chlamys jakloweciana*" come from different Early Badenian localities in Romania and Bulgaria (Studencka et al. 1998). According to personal communication with Barbara Studencka (2003) the latter authors based their designation on a specimen from Costei illustrated by Nicorici (1977, pl. 42, Figs. 2a–2e), representing however a different species related to *Manupecten*. Its presence in the Middle Badenian of Budapest is currently signalized to author by Kóky (personal communication). Fragments of "*Chlamys jakloweciana*" from the Badenian of Samsonhaza, illustrated by Csepregy-Meznerics (1960, pl. 16, Figs. 6–7) are not related to "*Chlamys*" *trilirata* and therefore the reference of its presence in the Karpatian of Püspökhatvan and Otnangian of Budapest-Cinkota in the same study must be doubted.

The extraordinary rich collection from Boujan in Southern France originally documented by Roger (1939) is dated to the "Helvetien" and can be referred to the Middle Miocene. The type locality is of Langhian age (Freneix et al. 1982). Seravallian and Tortonian occurrence of "*Chlamys jakloweciana*" is mentioned only by Dermitzakis & Georgiades-Dikeoulia (1984), but without material evidence it is doubted in the present study.

Genus *Hinnites* DeFrance, 1821

Type species: *Ostrea crispa* Brocchi, 1814

Hinnites crispa (Brocchi, 1814)
(Fig. 4.6,7)

1867 *Hinnites defrancei* Micht. — Hörnes, p. 423 (pars), pl. 2, Figs. 1–2

1928 *Hinnites leufroyi* Serr. — Kautsky, p. 264

1947 *Hinnites leufroyi* Serr. — Sieber, p. 112

1939 *Chlamys crispa* (Brocchi, 1829) — Roger, p. 172, pl. 23, Figs. 11, 12, pl. 24, Fig. 6, pl. 25, Figs. 1, 4, pl. 28, Fig. 2

2001 *Hinnites brussoni leufroyi* (de Serres, 1829) — Schultz, p. 221 (pars), pl. 20, Figs. 2a–b, 4a–b

Type: Rossi-Ronchetti (1951–1957) referred to an articulated specimen illustrated by Brocchi (1814) and housed in the Natural History Museum in Milan (Brocchi collection; No. 460) for the holotype. It derived from Asti in NW Italy (cf. Roger 1939). The age of that occurrence originally regarded as Piacentino is Piacenzian (early Late Pliocene).

Material: Specimens from Windpassing (Coll. NHMIs) and Grund (Coll. NHMs).

Dimensions: Right valve — disc height = 46.2 mm, disc length = 42 mm, disc convexity = 4 mm, umbonal angle = 102°, ears length = 26.7 mm, ears height = 10.2 mm; left valve — disc height = 62.3 mm, disc length = 57 mm, disc convexity = 13 mm, umbonal angle = 106°, ears length = 34.6 mm, ears height = 15 mm.

Remark: The studied specimens were previously erroneously identified with *Hinnites brussoni* (compare Schultz 2001) yet also the most careful reinvestigation could not detect any traces of shagreen microsculpture which is its main distinctive feature toward *Hinnites crispus* (compare Roger 1939; Waller 1993). The apparent difference between former species is indeed only the absence of shagreen microsculpture in *Hinnites crispus* (cf. Roger 1939). Indeed both species are represented in the Middle Miocene of Paratethys. Hence the specimens from Grund identified by Schultz (2001) as *Hinnites leufroyi* and *Hinnites defrancei*, bear no shagreen microsculpture and consequently represent *Hinnites crispus* morphology. In contrast the specimen illustrated by Nicorici (1977, Pl. 44, Fig. 1a–1c) and identified as *Chlamys brussoni defrancei*, from the Badenian of SW Romania show shagreen microsculptural pattern and consequently represent typical *Hinnites brussoni*. With minor exceptions the present author principally follows revisions introduced by Waller (1991 and 1993). One such exception is the status of *Hinnites crispus* which is in the present study considered as a direct descendant of *Hinnites brussoni*. This interpretation supported by related shell morphologies as well as by their stratigraphic ranges, stays in discordance with the inference by Waller (1993) advocating the branching of *Hinnites crispus* off a *Laevichlamys* representative.

Stratigr./Geogr. range: Middle Miocene to Pliocene, ?Recent/Central Paratethys, Mediterranean. In the Central Paratethys it is restricted to the Badenian, in the Mediterranean and E Atlantic regions it is typically present from the Middle Miocene to Pliocene (Roger 1939). Waller (1993) refers the living *Hinnites* from the tropical West Africa offshore also to *Hinnites crispus*. It is possible that the latter region represents the current refugium of this termophylic taxon.

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

Type species: By original designation (Bernard, 1986), *Lima gigantea* Gray; Miocene to Recent of the eastern Pacific (Baja California to Alaska).

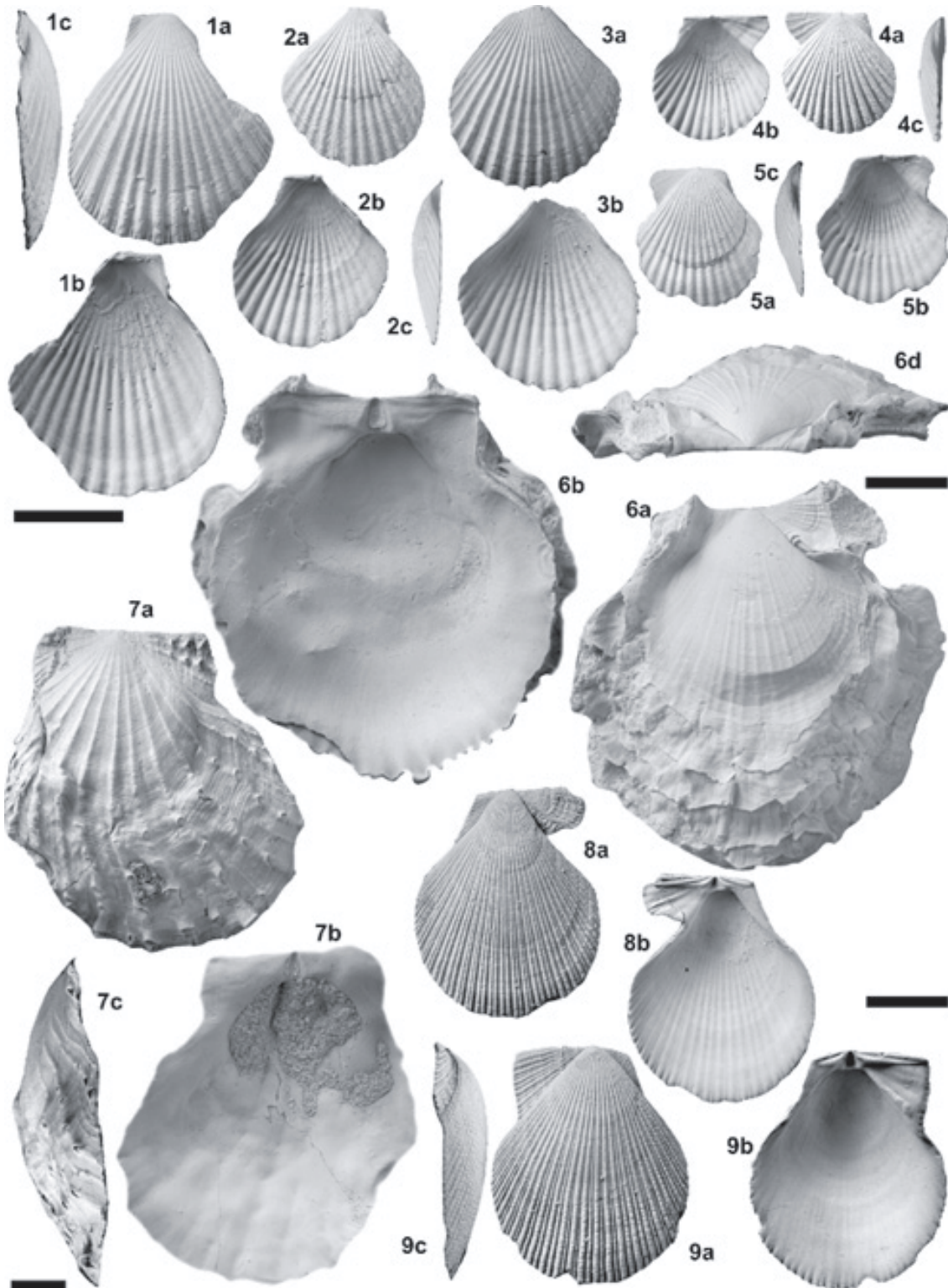


Fig. 4. “*Chlamys*”, *Hinnites* and *Crassadoma* from the Grund Formation. 1–5 — “*Chlamys*” *trilirata* (Almera et Bofill); locality: E Grund; collection: DPUV2 (compare text for abbreviations). 1 — anterodorsally fragmented right valve showing distal introduction of secondary radial sculpture. 2 — left valve with missing anterior ear. 3 — right valve with missing ears and proximal disc region. 4 — a complete right valve showing intensive shagreen microsculpture. 5 — right valve with marginally fragmented disc showing almost completely reduced shagreen microsculpture and well developed commarginal bars on rib tops characterizing the early growth stage. 6–7 — *Hinnites crispus* (Brocchi). 6 — a complete right valve; locality: Windpassing; collection: NHMls. 7 — a complete left valve; locality: Grund; collection: NHMs. 8–9 — *Crassadoma multistriata* (Poli) — locality: E Grund; collection: DPUV2. 8 — right valve with fragmented ventral margin. 9 — left valve with fragmented ventral margin. (The single scale bars (1 cm) refer to specimens 6 and 7 and to specimen groups 1–4 and 8–9. The letters imply the view: (a) exterior, (b) interior, (c) posterior and (d) dorsal.)

Crassadoma multistriata Poli (1795)
(Fig. 4.8,9)

- 1993 *Crassadoma multistriata* (Poli, 1795) — Waller, p. 212, Figs. 5a,d,g; 6c-j
2001 *Crassadoma? multistriata* s.l. (Poli, 1795) — Schultz, p. 176, pl. 16, Figs. 6, 9–12, pl. 17, Fig. 1–4

Type: Waller (1993) defined the original figure of Poli (1795, Fig. 14) as lectotype, although the original specimen, from the Holocene of Sicily (Italy) got lost. In consequence the author defined additionally three syntypes (Coll. NHM London).

Material: Numerous specimens from the field ditch E Grund (Coll. DPUV2) and from the excavation Grund 1998 (Coll. DPUV1 and NHMlv).

Dimensions: Right valve — disc height = 27 mm, disc length = 22.2 mm, disc convexity = 3.6 mm, umbonal angle = 81°, ears length = 16.1 mm, ears height = 6.5 mm; left valve — disc height = 28.9 mm, disc length = 23.8 mm, disc convexity = 5.2 mm, umbonal angle = 82.5°, ears length = 16 mm, ears height = 9 mm.

Remark: It can be easily distinguished from similar species like *Chlamys costai* (Sowerby in Smith) or *Chlamys justiniana* (Fontannes) by completely lacking the shagreen microsculpture. *Chlamys varia* (Linné) differs by its fixed number of ribs early in the ontogeny.

Stratigr./Geogr. range: Late Eggenburgian to Badenian of the Central Paratethys, Burdigalian Upper Marine Molasse of the Western Paratethys and Sakaraulian to Tarkhanian and Konkian of the Eastern Paratethys; Priabonian?, Burdigalian to Recent of the Mediterranean, E Atlantic and Indian Ocean.

Crassadoma multistriata inhabited at least since Burdigalian the regions between the Atlantic and the Indian Ocean, although its oldest reference is dated to the Priabonian (cf. Waller 1993). Its Central Paratethyan record apparently begins with the Late Eggenburgian when it immediately becomes common and characteristic within the shallow water successions (cf. Mandic & Steininger 2003).

Genus *Aequipecten* Fischer, 1886

Type species: By original designation (Fischer 1886) *Ostrea opercularis* Linnaeus, 1758 — Recent eastern Atlantic and Mediterranean.

Aequipecten macrotis (Sowerby in Smith, 1847)
(Fig. 5.1,2)

- 1949 *Chlamys macrotis* Sow. — Sieber, p. 112
2001 *Aequipecten macrotis macrotis* (Sowerby, 1847) — Schultz, p. 192, pl. 18, Fig. 2

Type: The holotype was originally not designated, yet Čtyroký (1969) regarded the left valve illustrated by Sowerby in Smith (1847, pl. 17, Fig. 15) as the holotype by monotypy. The specimen was collected at Adica, S Lisbon or Piedade region in Portugal. Apparently the type series included specimens from both localities and according to ICZN 1985, Art. 74b, Čtyroký (1969) must be deemed to have designated the

lectotype. Veiga Ferreira (1969) referred the occurrence at Adica to the Tortonian.

Material: Numerous juvenile to adult specimens from the field ditch E Grund (Coll. DPUV2) from the Grund excavation 1998 (Coll. DPUV1 and NHMlv) and from Immen-dorf (Coll. NHMls).

Dimensions: Right valve — disc height = 30.1 mm, disc length = 30.1 mm, disc convexity = 6.5 mm, umbonal angle = 82.5°, ears length = 21.2 mm, ears height = 8.5 mm; left valve — disc height = 25.8 mm, disc length = 27 mm, disc convexity = 6 mm, umbonal angle = 98°, ears length = 17 mm, ears height = 7 mm.

Remark: With 18 to 24 ribs this characteristic species has significantly fewer ribs than *Aequipecten malvinae*. *Aequipecten macrotis* is typically represented in the Early Badenian sediments of Grund and Niederleis. At Niederleis, it is the most typical molluscan species of the maerl facies (Mandic et al. 2002). In the latter locality it has been characteristically found in a marl facies. In the Paratethys it is present in the Burdigalian Upper Marine Molasse of the Western Paratethys. In the Central Paratethys the oldest findings are from the “late Ottnangian” of Bantapuszta in Hungary (see Schultz 2001).

Stratigr./Geogr. range: Late Ottnangian to Badenian of the Central Paratethys. Miocene of the Mediterranean to NE Atlantic.

Aequipecten malvinae (Dubois, 1831)
(Fig. 5.3,4)

- 1986 *Chlamys (Aequipecten) malvinae* (du Bois de Montpereux, 1831) — Studencka, 35, pl. 4, Figs. 4, 7 and 10a–b
2001 *Aequipecten flavus* (Dubois, 1831) — Schultz, p. 191, pl. 18, Fig. 1
2001 *Aequipecten malvinae* (Dubois de Montpereux, 1831) — Schultz, p. 197, pl. 18, Fig. 4 and 5

Type: Specimens illustrated by Dubois de Montpereux (1831, Pl. 8, Figs. 2 and 3) are from Shushkivitsky (former Szuszkowce, spelling by Dubois as Szuskowce) in the Ternopol region, NW Ukraine. Occurrence is dated to the Late Badenian (Muratov & Nevesskaja 1986; Studencka & Popov 1996). *Aequipecten flavus* (Dubois) and *Aequipecten diaphanus* (Dubois) types are from the same locality.

Material: Specimens from the field ditch E Grund (Coll. DPUV2) and from the Grund excavation 1998 (Coll. NHMlv).

Dimensions: Right valve — disc height = 15.6 mm, disc length = 15 mm, disc convexity = 3 mm, umbonal angle = 95°, ears height = 3.5 mm; left valve — disc height = 22.1 mm, disc length = 21.6 mm, disc convexity = 4.9 mm, umbonal angle = 95°, ears length = 13.8 mm, ears height = 5 mm.

Remark: The reunion of *Aequipecten flavus* and *Aequipecten malvinae* follows a great deal of evidence provided by Studencka (1986). The decision was moreover facilitated by the fact that the type series of the latter species derived from the same locality. The extremely detailed reinvestigation of numerous specimens from the type region could show that *Ae. flavus* represent apparently the young adult stage of *Ae. malvinae*. This correlates with the fact that specimens derived from the Grund Formation, varying by the rib number between 37 and 43, hence corresponding with *Ae.*

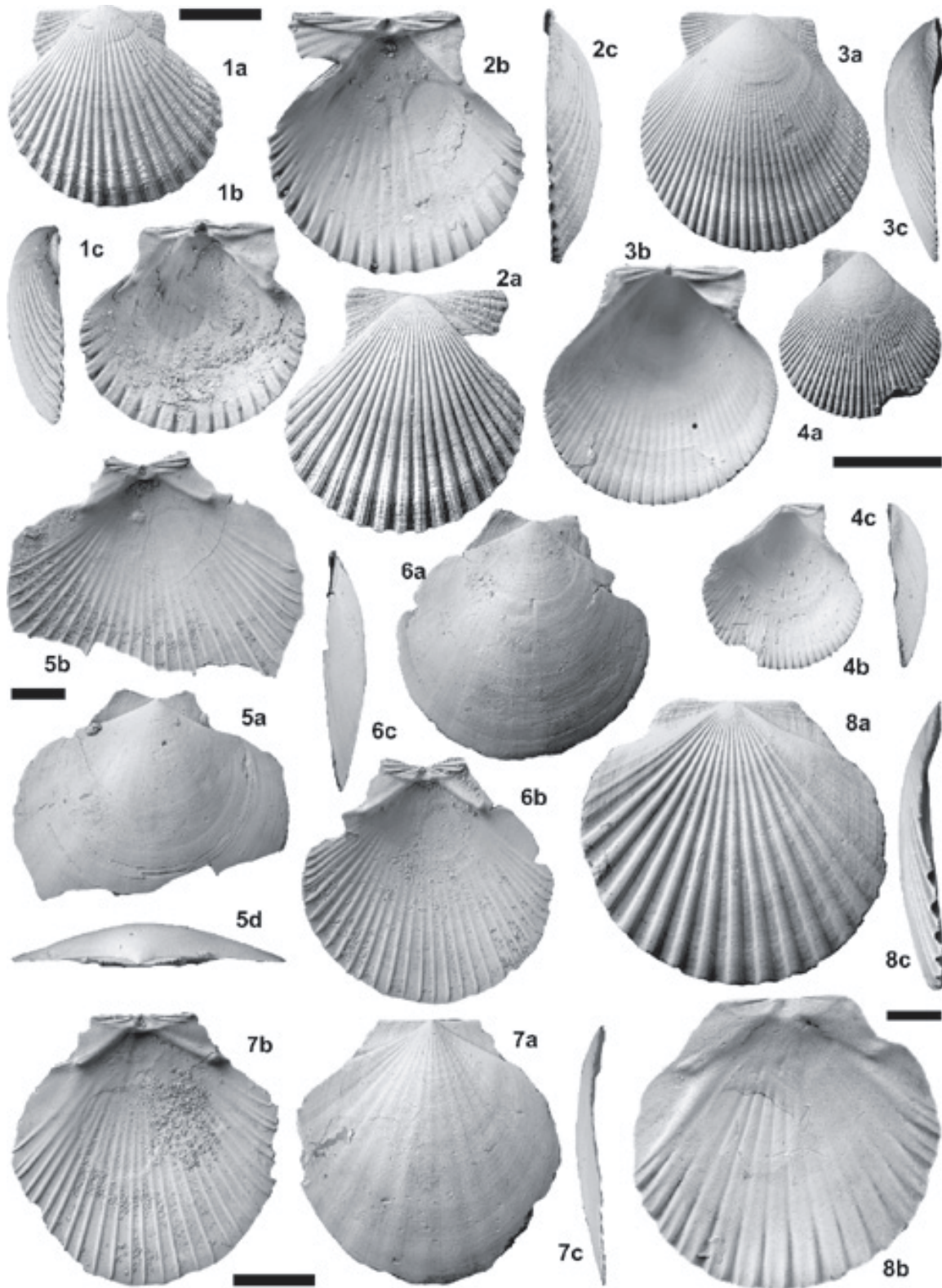


Fig. 5. *Aequipecten*, *Costellamussiopecten* and *Oopecten* from the Grund Formation. 1-2 — *Aequipecten macrotis* (Sowerby in Smith) — locality: Immendorf; collection: NHMIs (compare text for abbreviations). 1 — left valve with missing anterodorsal ear portion. 2 — a complete right valve. 3-4 — *Aequipecten malvinæ* (Dubois) — locality: Grund; collection: DPUV2. 3 — a well preserved left valve. 4 — right valve missing the anterior ear. 5-7 — *Costellamussiopecten cristatus badense* (Fontannes) — locality: Windpassing; collection: NHMIs. 5 — right valve with fragmented ventral disc portion. 6 — right valve with fragmented postero- and anterodorsal margins. 7 — left valve with abraded margins. 8 — *Oopecten solarium* (Lamarck) — locality: Windpassing; collection: NHMIs. 8 — a single left valve. (The single scale bars (1 cm) refer to specimens 5 and 7 and to specimen groups 1-2, 2-4 and 6-7. The letters imply the view: (a) exterior, (b) interior, (c) posterior and (d) dorsal.)

flavus are all smaller than 22 mm in height. According to Schultz (2001) *Ae. malvinae* has, besides better-developed secondary sculpture, also the lowered rib number (27–30 with 2–3 lateral ones).

Stratigr./Geogr. range: Badenian of the Central Paratethys, Tarkhanian and Konkian of the Eastern Paratethys, Burdigalian to Tortonian of the Mediterranean to NE Atlantic.

Specimen from the Late Ottnangian (Bohn-Havas et al. 1985) of Bantapuszta in the Central Hungarian Várpalota Basin identified by Kóky in Steininger et al. (1973) with *Aequipecten malvinae* apparently has a smaller number of ribs and represents another *Aequipecten* related species. As discussed above, the Karpatian occurrence from the same basin (Kóky 1967) is reconsidered for being Early Badenian in age. This species remains in consequence unknown from layers older than Badenian. Subsequently also *Aequipecten flavus* is definitely restricted to the Badenian (e.g. Bohn-Havas et al. 1987).

Genus *Costellamussiopecten* Bongrain, Cahuzac et Freneix, 1994 [emend.]

Type species: By original designation (Bongrain et al. 1994) *Pecten haueri* Michelotti from the Miocene of the NE-Atlantic, Mediterranean and Paratethys.

Diagnosis: Following Bongrain et al. (1994), a list of features characterizing the genus can be given: (1) right hinge with 3 tooth pairs, whereby the dorsal tooth pair dominates, (2) spiny to scaly radial secondary sculpture at least early in the ontogeny, (3) dentition of the right dorsal edge (= crista), (4) presence of *Camptonectes* microsculpture, (5) smooth pre-radial stage in the left valve and (6) distinct aragonite layer intercalated within the umbonal region. A diagnosis emendation given herein pertains to the presence of aequipectinoid in addition to amussiopectinoid disc shapes in the genus.

Remarks: *Costellamussiopecten* included according to the original designation by Bongrain et al. (1994) a group of secondarily, scaly sculptured species, previously classified with *Aequipecten* and related to *C. haueri*. It has been defined as a subgenus of *Amussiopecten* based on its apparent relationship to *C. baranensis* (a Middle Miocene NE-Spain species closely related to *C. cristatus badense*), classified erroneously with the latter genus. Yet, *Amussiopecten*, along with *Amussium* never develop the scaly secondary sculpture, at best exemplified by the dorsal crista and can therefore not be related to *Costellamussiopecten*. Representing apparently an independent taxonomic unit, it has been elevated by the present study onto the genus level.

The ongoing investigations by the present author (Mandic, in prep.) shows that the genus has Oligocene to Pliocene range and NE-Atlantic, Mediterranean and Paratethys distribution. The following species recorded in the Paratethys are tentatively considered to be related to the genus: *Costellamussiopecten haueri* (Michelotti, 1847), *C. koheni* (Fuchs, 1876), *C. spinulosus* (Münster in Goldfuss, 1834–1840), *C. pasinii* (Meneghini, 1857), *C. cristatus badense* (Fontannes, 1882), *C. deletus* (Michelotti, 1861), *C. telegdirothi* (Csepregy-Meznerics, 1960), *C. northamptoni* (Michelotti, 1839). Additional species possibly included are *Costellamussiopecten?*

schreteri (Noszky, 1936), *C.? oligosquamosus* (Sacco, 1897), *C.? ferrugosus* (Sacco, 1897), and *C.? martelli* (Ugolini, 1906).

Costellamussiopecten cristatus badense (Fontannes, 1882)
(Fig. 5.4,6)

1867 *Pecten cristatus* Bronn. — Hörnes (pars.), p. 419, pl. 66, Figs. 1a–d
1928 *Amussium cristatum* Bronn. var. *badensis* Font. — Kautsky, p. 253
1947 *Amussium cristatum* Bronn. var. *badensis* Font. — Sieber, p. 158
2001 *Amussium cristatum badense* (Fontannes, 1882) — Schultz, p. 157, pl. 15, Figs. 13a–b

Type: The type is the articulated specimen illustrated by Hörnes (1867) housed in the NHM's collection. It derived from marls at Möllersdorf in Lower Austria, dated as Upper Lagenidae Zone (Early Badenian).

Material: Specimens from Windpassing (Coll. NHMIs).

Dimensions: Right valve — disc height = 28 mm, disc length = 29.8 mm, disc convexity = 3.1 mm, umbonal angle = 119.5°, ears length = 15 mm, ears height = 6 mm; left valve — disc height = 33.8 mm, disc length = 33 mm, disc convexity = 3 mm, umbonal angle = 121°, ears length = 19 mm, ears height = 5.5 mm.

Remarks: This taxon belongs to a lineage of amussiopectinoid shaped *Costellamussium*, which originated in the Oligocene, possibly from *Costellamussiopecten deletus*. Its oldest representative is *C. pasini* (Meneghini). The lineage becomes extinct in the Pliocene. Its last representative was the European "*Amusium*" — "*Amusium*" *cristatum* (Bronn.). The morphologically homologue *Amussiopecten-Amusium* lineage originated likely in the Oligocene, but as mentioned above never developed the scaly ornament and the dorsal crista.

Costellamussiopecten cristatus badense is morphologically closely related to its Pliocene successor, hence some authors tend to regard them as synonymous (e.g. Studencka et al. 1998). In contrast Schultz (2001) following Kautsky (1928) consider the difference as allowing the subspecies level division. Principally *Costellamussiopecten cristatus* has mostly completely suppressed ribs of the left umbonal region being moreover dorso-ventrally elongated.

Stratigr./Geogr. range: Karpatian to Badenian of the Central Paratethys, Burdigalian to Messinian of the Mediterranean to NE Atlantic (Schultz 2001).

Genus *Oopecten* Sacco, 1897a

Type species: By original designation (Sacco 1897a) *Pecten rotundatus* Lam., Burdigalian of southeastern France.

Oopecten solarium (Lamarck, 1819)
(Fig. 5.7)

1867 *Pecten bessi* Andr. — Hörnes, 404 (pars), pl. 62, Figs. 1–2, (? pl. 63, Figs. 1–5)
1928 *Pecten (Amussiopecten) solarium* Lamarck — Kautsky, p. 250
1947 *Pecten (Amussiopecten) solarium* Lam. — Sieber, p. 158
2001 *Flabellipecten solarium* (Lamarck, 1819) — Schultz, p. 236 (pars)

Type: The holotype is not designated. The type series of Lamarck (1819) derived from the Doue environ in the Loire Basin (NW France) (cf. Dollfus & Dautzenberg 1902–1920).

According to Bongrain (1988) those sediments bear land mammal association of the MN9 European Faunal Zone correlating with the Tortonian (cf. Steininger et al. 1996).

Material: Two left valves from Windpassing (NHMW l.c.).

Dimensions: Left valve — disc height = 54 mm, disc length = 58 mm, disc convexity = 7.5, umbonal angle = 125°, ears length = 38 mm, ears height = 10.5 mm.

Description: The left valve is of moderate size, with disc rounded for most of the outline except for slightly concave postero- and anterodorsal margins, very slightly elongated posteroventrally, weakly convex in dorsoventral cross-section, with umbonal angle attaining about 125°, with flattened proximal region, lateral disc areas moderately arched, broadly triangular in left view, similarly broad but anterior one distinctly shorter than the posterior one, anterior lateral area with 3 ribs on its posterior half, the middle one marks the maximum convexity axis, the anterior half smooth; the posterior disc area with 6 smooth ribs on its anterior two thirds, the 3 one marks the axis of maximum convexity, the posterior third is smooth; disc with 14 first order, prominent, flat-topped ribs, trapezoidal in cross-section, as broad as flat-bottomed interspaces, the latter with extremely weak mediate riblet, disc surface covered with slightly eroded commarginal lamellae being proximally loosely and distally densely arranged. Preradial stage about 2 mm in height. Ears very long but low, with straight dorsal and convex lateral margins, posterior ear larger than the anterior ear, with the summed length about three quarters of the disc length, the anterior one low, the posterior one moderately high, posterior ear flattened anterior ear radially concave, with 4 dorsally prominent riblets, the contacts with the disc low but distinct. Interiorly 15 and a half pairs of prominent interior rib carinae. Cardinal crura with the paired posterior denticle. Hinge with 3 to 4 tooth pairs.

Remark: The present study provides the first illustration of an *Oopecten solarium* from the Grund Formation.

This species is much confused in the literature although showing apparent distinctive features. Indeed the combination of a rounded disc outline, extremely wide umbonal angle, very long but low ears, numerous, typically flattened, but prominent ribs, with single weak, intercalated riblet in interspaces, wide marginal disc areas and symmetrical radiating riblets on ears of the left valve reaching in the adult stage gigantic dimensions allow an easy species identification.

Initially Hörnes (1867) classified *Oopecten solarium* specimens together with specimens of *Pecten subarcuatus styriacus* and *Pecten besseri* under the latter name. Deperet & Roman (1902–1912) following Ugolini (1908) regarded the specimens illustrated by Hörnes (1867) as independent species and denoted it with *Pecten (Amussiopecten) incrassatus* Partsch. The latter name is however a nomen nudum of Partsch in Hörnes (1848) that have been made available by bibliographic reference (cf. ICZN 1985, Art. 11,d,ii and Art. 12) by Hörnes (1867). Actually the latter author included the Partsch designation into his *Pecten besseri* synonymy. Dollfus & Dautzenberg (1902–1920), referring neither to Ugolini (1908) nor to Deperet & Roman (1912), included the specimens illustrated as *Pecten besseri* by Hörnes (1867) into *Pecten (Oopecten) solarium*. Finally Roger (1939), following Kautsky (1928) and Friedberg (1936), reunited all those references into *Chlamys solarium* (Lamarck).

Kojumdgieva (1960), Csepregy-Meznerics (1960), Nicorici (1977) and Steininger et al. (1978) document typical Central Paratethys morphologies of *Oopecten solarium*. In contrast, beside characteristic specimens illustrated by Švagrovský (1981, pl. 7 and 9) from the Upper Badenian of Devínska Nová Ves, Slovakia, an articulated valve from his pl. 8 with lowered number of prominent, rounded ribs and low umbonal angle, represents more likely a *Pecten* or a *Flabellipecten*. The same holds true for a right and a left valve documented by Schultz (2001, pl. 38, Fig. 1 and pl. 40, Figs. 1 and 2). Hence the left valve with marginal areas sculptured by prominent first order ribs and ears missing the radiating riblets is apparently not an *Oopecten solarium*. Yet, conspicuously, these specimens are referred as Hörnes (1867, pl. 63, Figs. 4 to 5; sic?: cf. Figs. 1 to 5, my rem.) originals, implying that the similarity of the latter drawings with actual *Oopecten solarium* must be a coincidence.

The present author follows Roger (1939) by classifying the species with *Oopecten*, Bongrain (1988) and Schultz (2001) classified it currently with *Flabellipecten*, but unfortunately failed to give the arguments.

Stratigr./Geogr. range: Common and characteristic during the whole range of the Badenian in the Central Paratethys. Its possible Karpatian occurrence (Kókay 1967) is discussed elsewhere in the text (see chapter — *Biostratigraphic inferences*). Based on the latter record Bohn-Havas et al. (1987) also referred to its questionable occurrence from the Karpatian. In the Mediterranean to E Atlantic region it ranges from the Burdigalian to the Messinian (Roger 1939).

Genus *Macrochlamis* Sacco, 1897a

Type species: By subsequent designation (Sacco 1897b) *Ostrea latissima* Brocchi from the Pliocene of Italy. Note that Bongrain (1988, p. 228) proposed replacement of the current type species by *Pecten ligerianus* Dollfus et Dautzenberg from the Middle Miocene of NW-France.

Macrochlamis nodosiformis (de Serres in Pusch, 1837) (Fig. 6.1,2)

1867 *Pecten latissimus* Brocchi — Hörnes, p. 395, pl. 56, Figs. 1–4, pl. 57, Figs. 1–4

1928 *Pecten (Oopecten) latissimus* Brocchi var. *austriaca* nov.var. — Kautsky, p. 252

1949 *Pecten (Oopecten) latissimus* Brocchi — Sieber, p. 112

2001 *Gigantopecten nodosiformis* (Pusch, 1837) — Schultz, p. 249, pl. 36, Fig. 3, pl. 37, Figs. 1–2, pl. 38, Fig. 2, pl. 39

Type: The holotype was not designated; the specimen originally illustrated by Pusch (1837, Pl. 5, Figs. 9a–c) is from Skotniki, southern slopes of the Holy Cross Mts, Central Poland. The type series derived from Skotniki and Widuchowa near Busko and Kików near Stobnica. It is Early Badenian in age (Studencka & Studencki 1988).

Material: Specimens from Windpassing and Guntersdorf (Coll. NHMls).

Dimensions: Right valve — disc height = 71.5 mm, disc length = 76 mm, disc convexity = 23.5 mm, umbonal angle = 102°, ears length = 48 mm, ears height = 23 mm; left

valve — disc height = 119.8 mm, disc length = 137 mm, disc convexity = 39 mm, umbonal angle = 103°, ears length = 79 mm, ears height = 32 mm.

Remark: This characteristic species resembles somewhat the *Macrochlamis holgeri* (Geinitz) from the Eggenburgian deposits of Lower Austria. The latter species, however, never develops node series on rib tops.

The generic designation follows the argumentation of Smith (1991) regarding *Gigantopecten* for the junior synonym of *Macrochlamis* (see chapter — *Faunal composition and taxonomic revisions*).

Stratigr./Geogr. range: It is typical and common throughout the Badenian (cf. Schultz 2001). Its record from the deposits underlying the “Grund Horizon” of the Várpálot Basin, discussed above in the text, is Karpatian to Early Badenian in age. Its first occurrence in the Mediterranean to NE Atlantic region is in the Late Burdigalian. The species is correspondingly commonly present there in the Middle and also in the Late Miocene. In the Late Miocene (Roger 1939) or Pliocene (Bongrain 1992) it gets replaced by the *Macrochlamis latissima*.

Macrochlamis tournali (de Serres, 1829)
(Fig. 6.3,4)

- 1867 *Pecten tournali* Serres — Hörnes, p. 398, pl. 58, Figs. 1–6
1928 *Pecten (Oopecten) tournali* de Serr. — Kautsky, 252
1947 *Pecten (Oopecten) tournali* Serr. — Sieber, p. 158
1949 *Pecten tournali* Serr. — Sieber, p. 112
2001 *Gigantopecten tournali* (de Serres, 1829) — Schultz, p. 254, pl. 41, Figs. 1–2

Type: Holotype was not designated. The accurate origin of the left valve illustrated by Serres (1829) is unknown. The collection is derived from the “marine Tertiary of southern France” (“terrains marins tertiaires du midi de la France”). Indications by Roger (1939), Bongrain (1992) and Schultz (2001) point out that the occurrence of this species in southern France could be restricted to the upper Burdigalian.

Material: Specimens from Windpassing and Immendorf (Coll. NHMIs)

Dimensions: Right valve — disc height = 29.5 mm, disc length = 27.1 mm, disc convexity = 5.7 mm, umbonal angle = 100°, ears length = 19 mm, ears height = 8.5 mm; left valve — disc height = 38 mm, disc length = 41.2 mm, disc convexity = 7.2 mm, umbonal angle = 92°, ears length = 26.8 mm, ears height = 12 mm.

Remark: Bongrain (1992) in her proposal for *Gigantopecten*, i.e. *Macrochlamis*, phylogeny restricted the range of *Macrochlamis tournali* to the Middle to Late Burdigalian. She derived *M. tournali* from *Macrochlamis ziziniæ* (Blanckenhorn) which is a species indeed closely related to it. Yet the author also let *M. ziziniæ* terminate shortly above the Burdigalian/Langhian boundary. Its successor, an unnamed species termed “*G. sp.?*” arose by gradual transition already in the Early Langhian. The latter represents a morphological stage preceding the last stage of the transition provided by the mid-Serravalian to Tortonian *Macrochlamis albina* (Teppner). The

actual FOD of *Macrochlamis albina* is still within the Early and not the Middle Miocene. Hence *M. albina* reaches its maximum already in the Early Badenian deriving forms larger than 20 cm (e.g. Schultz 2001).

Stratigr./Geogr. range: “Late Ottnangian” to Badenian of the Central Paratethys. Upper Marine Molasse of the Western Paratethys, Burdigalian to Tortonian of the Mediterranean to NE Atlantic.

Genus *Pecten* Müller, 1776

Type species: By subsequent designation (Schmidt 1818), *Ostrea jacobaea* Linneus, Pliocene to Recent of the Mediterranean and northeastern Atlantic.

Pecten subarcuatus styriacus Hilber, 1879
(Fig. 7)

- 1879 *Pecten styriacus* Hilb. — Hilber, p. 455, pl. 6, Figs. 13–15
1928 *Pecten subarcuatus* Tournouer. var. *styriaca* Hilber. — Kautsky, pl. 7, Figs. 9–10
1947 *Pecten subarcuatus* Tourn. var. *styriaca* Hilb. — Sieber, p. 158
2001 *Pecten subarcuatus styriacus* Hilber, 1879 — Schultz, p. 271, pl. 42, Figs. 2–3

Type: The holotype was originally not designated. The type series consists of at least three specimens illustrated by Hilber (1879, pl. 6, Figs. 13–15). Schultz (2001) referred the holotype, that is indeed the potential lectotype, as being housed in the Collection of the Joanneum Museum at Graz (SE Austria). The type series derives from the St. Florian (= Groß St. Florian) in Styria, from sandy marls. The sediments belong to the Florian Formation of the western Styrian Basin and are dated correspondingly to the Grund Formation with the regional Lower Lagenidae Zone of the Early Badenian (Tollmann 1985; Schultz 2001).

Material: Numerous juvenile to adult specimens from the field ditch E Grund (Coll. DPUV2) and excavation Grund 1998 (Coll. NHMlv) and Windpassing (Coll. NHMIs).

Dimensions: Left valve — disc height = 38 mm, disc length = 42.5 mm, disc convexity = 1.5 mm, umbonal angle = 113°, ears length = 27.9 mm, ears height = 11 mm; right valve — disc height = 38 mm, disc length = 43.3 mm, disc convexity = 11 mm, umbonal angle = 94°, ears length = 23.8 mm, ears height = 9 mm.

Remark: Studencka (1986) reunited *P. subarcuatus* with *P. styriacus* which was followed by Studencka et al. (1998). Yet, *P. subarcuatus styriacus* has always flat-topped ribs, as confirmed in numerous specimens from the Grund Formation. *P. s. subarcuatus* differs in that its ribs on the left and on the right valve are convexly rounded and *P. subarcuatus fuchsi* has left ribs sub-trapezoidal and the right ribs convexly rounded to sub-trigonal as documented by numerous specimens from the Late Burdigalian of the Suez region in NE Egypt (Coll. Mandic, Natural History Museum Vienna). Indeed these differences are minute and reflect maximally the subspecies level taxonomy, but coincide apparently with the paleogeographical distribution of those otherwise coeval taxa.

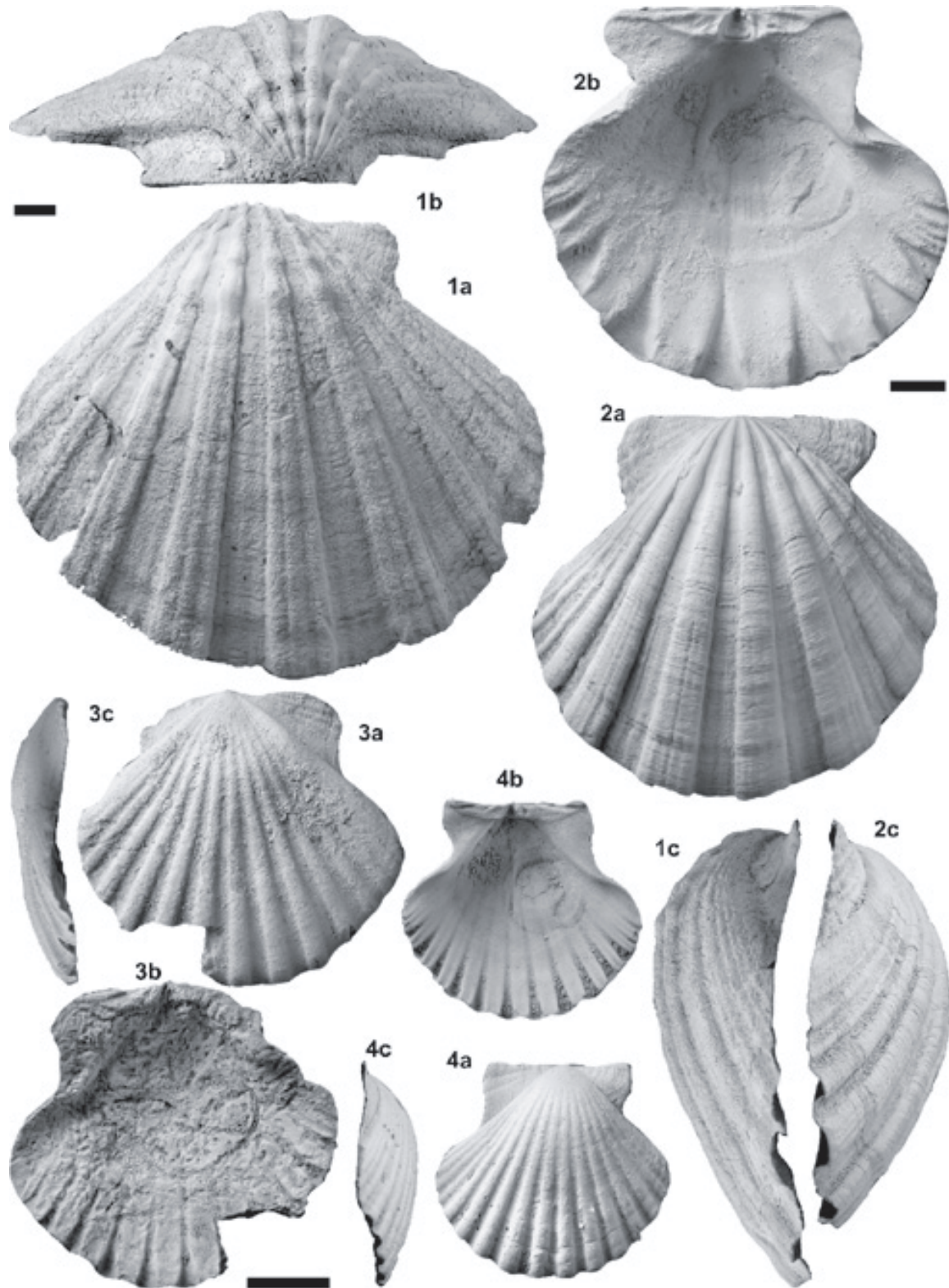


Fig. 6. *Macrochlamis* from the Grund Formation. 1–2 — *Macrochlamis nodosiformis* (de Serres in Pusch). 1 — left valve missing the anterior ear; locality: Guntersdorf; collection: NHMIs (compare text for abbreviations). 2 — right valve; locality: Immendorf; collection: NHMIs. 3–4 — *Macrochlamis tournali* (de Serres). 3 — left valve missing the portions of anterodorsal ear and the ventral disc margin; locality: Immendorf; collection: NHMIs. 4 — a complete right valve; locality: Windpassing; collection: NHMIs. (The single scale bars (1 cm) refer to specimens 1 and 2 and to specimen group 3–4. The letters imply the view: (a) exterior, (b) interior, (c) posterior and (d) dorsal.)

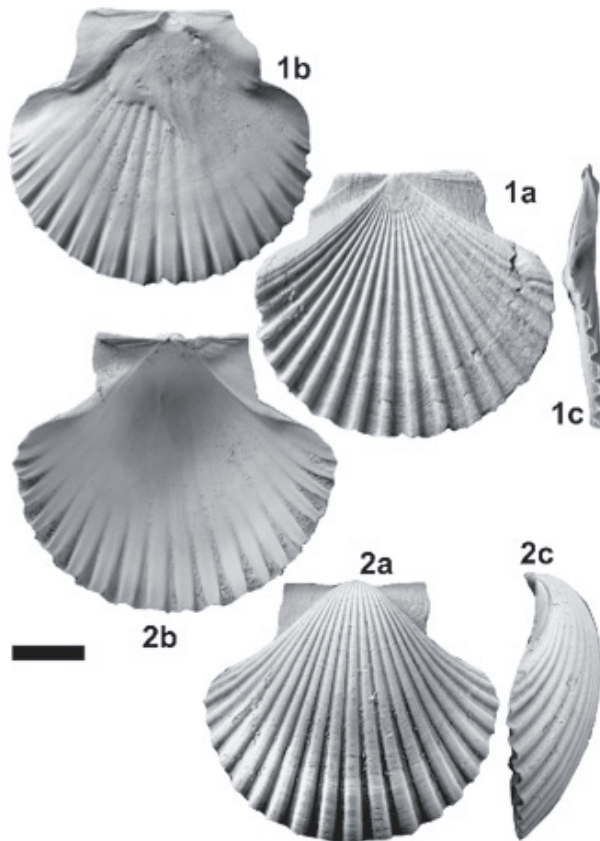


Fig. 7. *Pecten subarcuatus styriacus* Hilber from the Grund Formation — locality: Grund; collection: DPUV2. **1** — left valve with fragmented anterodorsal ear portion. **2** — a complete right valve. (The scale bar = 1 cm. The letters imply the view: (a) exterior, (b) interior and (c) posterior.)

Hence *P. s. subarcuatus* inhabited the northeastern Atlantic, *P. s. styriacus* the Central Paratethys and *P. s. fuchsi* the proto-Mediterranean region.

Stratigr./Geogr. range: Restricted to the Late Eocene to Late Badenian of the Central Paratethys (cf. Schultz 2001).

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