

The utility of late Early to Middle Cambrian small shelly fossils from the western Mediterranean

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ABSTRACT: New data on Cambrian small shelly fossils from Germany and Sardinia, and Spain are discussed with respect to their stratigraphical, paleogeographical, and paleoecological value. It is shown that these small shelly assemblages represent very useful tools for reconstruction of geological processes and of the Perigondwanan history in the Mediterranean area, especially, if trilobites are absent or hard to recover from the rocks. The German and Sardinian assemblages reflect distinct ecological conditions on shallow platform and shelf areas and mirror any changes in these habitats. Thus, lateral and vertical transitions from restricted inner platform to deep subtidal conditions are documented by characteristic successions of Sardinian assemblages. German assemblages show clearly distinct paleogeographic/ecological developments. The reorganization of the ecosystems is linked to shelf-wide processes which can be stratigraphically correlated in their single phases (e.g., drowning of platforms, breakup of the Perigondwanan realm, origin of terranes). Broader paleogeographic relationships of small shelly fossils to the Far East and Australia are proposed and support earlier controversial assumptions based on trilobites. Because of the small shelly fossils distribution patterns, a pre-Late Cambrian separation of terranes from the so called European shelf of western Gondwana is unlikely. During the Early to Middle Cambrian a rather uniform and weakly differentiated facies belt across most of the European shelf is indicated, and this contradicts earlier concepts of more-or-less isolated depositional basins. Despite recent progress in knowledge of Mediterranean small shelly fossil assemblages, further improvements will lead to a better understanding and a much more detailed picture of the Cambrian history of Perigondwana and its relationships to other paleocontinents.

Key words: small shelly fossils, Cambrian, Gondwana, Mediterranean

1. INTRODUCTION

The late Early to Middle Cambrian marine shelly fauna is commonly dominated by trilobitic arthropods, brachiopods and echinoderms. Additional typical elements are represented by poriferans and hyoliths (Zhuravlev, 2001). Over the previous several decades many other, mainly microscopic fossils were described from Cambrian strata. These fossils show a surprisingly well-developed morphology and complexity and are part of highly diverse, shallow-water assemblages. The paleobiological affinity of many of these taxa is not clear, and their classification is often highly speculative. Because of limited systematic knowledge and the large number of problematic taxa, for such remains the term “small shelly fossils” was introduced by Matthews and Missarshevski

(1975) for phosphatized and calcareous remains.

Small shelly fossils from the Early to Middle Cambrian interval were more intensely studied over the last few decades of the 20th century. Small shelly biota from Asia (Siberia, China, Himalaya Mountains), Laurentia, Avalon, and Australia, but also from other regions were extensively described (e.g., Landing et al., 1980, 1989; Brasier and Singh, 1987; Landing, 1988, 1991; Missarshevski, 1989; Qian and Bengtson, 1989; Bengtson et al., 1990; Hamdi, 1995; Alexander et al., 2001; Skovsted, 2003; Lauri, 2004; Wrona, 2004 and others). After initial euphoria on the utility of these rich microfossil contents as an aid in biostratigraphic correlation of Cambrian strata, a facies control that limited their biostratigraphic value and long stratigraphic ranges were observed for many of these remains (Landing, 1992).

This report deals with important small shelly taxa from the western Mediterranean, and highlights their use in clarification of stratigraphical and paleogeographical relations and in paleoecological, tectonostratigraphical, and process reconstructions.

2. SMALL SHELLY FOSSILS FROM THE WESTERN MEDITERRANEAN

The Cambrian small shelly assemblages from the western Mediterranean (Spain, France, Sardinia, Germany) are rather poorly known. Apart from some single sporadic discoveries (e.g., Doré and Reid, 1965; Sdzuy, 1969; van den Boogaard, 1983; Cherchi and Schroeder, 1984; Mostler, 1985), intensive systematic investigations took place only over the last fifteen years. The first extensive data from this area were published by Kerber (1988) on small shelly fossils from the Montagne Noire (Massif Central, Southern France). Some years later, rich faunas were reported from eastern Germany (Elicki, 1992, 1994, 1996, 1998), Spain (Fernández-Remolar, 1999, 2001a, 2001b, 2002; Gozalo and Hinz-Schallreuter, 2002; Gubanov et al., 2004a), and Sardinia (Elicki, 2002; Elicki and Wotte, 2003; Elicki et al., 2003; Elicki and Pillola, 2004; Mergl and Elicki, 2004).

2.1. Small Shelly Fossils from Central Europe: Germany

In Central Europe Early to Middle Cambrian small shelly fossils are known from only a few sites (Elicki, 1998). The

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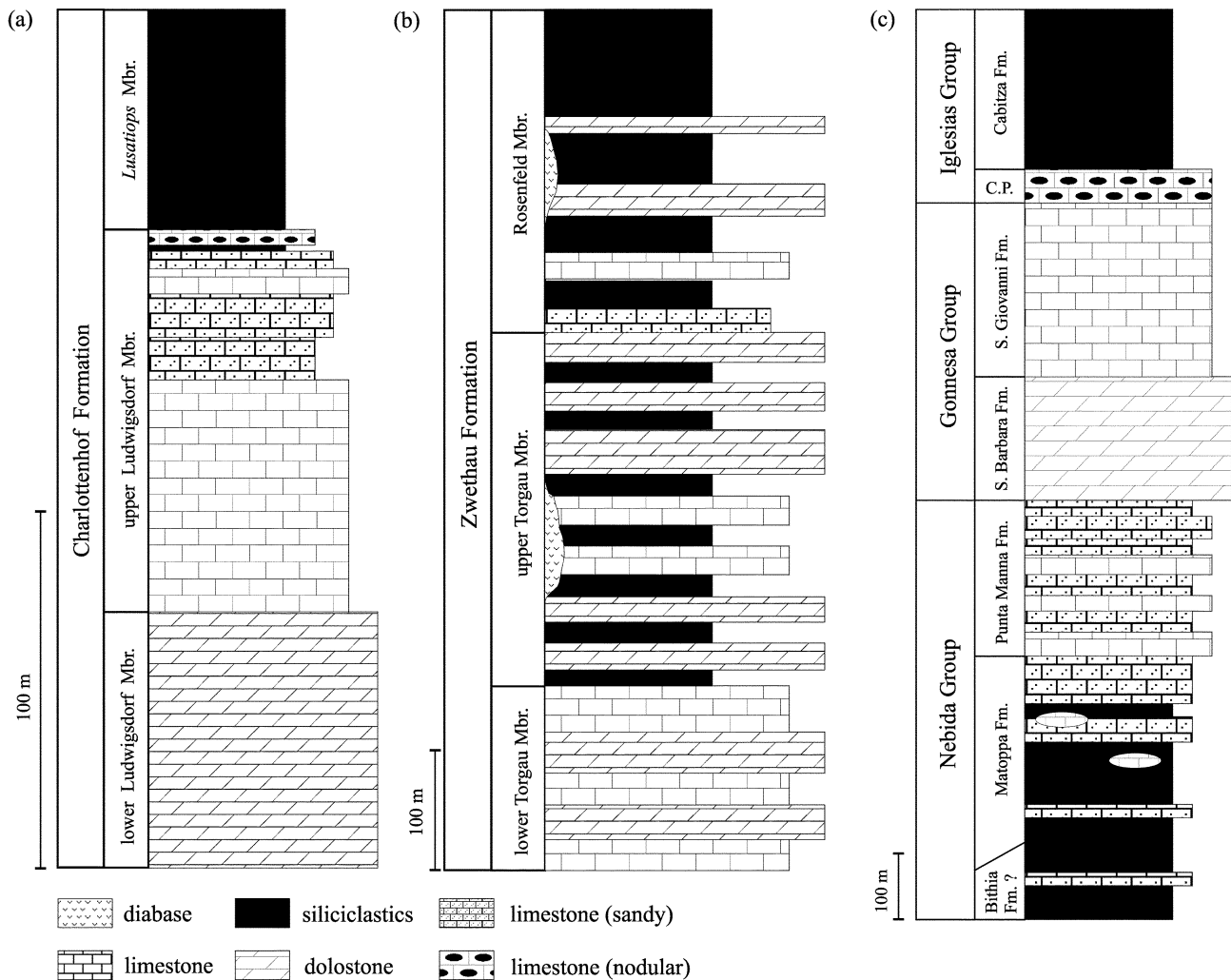


Fig. 1. Lithological columns of the German and Sardinian successions. (a) Early Cambrian succession of the GS area (higher Banian=upper Atdabanian): small shelly fossils occur in the upper half of the upper Ludwigsdorf Member. (b) Early Cambrian (middle Issendalenian=early Atdabanian) succession of the TDS area: small shelly fossils were found within the upper Torgau Member. (c) Cambrian succession of SW Sardinia: Early-Middle Cambrian boundary is located slightly above the onset of the small shelly fossils-bearing Campo Pisano Formation ("C.P").

most important and diverse fauna comes from the upper Lower Cambrian of eastern Germany (Elicki, 1994, 1997) where they have been discovered in carbonates of the Görlitz Syncline (=GS) and of the Leipzig area (Torgau-Doberlug Syncline=TDS). The GS succession (Fig. 1a) represents a fragmentary preserved higher Banian (=uppermost Atdabanian to Botoman) succession (thickness less than 300 m, surface outcrop) of mixed carbonates and siliciclastics (Elicki and Schneider, 1992). The TDS (thickness ca. 1500 m, drilling cores) is a middle Issendalenian (=lower Atdabanian) ramp characterized by a mixed carbonate-siliciclastic shoal-related system (750 to 800 m; Fig. 1b) followed by about 750 m of Middle Cambrian siliciclastic shelf sediments (Elicki, 1999a, 1999b; Buschmann et al., in press).

The fossils from GS are from the so called upper Ludwigsdorf Member (up to 80 m) of the Early Cambrian Charlottenhof Formation, and is characterized by mainly poriferans,

echinoderms, cancelloriids (all disarticulated), and hyoliths. In addition, trilobites, brachiopods, as well as bivalve, archaeogastropod, and monoplacophoran molluscs, occur (Table 1). Additional but rarer elements of the Görlitz fauna are represented by phosphatic microproblematica and cyanobacteria. This fossil assemblage shows distinct changes in its vertical occurrence. The oldest level (a) yields poorly identifiable brachiopod and poriferan remains followed by the more diverse association (b) of brachiopods, poriferans and hyoliths (with minor trilobites and cancelloriids). Level (b) is overlain by strata (c) which contain only some problematic remains (echinoderms?) followed by (d) a poriferan-dominated fauna with minor trilobite and cancelloriid remains. The most fossiliferous level (e) bears a hyolith-poriferan-echinoderm-trilobite-dominated association with cancelloriids, molluscs, and phosphatic small shelly fossils. The youngest carbonate strata (f) yield a limited porife-

Table 1. Early Cambrian fossils of the GS and TDS regions (Germany) based on Freyer (1977), Elicki (1992, 1994, 1996, 1998), Gozalo and Hinz-Schallreuter (2002). For trilobites see Sdzuy (1962) and Geyer and Elicki (1995), for brachiopods Freyer (1981b). For archaeocyaths and calcimicrobes see Elicki and Debrenne (1993) and Elicki (1999a).

	molluscs	<i>Pojetaia runnegari</i> , <i>Fordilla germanica</i> , <i>F. troyensis</i> , <i>Beshdashella tortilis</i> , <i>Yuwenia juliana</i> , <i>Y. (?) cf. bentleyi</i> , <i>Pelagiella subangulata</i> , <i>P. lorenzi</i> , <i>P. aff. adunca</i> , <i>P. sp.</i> , <i>Obtusoconus sp.</i> , <i>Planutenia inclinata</i> , <i>P. flectata</i> , <i>Anabarella australis</i> , <i>Bemella aff. jacutica</i> , <i>B. sp.</i> , <i>Khairkhania evoluta</i>
	hyoliths	<i>Burithes sp.</i> , <i>Conotheca circumflexa</i> , <i>Egdetheca cf. aldanica</i> , <i>Lenalitus pusillus</i> , <i>Microcornus elongatus</i> , <i>M. parvulus</i> , <i>Obliquatheca aldanica</i> , <i>Orthotheca sp.</i> , <i>Tchuranitheca curvata</i> , <i>Trapezovitus mirus</i> , <i>Hyolithes divaricatus</i> , <i>H. sp.</i> , sulcavethids indet.
Görlitz Syncline	chancelloriids	<i>Allonnia tripodophora</i> , <i>A. tetrathallis</i> , <i>A. sp. Archiasterella pentactina</i> , <i>A. hirundo</i> , <i>Chancelloria primaria</i> , <i>C. sp.</i>
	poriferans	<i>Dodecaactinella cynodontota</i> , <i>Eiffelia araniformis</i> , unidentified heteractinid remains
	miscellaneous microfossils	<i>Rhombocorniculum cancellatum</i> , <i>Atholicopalla adnata</i> , <i>Coleoloides typicalis</i> , <i>Microcornus cephalata</i> , <i>Cambroclavus ludwigsdorfensis</i> , <i>Halkieria sp.</i> , <i>Cambrotubulus decurvatus</i> , <i>C. corniformis</i> , <i>Torelrella lentiformis</i> , <i>T. mutila</i> , <i>Hyolithellus cf. micans</i> , unidentified echinoderm remains
	bradoriids	<i>Hipponicharion elickii</i> , lipabdominids indet.
Torgau-Doberlug Syncline	chancelloriids	<i>Allonnia tripodophora</i> , <i>A. tetrathallis</i> , <i>Archiasterella pentactina</i> , <i>A. hirundo</i> , <i>Chancelloria sp.</i>
	miscellaneous microfossils	<i>Halkieria sp.</i> , <i>Tiksitheka licis</i> , <i>Cambrotubulus cf. decurvatus</i> , <i>Torelrella lentiformis</i> , <i>T. curva</i> , <i>Cambroclavus sp.</i> , <i>Tintinnoidella praecursa</i> , unidentified poriferan and echinoderm remains

ran-brachiopod fauna with some hyoliths and chancelloriids. The immediately overlaying pure shaly layers (*Lusatitops* Member) provided a dramatically depleted fauna consisting of some trilobites, scarce brachiopods, and very rare hyoliths.

Generally, within the Görlitz Cambrian it is possible to recognize a succession from higher salinity, restricted-marine facies (dolomitic limestones and dolostones) overlying open-marine shallow-shelf facies (partly silty to argillaceous limestones) and uppermost open-marine and deeper shelf environments (mud- and siltstones), (Elicki, 1994). It is conspicuous that the lowest fauna occurs in the open-marine horizons and is most diverse relatively close to the transition from carbonate to siliciclastic deposition (above level e). In particular, some of the problematic phosphatic small shelly fossils (e.g., *Rhombocorniculum*) occur only close to these transitional strata, which contain larger amounts of argillaceous material and a more-or-less nodular texture. The transition into the most diverse fauna (level e) occurs a few meters beneath this transition where the siliciclastic input is slightly increased. Whereas the taxonomic diversity is highest within this portion, only one group (hyoliths) clearly predominates by about 90 % of all individuals. The number of poriferans, chancelloriid, and echinoderm individuals is hard to calculate, because only disarticulated elements occur. Although many hundreds to thousands of sclerites are present in some samples, it is not surely known how many elements belong to one scleritome. Molluscs (bivalves, archaeogastropods, monoplacophorans), and hyoliths are abundant in level (e). Even the bivalves are common. Extremely rare elements are represented by the phosphatized halkieriid sclerites.

Trophic and habitat characteristics of the GS assemblage were recently investigated by Elicki (2003). Briefly stated, the Görlitz fauna is clearly dominated by suspension-feed-

ers and deposit-feeders (hyoliths, bivalves, other molluscs, echinoderms, chancelloriids, trilobites, brachiopods) followed by filter-feeders (poriferans). Predators are comparatively rare. Most of the individuals are related to a soft-bottom environment and a semi-infaunal habitat (e.g., *Lenalitus*, *Circotheca*, some helcionellids) or an infaunal mode of life (bivalves). Epibenthic forms (e.g., trilobites, brachiopods) were also common. Following the paleontological and the sedimentological data, the depositional area can be summarized as an open-marine, moderate wave-influenced and well-oxygenated shelf environment during a transgressive stage under mesothropic conditions. Restricted-marine, higher salinity areas were located locally in proximal position (Elicki and Schneider, 1992).

The fauna from subsurface Lower Cambrian carbonates of the TDS (Zwethau Formation) is quite different. The most conspicuous faunal elements are archaeocyaths and calcimicrobes (Freyer and Suhr, 1987, 1992; Elicki and Debrenne, 1993; Elicki, 1999a). Shelly fossils are rather rare and hard to recover in limited drill core material, and the knowledge about these fossils is limited (Elicki, 1994). Some single trilobite remains (Sdzuy, 1962), chancelloriids, poriferans, echinoderms (all disarticulated), and phosphatic arthropods, as well as some additional phosphatic small shelly fossils and problematic remains are described (Elicki, 1992) (Table 1). Some of these fossils are enriched in distinct layers (e.g., poriferans, tintinnoids, bradoriids). Of special importance are the bradoriids (*Hipponicharion*), which are poorly known from the Mediterranean Cambrian (Gozalo and Hinz-Schallreuter, 2002), and tintinnoids, which are only sporadically reported from Paleozoic strata and never before from the Cambrian (Elicki, 1994). In the TDS, cambroclaves – common elements of the Görlitz fauna – as well as halkieriids and molluscs are extremely rare. Wherever there are some

indications of very shallow-water or higher salinity conditions (lagoons or back shoal areas, see Elicki, 1999a), the abundance of all faunal elements decreases strongly. The highest shelly fossil content is in open-marine areas adjacent to archaeocyathan-calcimicrobial reef mounds and oolitic shoals. Generally, the abundant shelly biotic remains are distinctly less than in the GS area. The fossil-bearing facies of the TDS are very pure limestones – only limited siliciclastics reached the carbonate depocenters. Further, the common occurrence of archaeocyathans – commonly seen as adapted to low-nutrient conditions (e.g., Brasier, 1990, 1992; Debrenne and Zhuravlev, 1997) – support the interpretation as a rather oligotrophic environment. Bioturbation was not significant; hardgrounds are missing. The predominating mode of food production was by photosynthesis (cyanobacteria) and filter-feeding (archaeocyathans). The scarce shelly fauna was represented only by filter-feeders (poriferans), suspension- and deposit-feeders (chancelloriids, trilobites). The presence of predators is not surely indicated (armour-plate-protected halkieriids may represent potential prey of predators). The overwhelming majority of organisms were epibenthic. A synthesis of these paleontological and sedimentological data tends to reconstruction of the depositional environment as a ramp divided into oolitic shoals, open-marine reef-mound and inter-reef areas, and shallow areas of higher salinity. In the most proximal areas, intertidal flats were well developed (Elicki, 1999a).

Because of the complex structure of the TDS, the transition into the purely siliciclastic upper half of the Cambrian succession (Middle Cambrian Tröbitz Formation and Delitzsch Formation) remains unclear. From this siliciclastic portion trilobites and brachiopods as well as rare hyoliths, echinoderms, helcionellids, and trace fossils are known (Sdzuy, 1957, 1970; Freyer, 1981a).

2.2. Small Shelly Fossils from Southern Europe: Sardinia

In southwestern Sardinia, widely outcropping Cambrian rocks reach a thickness of about 1500 to 2500 m (Pillola, 1991). The well documented succession represents three

stages of development (Fig. 1c): siliciclastic to mixed siliciclastic-carbonate shelf stage (Nebida Group, Lower Cambrian), isolated carbonate platform stage (Gonnesa Group, late Early Cambrian), and drowning/drowned platform stage (Iglesias Group, uppermost Lower Cambrian to Lower Ordovician). The open-marine Nebida Group is mostly represented by siliciclastics, but, in its upper portion shallow-water carbonates became widespread. The overlaying Gonnesa Group consists of often laminated dolostones and limestones (no siliciclastics). The youngest stage (Iglesias Group) has a few decimetres of argillaceous and more-or-less nodular carbonates at its base (Campo Pisano Formation, uppermost Lower to Middle Cambrian) which are overlain by clay-, silt-, and sandstones (Cabitza Formation, Middle Cambrian to Lower Ordovician). For a detailed model of the shelf and platform stages see Bechstädt and Boni (1994 and references therein), for that of the drowning stage, see Loi et al. (1995) and Elicki et al. (2003).

Shelly fossils from the Sardinian Cambrian are mainly known from siliciclastic intervals (Rasetti, 1972; Pillola, 1991; Pillola et al., 2002). The faunal investigation of the carbonates has focused on archaeocyathans (which occur in the Nebida and Gonnesa Groups) as a way to resolve biostratigraphic questions. Whereas shelly fossils from the Lower Cambrian are poorly known due to difficulty in extracting them, but also due to their limited occurrence and the current lack of research, the condensed and highly fossiliferous Campo Pisano Formation has arthropods, echinoderms, poriferans, brachiopods, chancelloriids, molluscs, and phosphatic small shelly fossils (Cherchi and Schroeder, 1984; Mostler, 1985; Elicki and Wotte, 2003; Elicki et al., 2003; Elicki and Pillola, 2004; Mergl and Elicki, 2004) (Table 2).

Southwest Sardinia has excellent outcrops – in contrast to the limited exposure in Germany in the GS and subsurface cores of the TDS. Consequently, vertical and lateral trends in the distribution of shelly remains are recognizable in Sardinia. The southeastern part of the study area in Sardinia has generally poorer fossil content than in northwestern areas. The highest fossil content is always at the base of the

Table 2. Shelly fossils of the Campo Pisano Fm. (Sardinia) based on Cherchi and Schroeder (1985), Mostler (1985), Pillola (1991), Elicki (2002), Elicki and Wotte (2003), Elicki et al. (2003), Elicki and Pillola (2004). For trilobites see Elicki and Pillola (2004), for brachiopods Mergl and Elicki (2004).

	molluscs	<i>Pelagiella subangulata</i>
	hyoliths	<i>Microcornus</i> sp.
	chancelloriids	<i>Allonnia tripodophora</i> , <i>Chancelloria sardinica</i> , <i>C. maroccana</i> , <i>Archiasterella pentactina</i> , <i>A.</i> sp.
Campo Pisano Fm.	poriferans	<i>Eiffelia araniformis</i> , <i>Dodecaactinella cynodontota</i> (including <i>Sardospongia triradiata</i> and <i>Polyactinella furcata</i>), <i>Phobetractina polymorpha</i> , <i>Protospongia</i> sp., <i>Kiwetinokia</i> sp., unidentified monaxons
	bradoriids	<i>Hipponicharion ichnusum</i>
	miscellaneous microfossils	<i>Hyolithellus</i> cf. <i>filiformis</i> , <i>Hadimopanella oezgueli</i> , <i>H.</i> cf. <i>oezgueli</i> , <i>H.</i> sp., <i>Cambroclavus</i> sp., <i>Olivoides multisulcatus</i> , <i>Zeugites</i> sp., <i>Hemisphaerammina</i> cf. <i>cecillalickeri</i> , <i>Ammodiscus</i> sp., <i>Psammosphaera</i> sp., <i>Atholicopalla adnata</i> , unidentified echinoderm remains

Campo Pisano Formation. This succession commences with a poriferan spiculite. Above this spiculite, a sudden abundance of eocrinoid remains associated with trilobite and brachiopod remains is observed. Minor faunal elements are represented by cancelloriids, pelagiellids, some hyoliths and sponge spicules. Of particular interest is the occurrence of phosphatic small shelly fossils restricted to this interval. A next biofacies developed by a gradual transition from below. The overlying assemblage is characterized by more-or-less the same fossil groups as that below, but trilobites are dominant. Other important constituents are echinoderms, but brachiopods, poriferans, hyoliths, and cancelloriids may be present. This second assemblage persists until nearly the top of the Campo Pisano Formation. Only in the uppermost part, the fossils become fewer and smaller and larger amounts of abraded remains occur.

As interpreted by Elicki et al. (2003) the Campo Pisano microfauna is autochthonous and significant for the reconstruction of habitats and depositional environments. The succession is ecostratigraphic characterized by the very sudden appearance of the nodular Campo Pisano carbonates. This indicates an abrupt flooding of the (Gonnesa-) carbonate platform. The first well-documented fauna after that distinct sea-level rise consists nearly exclusively of poriferans. This pioneer-fauna of epibenthic filter-feeders may have benefited from the drowning of the depositional surface into greater subtidal depth (Elicki et al., 2003). The following transition from spiculite biofacies to echinoderm biofacies marks a conspicuous biotic change across the entire depositional area in the lower Campo Pisano Formation. Now, the predominance and persistence of sessile epibenthic suspension feeders coincides with an increased and permanent influx of suspended material into this subtidal setting. Reason could be an intensified erosion of the hinterland due to the raised sea-level and/or the paleogeographic movement of the area from the tropical-arid realm into higher southern latitudes as speculated by Elicki et al. (2003). The succeeding trilobite-dominated fauna contains fewer sessile-benthic organisms than below and is interpreted to represent deep subtidal conditions. Near the lithological transition into the overlying siliciclastic Cabitza Formation, the abrupt change in the fossil content (decrease and more allochthonous elements) is interpreted as a further distinct drowning. Elicki et al. (2003) on the basis of the ecological successions and of a revised stratigraphic framework have interpreted a deep subtidal depth for the most of the Campo Pisano Formation (between the two drowning impulses) and probably upper bathyal conditions for the overlying siliciclastics of the lower Cabitza Formation.

3. DISCUSSION

3.1. Paleocology and Sedimentary Systems

The small shelly faunas of the described German Cam-

brian show distinct regional variations. Based on the paleontological and lithological data, the Görlitz biotic assemblages clearly indicate a normal-marine mesotrophic environment characterized by large numbers of semi-infaunal and infaunal suspension- and deposit-feeders (hyoliths, bivalves, archaeogastropods, monoplacophorans). The high biodiversity and the occurrence of different ontogenetic stages (of trilobites, molluscs and echinoderms) point to an unstressed, open-marine community. The location of this molluscan-dominated habitat is interpreted as relatively proximal (Elicki and Schneider, 1992). Changes in the physical conditions (sea-level fluctuations, siliciclastic influx, maybe climate changes) were mirrored by changes in the diversity and composition of the assemblages. This is clearly indicated, for example, by the occurrence and disappearance of molluscs, cambroclaves, and pseudoconodonts. As an example, the pseudoconodont *Rhombocorniculum* is strictly bound to the final drowning stage (a phenomenon which is also observed in Sardinia, Elicki and Wotte, 2003) and to distinct higher levels of siliciclastic influx (argillaceous limestone to marlstone). In summary, the Görlitz fauna is very useful for reconstructing not only trophic characteristics and so special conditions of the environment, it is also useful to clarify the evolution of the depositional conditions and habitats of the Görlitz Cambrian biota.

The fauna of the TDS area is characteristic of a quite different type of environment. In comparison to the GS region, shelly fossils are rather rare, but photosynthetic microbes and filter-feeding sponges (archaeocyathans) are most common. In contrast to the GS, the TDS fauna represents a palaeoecological different system. The predominance of archaeocyathans together with some sedimentological data (Elicki, 1999a) led to the reconstruction of an oligotrophic water column. In the TDS the value of the early shelly fossils lays in their role in paleobiogeographical reconstruction (see below).

The Sardinian Cambrian allows another application of shelly fossil assemblages. In contrast to the German GS environment (drowning shelf) and TDS environment (siliciclastic-carbonate ramp with shoals), the Sardinian Campo Pisano Formation represents the drowning stage of an isolated platform (Bechstädt and Boni, 1994; Loi et al., 1995; Pillola et al., 2002). The appearance and the disappearance of distinct fossil groups and the related succession of preferred feeding strategies and habitat types (see above, Elicki et al., 2003) are very useful tools for the reconstruction of processes that affected habitats. The main external, non-biotic control is identified as water depth (Elicki et al., 2003). As a result of their ecological requirements, the shelly fossil assemblages not only show the timing of the drowning (from onset to drowning pulses and phases of stagnation), they also indicate the water depth for each drowning stage as well as the lateral topography of the depositional area. Within a sequence where sedimentological data are practi-

cally absent (as in the Sardinian condensed Campo Pisano Formation) due to a strong late-diagenetic overprint (Elicki, 2001), such paleontological data are the only source for reconstruction and so of very special value.

3.2. Bio- and Ecostratigraphic Aspects

The use of post-basal Cambrian small shelly fossils for biostratigraphy is limited due to the rather poor knowledge (compared to trilobites) on taxonomic and phylogenetic aspects as well as the assumed degree of facies control (Landing, 1992, Landing and Westrop, 2004). Additionally, the ranges of many small shelly taxa are often very long. Result of this situation is that the stratigraphic resolution is not very high. However, if trilobites (or archaeocyathans) are absent or hard to recover from the rock, small shelly fossils are the only biostratigraphic aid. So, for the small shelly fossils from the GS an assemblage-zone correlation has been utilized (Elicki, 1994). Following Brasier's (1989a) biostratigraphy for the lowermost to higher Early Cambrian of the Tethyan belt, different assemblage zones can be distinguished. The association of the Görlitz biota (particularly *Rhombocorniculum cancellatum* and *Pelagiella lorenzi* with the trilobites *Calodiscus lobatus* and *Serrodiscus silesius*) allows correlation with the *Lapworthella cornu* to *Rhombocorniculum cancellatum* zone interval. This interval correlates to horizons of Comley (Ac3–Ac4) and Nuneaton (Purley Shale, both England), of Newfoundland (lower Brigus Formation), of Sweden (Gislöv Formation), and of Siberia (upper Atdabanian to early Botoman) (Brasier, 1989a). A correlation on the basis of the GS small shelly fossils into the Mediterranean regions is difficult because of the limited knowledge on their occurrence.

A further important use of Mediterranean small shelly fossils is their application in eco-stratigraphy. Such an approach is very useful on a regional scale. The small shelly fossils from Sardinia show characteristic vertical changes through the sections (see above), that trace fundamental changes in ecological conditions. These conditions are essentially controlled by eustatic and tectonically caused relative sea-level fluctuations (e.g., Bechstädt and Boni, 1989, 1994) and, possibly, regional climate changes due to paleogeographic movements of the depositional area into higher latitudes (Elicki et al., 2003). Within a relatively small paleogeographic area such changes are temporally approximately correlative. Such changes led to a more-or-less coeval reorganization of ecosystems on a regional scale, which is mirrored by modifications of the faunal characteristics. As mentioned above, there are nearly identical faunal successions in the different Sardinian sections, although minor differences may occur locally. In the lower Campo Pisano Formation of Sardinia at the Campo Pisano type section, a single, important biostratigraphic datum is known: the lowest occurrence of *Protolenus cf. pisidianus* indicates

an uppermost Lower Cambrian level just above the base of the Campo Pisano Formation (Pillola in Loi et al., 1995). Interestingly, within the *P. cf. pisidianus*-bearing interval a characteristic and abrupt biofacies change from sponge-dominated to echinoderm-dominated habitats occurs exactly at the top of the *P. cf. pisidianus*-level. Because of the regional-scale facies reorganization, this means that the base of echinoderm-dominated biofacies coincides with the base of the Middle Cambrian in the study area. This characteristic biofacies transition is an excellent ecostratigraphic level that allows recognition of the Early–Middle Cambrian boundary in southwestern Sardinia. Using this concept, a stratigraphic correlation of the Sardinian sections is possible even where trilobites are absent. Recently, the validity of this technique has been further confirmed by new discoveries of *Protolenus cf. pisidianus* from other Sardinian sections by Pillola (pers. comm.) in exactly the position predicted by ecostratigraphy.

These examples show that associations of Mediterranean small shelly fossils can be used as a stratigraphic instrument. Whereas a global or intercontinental correlation is not possible, small shelly assemblages represent useful regional-scale stratigraphy tools. A further advantage consists in the kind of extraction from the rocks. Using chemical methods, a faster winning of large amounts of (selected) microfossils from carbonates is possible. Such remains are fundamental for paleobiological investigation. For biofacies analysis (basis of the ecostratigraphic concept), in contrast, the investigation of thin-section series is needed to get pristine patterns of the faunal contents.

3.3. Paleobiogeography and Tectonics

Paleogeographically (Fig. 2), known small shelly assemblages reveal important aspects of the evolution of the Gondwanan shelf and its relationship to other Cambrian continents. A Siberian connection was long discussed based on the archaeocyathan-bearing carbonate deposits of the TDS (Freyer and Suhr, 1987). However, a critical reinvestigation of the older material has led to the conclusion, that such an affinity is not supported by the archaeocyathans (Elicki and Debrenne, 1993). Indeed, the bradoriid ostracod *Hipponicharion* from the Early Cambrian Zwethau Formation (Elicki, 1994; Gozalo and Hinz-Schallreuter, 2002) is strongly restricted to western Gondwana, Baltica, and Avalonia and contradicts the former assumptions. In addition, the only Early Cambrian trilobite reported from the TDS (*Dolerolichia pretiosa*) also supports a Mediterranean affinity (Sdzuy, 1962). Middle Cambrian strata of the TDS, from which mainly trilobites are known, are in accordance with that Early Cambrian palaeogeographic picture (Sdzuy, 1972).

The small shelly fauna from the GS area is much more significant than that from the TDS. Because of its greater richness, there are several taxa of paleogeographic value.

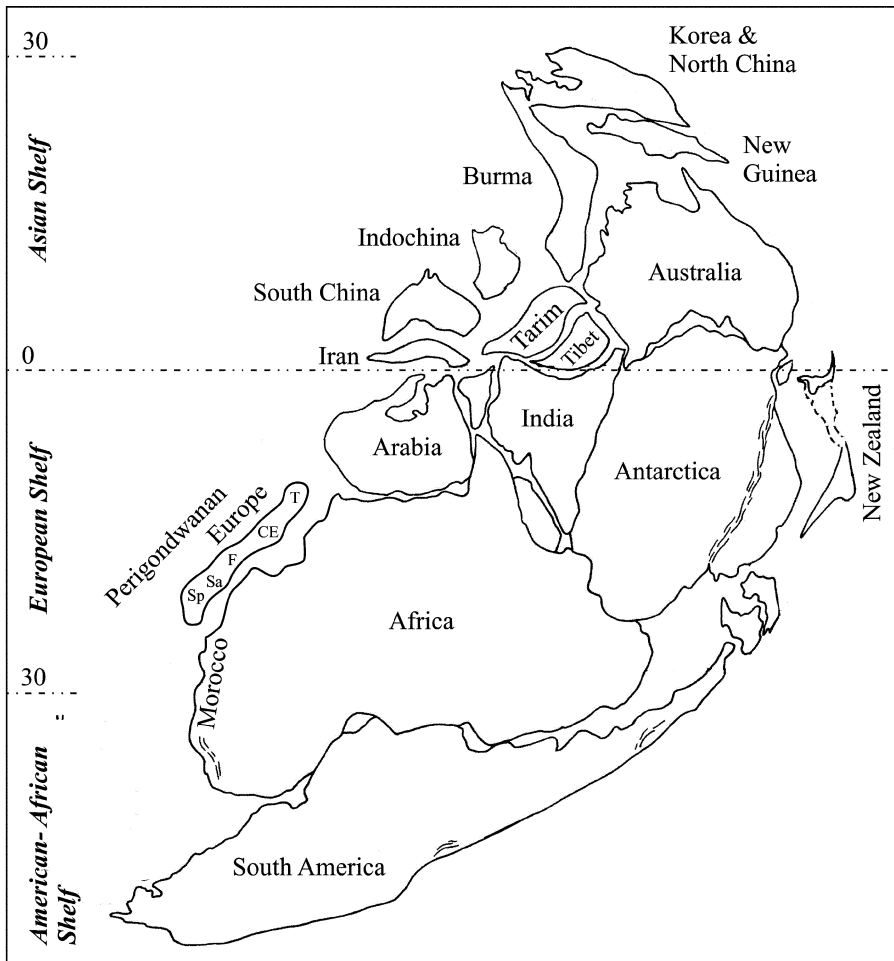


Fig. 2. Paleogeographic map of Gondwana (late Early to early Middle Cambrian); modified after Courjault-Radé et al. (1992), Landing and Westrop (2004) and Landing (2005). Sp, Spain; Sa, Sardinia; F, France; CE, Central Europe; T, Turkey.

Thus, the GS molluscan dominated assemblage is very similar to more-or-less coeval assemblages along the so-called "Paleotethyan belt" (Brasier, 1989b), of which the Mediterranean area can be regarded as a part. A high degree of similarity exists with small shelly assemblages in southern Australia (Bengtson et al., 1990; Brock et al., 2000), which is another part of "Paleotethys". In addition, from the Paleotethyan area *Anabarella australis* is known only from Australia and Germany (GS) (Elicki, 1996; Brock et al., 2000). The gastropod *Beshtashella tortilis* is described from the GS, but, also from Australia, southern China, Kazakhstan, and Spain (Elicki, 1994; Gubanov et al., 2004a). *Yuwenia* (gastropod) is known from the GS and southern Australia (Runnegar in Bengtson et al., 1990; Elicki, 1994). Common further molluscs which also occur in the GS are *Pelagiella* (gastropod), *Bemella* and *Obtusoconus* [both helcionellids; the latter described by Elicki (1996) as "*Tanuella*"] as well as the pelecypods *Fordilla* and *Pojetaia* (Elicki, 1994, 1996). The occurrences of all these taxa span the late Early to early Middle Cambrian interval. Because of this widespread distribution, Gubanov (2002) and Gubanov et al. (2004a) concluded that the Cambrian paleocontinents must have been situated closer together. A further argument

comes from the Cambrian diversification in gastropods. So, during Early Cambrian time there is an increase in the number of gastropod taxa, interpreted by Gubanov (2002) as an indication for a proceeding geographical separation of formerly well connected areas. A problem in this interpretation is the sometimes poor morphological definition of the taxa that can lead to taxonomic and systematic confusion. Nevertheless, other Mediterranean small shelly fossils point also to closer connections between areas which were hitherto assumed as positioned in great distance to each other: the pseudoconodont *Rhombocorniculum cancellatum* is known outside the GS from Avalonia, Baltica, Kazakhstan, Mongolia, southern China, and Siberia in approximately time-equivalent strata (e.g., Walliser, 1958; Landing et al., 1980; Brasier, 1989b; Elicki and Schneider, 1992). Additionally, cambroclaves – remains of uncertain systematic affinity – were hitherto known exclusively from Asia. In fact, specimens occur in upper Atdabanian strata of Kazakhstan and coeval beds of North and Central China as well as in the uppermost Lower Cambrian of Hainan (Mambetov and Repina, 1979; Bengtson et al., 1990; Jiang, 1992). The latter author reconstructed a centre of origin (Kazakhstan) and a migration path through northern to southern China during

the Early Cambrian. Newer finds came from South Australia (Bengtson et al., 1990), from Germany and Sardinia (Elicki and Wotte, 2003). However, evidence from the Mediterranean part of western Gondwana indicates that the reconstructed migration pattern (Jiang, 1992) may have to be revised. The German specimens are from early Atdabanian-equivalent strata and the Sardinian specimens are early Middle Cambrian in age (confirmed by trilobites, Elicki and Wotte, 2003). This means – after the recent state of knowledge – that the oldest and the youngest cambroclaves are from the Mediterranean region of Perigondwana. This observation is also paleobiologically remarkable in the context of the occurrence of the bradoriid ostracods (*Hipponicharion*): after recent investigation Gozalo and Hinz-Schallreuter (2002) mean that also this genus has his oldest representatives in the Mediterranean area (TDS). So, the new results from the few last years suggests that western Perigondwana could be an important region to evaluate true centers of origin and migration patterns of several groups of organisms. This region may also have functioned as a center of origination (as for a number of archaeocyathans, Debrenne and Zhuravlev, 1992). In any case, the small shelly fossils seem to support the probable paleogeographic relationship of the Mediterranean to the eastern Gondwana margin (Far East, Australia; Pillola, 1991 – Early Cambrian, Sdzuy, 1972 – Middle Cambrian, Shergold et al., 2000 – Late Cambrian). The high degree of morphological accordance of taxa along the Gondwanan margins suggests an intensive and more-or-less uninterrupted exchange of taxa.

Other small shelly taxa from the German and Sardinian Cambrian as special poriferans (e.g., *Dodecaactinella*, *Eiffelia*), cancelloriids (e.g., *Allonnia*, *Archiasterella*), hyoliths (e.g., *Lenalituus*, *Conotheca*, *Microcornus*) or microproblematica (e.g., *Microcoryne*, *Hadimopanella*, *Aetholicopalla*, *Coleoloides*, *Torellella*) are too poorly investigated for stratigraphic and paleogeographic conclusions.

In addition to these intercontinental paleogeographic relationships, the Mediterranean small shelly fossils contribute to the reconstruction of regional paleogeographic and tectonic processes. Because of the high sensibility of ecoenoses to environmental conditions and changes of base level, sea-level and climate fluctuations can be reconstructed (e.g., the gentle drowning of the German shelf area or the sudden drowning of the Sardinian platform).

Besides the drowning history of the Gondwanan European shelf and the related climate/sea-level changes, the small shelly fossils also give important arguments to the recent discussions on terrane-based tectonic models (including their derivation, evolution, relations) and local/regional basin evolution. For most of the central and southern European Mediterranean, Cambrian strata were deposited within separated pull-apart-basins, currently preserved as terranes, is widely accepted (Linnemann et al., 2000; Murphy et al., 2004). Although the knowledge on Cambrian small shelly

fossils from that terranes is comparatively poor, there are several reports on such faunas: France (Doré and Reid, 1965; Kerber, 1988; Álvaro et al., 2002), Spain (e.g., Geyer, 1986; Fernández-Remolar, 1999, 2001c; Vidal et al., 1999; Gozalo and Hinz-Schallreuter, 2002; Gubanov, 2002; Gubanov et al., 2004), Germany (e.g., Elicki and Schneider, 1992; Elicki, 1994, 1999a), Sardinia (e.g., Elicki et al., 2003; Elicki and Wotte, 2003; Elicki and Pillola, 2004), Jordan (Bandel, 1986; Elicki, 2004a, 2004b), Turkey (Gedik, 1989; Sarmiento et al., 2001). As demonstrated, there was a very active faunal exchange between these different regions. Wherever small shelly assemblages are described from the Mediterranean Europe, they show a large amount of sheared taxa. Because these taxa were highly sensible to environmental conditions, time-equivalent occurrences of the same species, genera and assemblages point to large and rather uniform facies belts and contradict strongly separated terranes. The content, the coinciding evolution patterns and the palaeogeographic relations of Perigondwana's Early to Middle Cambrian biota demonstrate that the separation and single evolution of terranes from western Gondwana's European shelf have not been started before the end of the Cambrian.

4. CONCLUSIONS

The knowledge on Cambrian small shelly fossils from the Mediterranean area is relatively limited, but, much progress has been made over the last years. So, rich assemblages are known from higher Lower to lower Middle Cambrian carbonates of Germany and Sardinia (Elicki, 1994, 1997; Elicki et al., 2003; Elicki and Pillola, 2004) and from France (Kerber, 1988). Similar faunas have been mentioned from Spain (Geyer, 1986; Fernández-Remolar, 1999, 2001b; Sarmiento, 2001; Gozalo and Hinz-Schallreuter, 2002; Gubanov et al., 2004a).

The investigation on these fossils led to new paleobiological insights into the character and functioning of Cambrian shallow-marine ecosystems. Using this information, a determination of the trophic organization, of the kinds of habitats, and water depths has been done for the German and Sardinian deposits at different Cambrian times. Because of the sensitivity of the small shelly assemblages to environmental conditions, they mirror any changes in these conditions. Thus, the vertical succession of associations from the German Cambrian (Charlottenhof Formation, GS) and from the Sardinian Cambrian (Campo Pisano Formation) represents a very useful tool for reconstruction of the ecological development of the depositional areas.

Because of the ecological sensitivity, changes of limited extent induced by regional tectonics or sea-level fluctuations are reflected by distinct faunal changes. So, the timing (onset, diachrony, development) of shelf-scale processes (e.g., the drowning of carbonate platforms along the west-

ern Gondwana margin and the origin of tectonic terranes) can be correlated.

In respect to the latter, there is important paleogeographic information from the Mediterranean small shelly fossils. The fossils indicate biotic migration between the different Perigondwanan regions until the Middle Cambrian at least. Together with sedimentological data this points to a rather uniform and weakly differentiated facies belt across most of the European shelf and contradicts the concept of isolated basins. A still open question in this respect is the probable endemism in Early Cambrian trilobites (e.g., Álvaro et al., 2003) which partly contradicts the data from the small shelly fossils. To clarify this problem, more information on the taxonomy and systematics of the small shelly fossils and trilobites is needed. Possible paleogeographic relationships of the Mediterranean Cambrian to the Far East (based on trilobites) are supported by the occurrences of related small shelly assemblages. Especially, some of the shared molluscan taxa (gastropods, bivalves) support such relationships.

Based on a number of species and genera, several centers of origin and succeeding migration paths hitherto assumed for distinct taxa (e.g., cambroclaves from Asia) must be rejected. New finds in the Mediterranean indicate that the recent knowledge is too poor for such an interpretation.

Stratigraphically, small shelly fossils are important and very useful where the higher biostratigraphic resolution allowed by trilobites is not available. Small shelly fossils often constitute characteristic assemblages which can be used for ecostratigraphic conclusions. If some of the assemblages are calibrated by trilobites then ecostratigraphic levels may correspond to biostratigraphic levels in regional extent (as shown in the case of the assemblages from Sardinia) and can be used to construct a regional stratigraphic framework.

In summary, Cambrian small shelly fossils of the Mediterranean area are important in the reconstruction of paleoecology, paleogeography, tectonics, sea-level fluctuations and as regional-scale stratigraphic tools. It can be expected that increased knowledge on Mediterranean small shelly fossil assemblages will lead to a better understanding and to a conspicuously more detailed picture of the Cambrian Perigondwana.

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