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Cambroclaves from the Cambrian of Sardinia (Italy) and Germany: constraints for the architecture of western Gondwana and the palaeogeographical and palaeoecological potential of cambroclaves

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Abstract

Cambroclaves represent a group of problematic microfossils previously known from strata close to the Early/Middle Cambrian boundary of only a few palaeogeographic regions (Kazakhstan, China, Australia). Because of their frequent occurrence as disarticulated remains, they have hitherto been assumed to be provincially restricted microfossils of unclear palaeobiological affinity. Discoveries of cambroclaves from the Early to early Middle Cambrian of southern (Sardinia) and central (Germany) Europe point to a much wider distribution during their short stratigraphic range, and imply closer palaeogeographic relations between the European shelf of western Gondwana and the areas from which cambroclaves were previously known. These relations are also supported by the common occurrence of other small shelly fossils. These facts support the existence of a widespread uniform facies belt (shelf) around parts of Gondwana during the Early–Middle Cambrian time interval, and contradict the interpretation of the European depositional areas as isolated basins or as distinctly separate Cambrian terranes. The western Gondwana cambroclaves occur in carbonate successions indicative of special palaeoecological conditions. The specimens are limited to distinct layers formed during transgressive phases that opened inner and partly restricted platform areas to open-marine and more distal (deeper subtidal) environments, possibly accompanied by a transition from a rather arid to more humid climatic conditions. Because of the short stratigraphic window of occurrence and of distinctive facies characteristics, cambroclaves are palaeoecologically and palaeobiogeographically useful, and consequently contribute important evidence for both the reconstruction of the Perigondwana realm and the relations to other palaeocontinents in the Cambrian.

Keywords: Cambrian; Gondwana; cambroclaves; small shelly fossils; palaeobiogeography; palaeoecology

1. Introduction

Cambroclaves are minute sclerites with a plate-like basal shield bearing a prominent elongate spine. The shield and the spine may have smooth

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or ornamented surfaces (Qian, 1978; Mambetov and Repina, 1979; Conway Morris and Chen, 1991). The original mineralogy was probably calcareous, but they were phosphatised during diagenesis. Possibly the hollow shield was originally filled with soft tissue.

Cambroclaves show a wide morphological variability that has led to many form-taxa, to an extensive number of synonyms, and to taxonomic confusion (Bengtson et al., 1990; Conway Morris et al., 1997). The latter authors have distinguished four morphological groups of cambroclaves: zhijinitids and paracarinachitids (oval base and prominent spine), cambroclavids (dumb-bell shaped base with spine at the anterior end), deiradoclavids (nearly circular base, spine may form a transverse ridge), and deltaclavids (tear-drop shaped base, short spine at the expanded anterior end). The first two groups are the most common and widespread.

Cambroclaves are mostly known from disarticulated remains. There are very few examples of some elements connected with each other (Kazakhstan, South Australia, China). These, and some particular morphological features, have contributed to several reconstructions of scleritomes (Mambetov and Repina, 1979; Bengtson et al., 1990; Conway Morris and Chen, 1991). Nevertheless, the shape of the complete animal is still unknown. Zhijinitids (with a more circular shield) may have been positioned on the animal's outer surface and separated from each other by soft tissue, or perhaps they were located in small interspaces within cambroclavid scleritomes. All the other cambroclave groups probably covered the animal totally (interconnected arrays or sheets; for discussion see Bengtson et al., 1990; Conway Morris and Chen, 1991). Most authors agree in interpreting a protective function for the sclerites against predators or physical abrasion. Some special morphologies (e.g. curved spines) may also point to a grasping behaviour.

The cambroclave-bearing animal is regarded as bilaterally symmetrical – maybe slug-like – with an unclear systematic position. Tentative interpretations range from protoconodont-related (Mambetov and Repina, 1979) to endoparasitic worms (Acanthocephala according to Qian and Yin, 1984) or to animals with affinity to priapulid worms or to aschelmiths (Conway Morris et al., 1997). Dzik (1994) compared such remains with receptaculids (usually interpreted as algae, but seen as sponge-related by that author). A more reliable systematic decision will not be possible until discovery of articulated specimens.

Cambroclaves are typical Cambrian, but otherwise rather unusual microfossils. They were first reported nearly simultaneously from South China and Kazakhstan (Qian, 1978; Mambetov and Repina, 1979), and they were subsequently found in North China (Tarim), South Australia, and Germany (for a summary of previously known occurences see Conway Morris et al., 1997; Fig. 2).

2. General characteristics of the Early/Middle Cambrian transition interval on the European shelf

During the Cambrian period several major continents (Gondwana, Laurentia, Siberia, Baltica) and several minor landmasses existed (Brasier, 1992; Kirschvink, 1992; McKerrow et al., 1992; Torsvik et al., 1996; Seslavinsky and Maidanskaya, 2001; Smith, 2001). Many sections representing this time interval (especially those of Perigondwana origin) occur today on terranes (e.g. Matte et al., 1990; Erdtmann, 1991; Narebski, 1994; Oczlon, 1994; Linnemann, 1995; Tolluoglu and Sümer, 1995; Tait et al., 1997; Debrenne et al., 1999; Zulauf et al., 1999; Belka et al., 2000; Cocks, 2000; Linnemann et al., 2000; Demange, 2001).

During Early Cambrian time, the European shelf of the western Gondwana margin was marked by a generally transgressive trend accompanied by a warming of the climate to arid–subtropical conditions (Álvaro and Vennin, 1998; Álvaro et al., 2000a,b,c). Thus, middle, southern and southwestern Europe are characterised by transition of the marine environments from siliciclastic (deeper and shallow shelf areas) to carbonate (archaeocyath-bearing shallow ramps and shelfs) under equatorial/subequatorial conditions (Debrenne, 1964; Perejón, 1986; Gandin, 1987; Bechstädt and Boni, 1994; Elicki, 1999; Álvaro et al.,

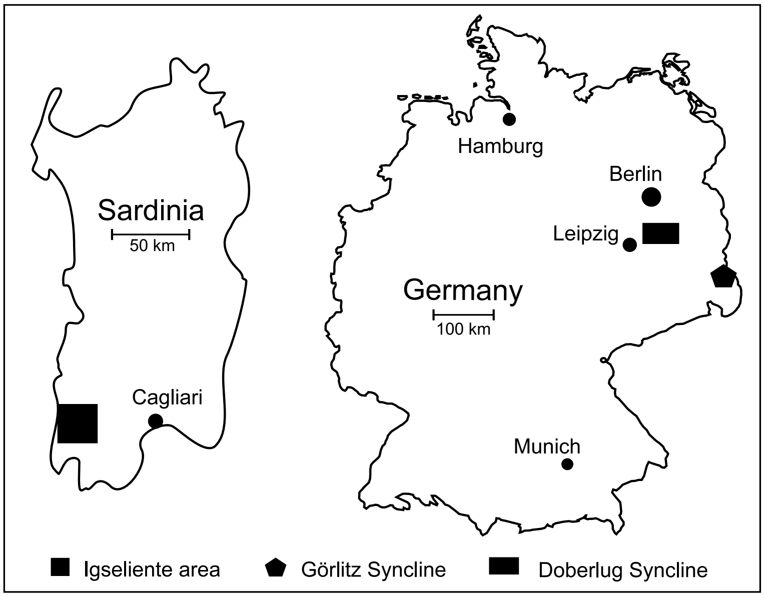


Fig. 1. Location map of the working areas in Sardinia (Italy) and Germany.

2000a,b; Fernández-Suárez et al., 2000; Seslavinsky and Maidanskaya, 2001).

In contrast, Middle Cambrian sediments of the European shelf are predominantly siliciclastic. Only at the beginning some carbonates were deposited on deepened shelfs and ramps (Gandin, 1979; Courjault-Radé, 1990; Liñán and Quesada, 1990; Loi et al., 1995; Álvaro et al., 2000b; Álvaro et al., 2001; Elicki, 2001). The reasons for these dramatic changes were complex (e.g. diachronous tectonics of different local intensity, changing climate, sea-level rise, palaeogeographic movements) and are not completely understood.

This general sedimentological evolution during the Early/Middle Cambrian transition produced a very uniform stratigraphic pattern over most of the Mediterranean region, including the Cambrian deposits in Spain, France, Sardinia (Italy), and Germany, but also shows similarity to Morocco, Turkey and the Middle East (Haude, 1969; Sdzuy, 1972; Önalan, 1986; Courjault-Radé et al., 1991; Álvaro et al., 1993; Liñán and Gámez-Vintaned, 1993; Pillola et al., 1994; Geyer and Landing, 1995; Elicki, 1997). Faunal similarities between these areas (see also Álvaro et al., 2003, this issue) are further support for such palaeogeographic relations. Many of these deposits in Europe are incorporated in tectonostratigraphic terranes (e.g. the German successions). The incompleteness of the sections, their isolation and poor preservation have led to many problems in correlation and in palaeogeographic and tectonic reconstruction.

In recent years an improved correlation of the European deposits has been worked out. In addition to intensive biostratigraphic work, the detection of sea-level-related regional and global events (e.g. Daroca event, Valdemiedes event) as well as provenance data from detrital minerals have helped to clarify the structural evolution of the European shelf area (Álvaro et al., 1993; Liñán and Gámez-Vintaned, 1993; Pillola, 1993; Geyer and Elicki, 1995; Álvaro and Vizcaïno, 1997, 1998; Chang, 1998a; Vidal et al., 1999; Belka et al., 2000; Cocks, 2000)

3. The cambroclaves from the western Gondwana European shelf

After having been reported for the first time in 1978, for a long time cambroclaves were known only from Asia. Following discoveries in southern Australia (Bengtson et al., 1990), cambroclaves

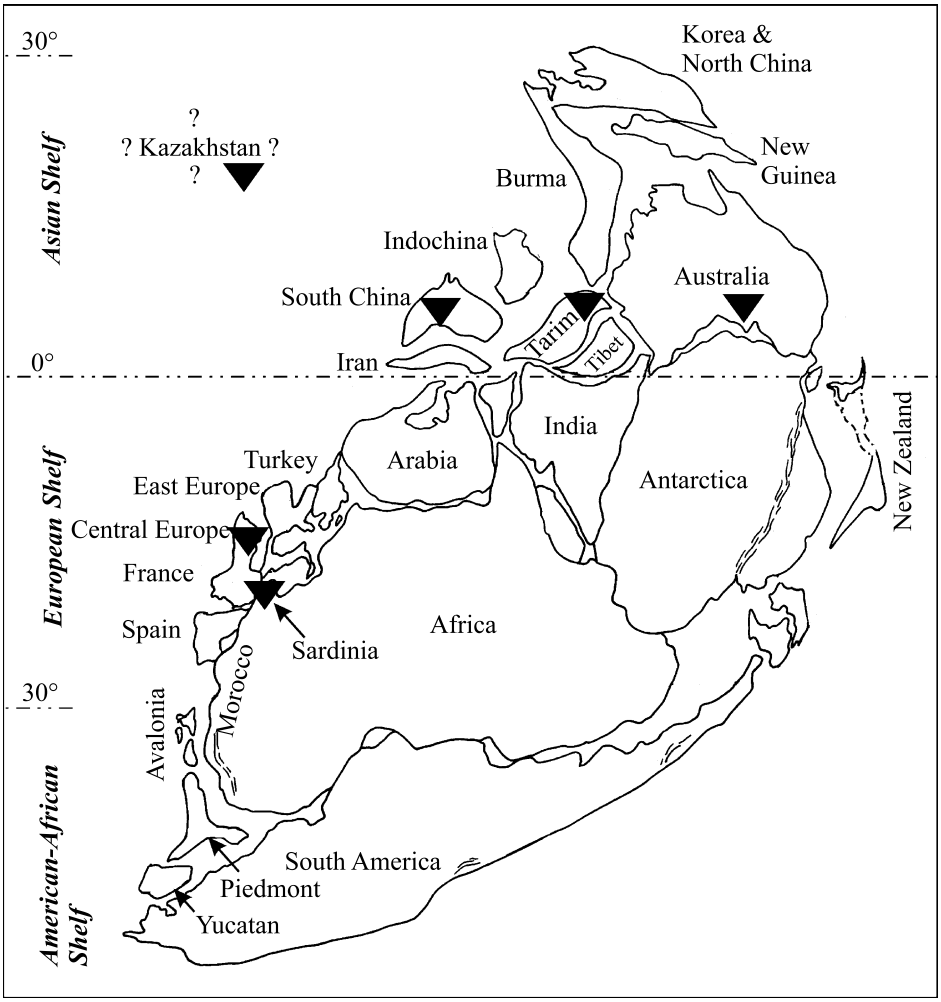


Fig. 2. Palaeogeographic reconstruction of Gondwana during the latest Early Cambrian (modified after McKerrow et al., 1992; Courjault-Radé et al., 1992; Seslavinsky and Maidanskaya, 2001). Localities of cambroclaves are indicated by black triangles.

were first reported from western Perigondwana by Elicki and Schneider (1992). Later these fossils – on the basis of more specimens – were revised and described as *Cambroclavus ludwigsdorfensis* (Elicki, 1994). The most recent findings come from southwestern Sardinia (Elicki, 1998–2000).

3.1. Cambroclaves from southwestern Sardinia (Italy)

The Cambrian succession of southwestern Sardinia (Fig. 1) has been investigated palaeontologically (trilobites, archaeocyaths) and sedimentologically over many years, but especially extensively during the last decades (for results and summaries of research, see Bechstädt et al., 1985; Bechstädt et al., 1988; Pillola, 1991; Bechstädt and Boni, 1994; Loi et al., 1995; Pillola et al., 1995). The succession (Fig. 3) represents an evolution from a clastic tidal shelf via a mixed shelf stage (both Nebida Group, Ovetian to Marianian) to an isolated carbonate platform (Gonnesa Group, upper Marianian to Bilbilian) which was subsequently disrupted and flooded (basal Iglesias Group, uppermost Bilbilian to Caesaraugustian) and then covered by clastic shelf deposits

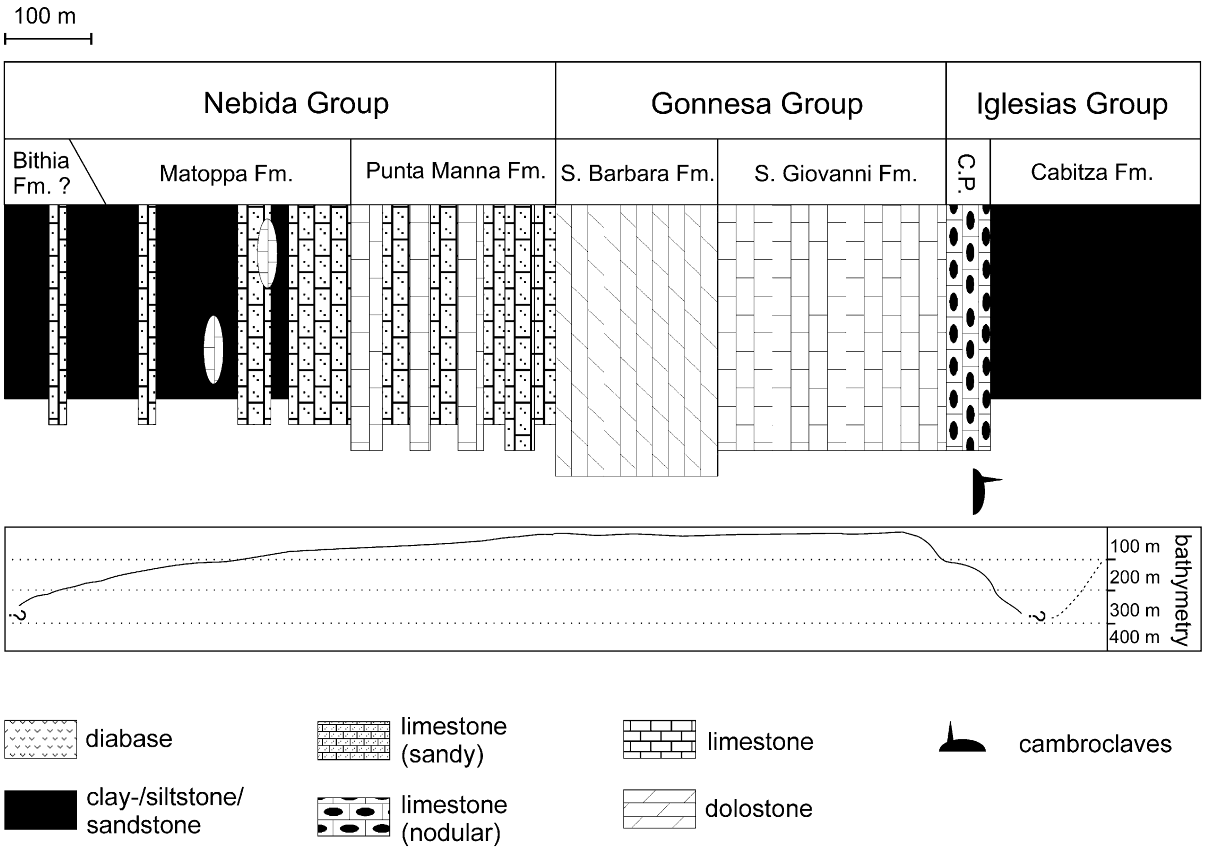


Fig. 3. Generalised geological section of the Cambrian succession of SW Sardinia (Italy) and sketch of the bathymetric history. C.P. = Campo Pisano Formation. Whether a 'Bithia Fm.' is really existing or only a synonym for a local equivalent of the lower Matoppa Fm. is under discussion. The position of cambroclaves is indicated.

(upper Iglesias Group, middle Caesaraugustian up to Lower Ordovician; Bechstädt et al., 1988; Pillola et al., 1995).

Despite the extensive knowledge of the Sardinian Cambrian, the drowning stage (basal Iglesias Group, Campo Pisano Formation, condensed nodular limestones) has until recently not been investigated in detail. Sedimentologic and facies data have been published by Gandin (1987), Cocozza and Gandin (1990) and Elicki (2001), while some palaeontologic work comes from Cherchi and Schroeder (1984), Mostler (1985), Pillola (1991) and Elicki (1998–2000). Following Pillola et al. (1995), the Campo Pisano Formation starts stratigraphically (trilobites) within the highest Lower Cambrian (upper Bilbilian) and extends to the mid-Middle Cambrian (early/middle Caesaraugustian).

The Sardinian cambroclaves were found in the Su Corovau section, which is situated about 6 km NE of the town Iglesias. They occur in a relatively thin (0.15 m) and distinct interval, about 1.8 m above the base of the Campo Pisano Formation. About 40 cambroclavid morphs have been identified (Fig. 7; special publication in progress). Whereas the biofacies of the directly underlying carbonate succession (basal part of the Campo Pisano Formation) is characterised by a predominance of poriferids (a phenomenon often recognised in Campo Pisano sections), the cambroclave-bearing level shows a more diverse fossil content that includes disarticulated echinoderm

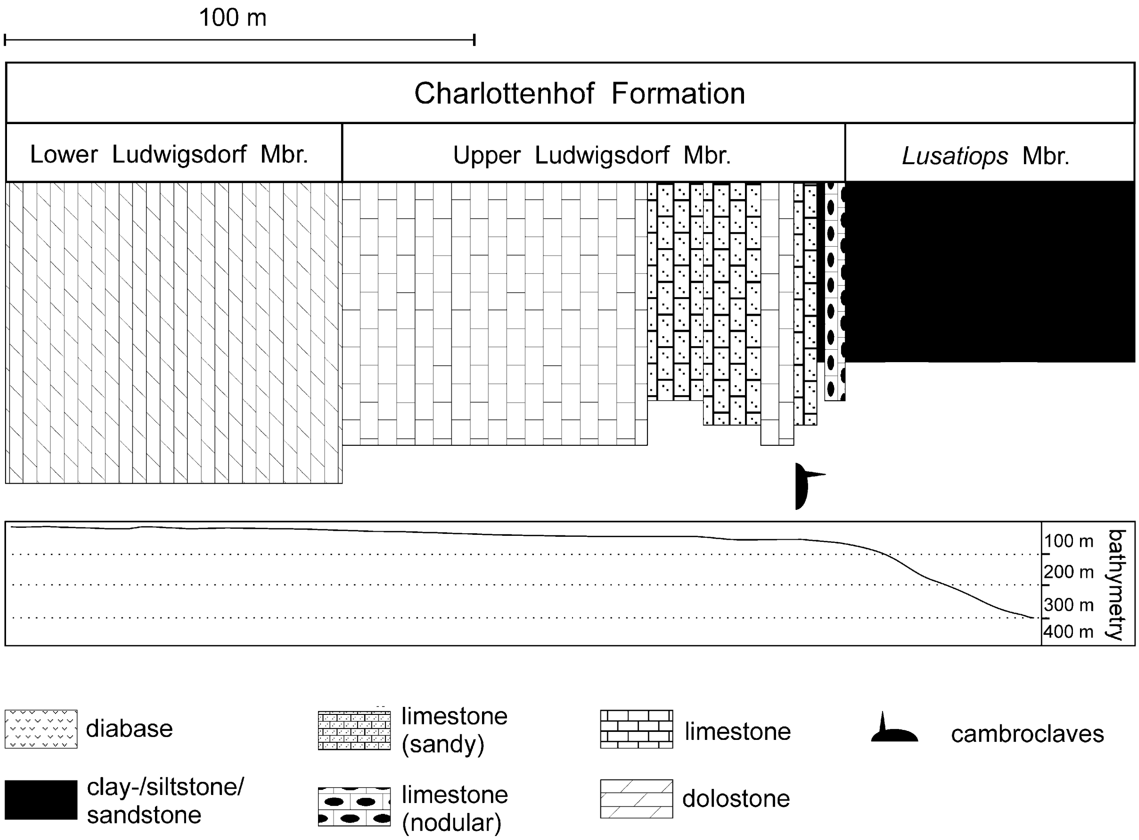


Fig. 4. Geological section of the Cambrian succession of the Görlitz Syncline (Germany) and sketch of the bathymetric history. The position of cambroclaves is indicated. For legend see Fig. 3.

remains, lingulate brachiopods, small trilobites, archaeogastropods (*Pelagiella*), and rare hyoliths (among others *Microcornus*) and chancelloriids. The sponge remains are nearly completely absent from this level upward for the rest of the section.

After investigation of nearly 20 sections of the Campo Pisano Formation it seems that there is a more or less regular vertical sedimentological and biofacies pattern that reflects the evolution of the Campo Pisano environment: thus, the sometimes nodular limestones of the lower Campo Pisano Formation follow the shallow isolated platform stage of the Gonnesa Group (Fig. 3). This transition represents a brief subsidence pulse (local breccias, abrupt changing of the biocoenoses, sudden onset of terrigenous influx) below the carbonate production optimum zone (probably middle subtidal). The fauna here is rather monotonous (mainly sessile–benthic filter-feeding poriferids). After that, the biofacies succession indicates a slight deepening to a greater subtidal depth which is the primary depositional regime for most of the Campo Pisano Formation. The fauna of this facies is typically open marine. Only toward the top of the formation can a second important subsidence impulse be observed (biota smaller and transported, decrease of carbonate content, alternation of carbonate and shaly layers), which led to a drop of the platform into deeper water. At this point, deposition became completely siliciclastic (Cabitza Formation; Fig. 3).

The Sardinian cambroclaves occur only in the transition zone from the very shallow to the presumed middle subtidal, and from a rather restricted to an open marine and terrigenous-influenced environment (more complex shelly-fossil

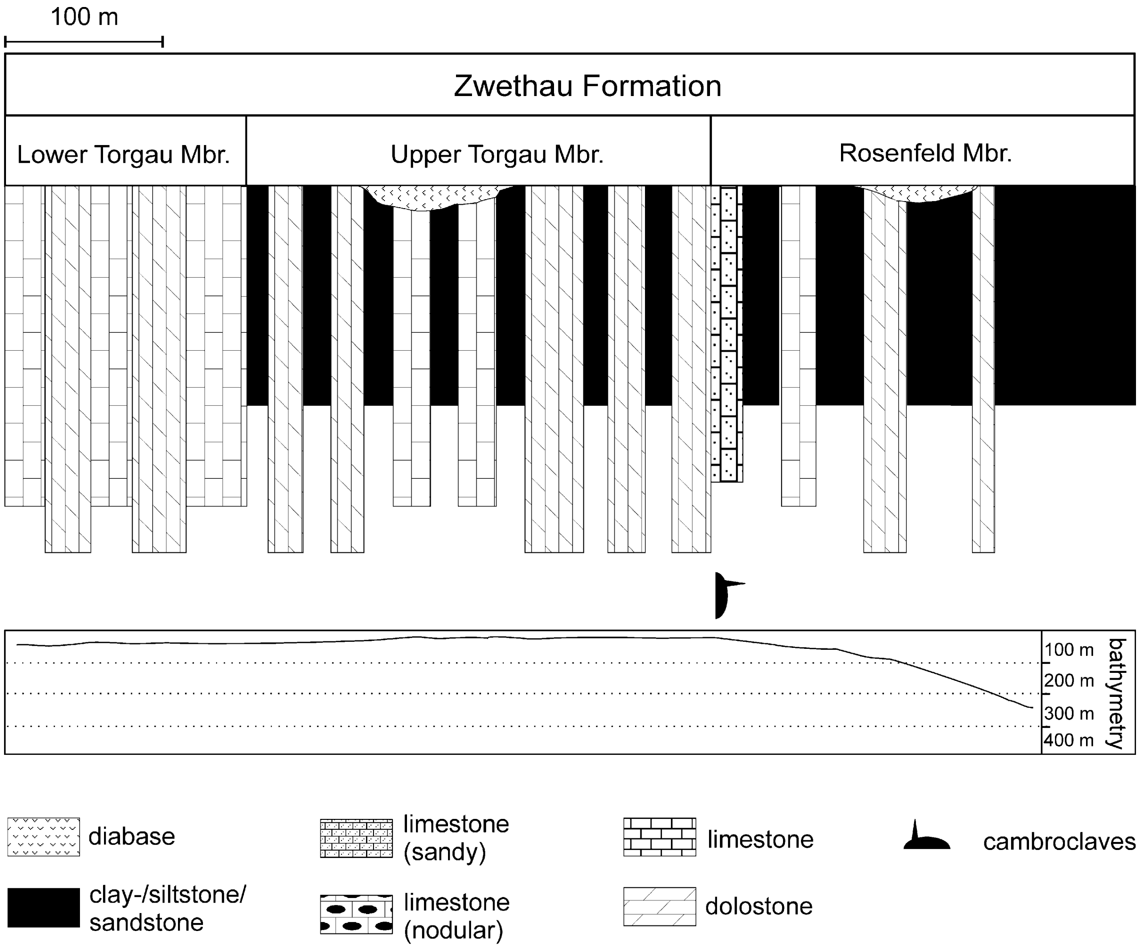


Fig. 5. Geological column of the Cambrian succession of the Doberlug Syncline (Leipzig area, Germany) and sketch of the bathymetric history. The position of cambroclaves is indicated. For legend see Fig. 3.

biocoeonoses; distinct decrease of passive filter feeders: no archaeocyaths, loss of the other poriferids; no photosynthetic organisms).

This dramatic reorganisation of the depositional area may have had different causes: Bechstädt et al. (1985), Gandin (1987), Bechstädt and Boni (1989), and Álvaro and Vennin (1996) have suggested tensional tectonics. However, when other sequences of this time interval in western Gondwana are taken into account, a general rise in relative sea level must also be considered. These processes may have been accompanied by general climate changes. Thus, arid conditions are assumed for the isolated platform stage of the Gonnesa Group, whereas more humid conditions may be assumed for near the end of the group (Gandin, 1987; but see Bechstädt and Boni, 1989). A further source of change is the movement of this palaeogeographic area to higher southern latitudes (e.g. Courjault-Radé et al., 1992; Kirschvink, 1992; Seslavinsky and Maidanskaya, 2001). Therefore, the strong sedimentologic and palaeoecologic changes that are expressed by the beginning of the Campo Pisano Formation may have been caused by a complex of tectonic, climatic, palaeogeographic, and sea-level events.

The biostratigraphic position of the Sardinian cambroclaves can be constrained by correlation to the Campo Pisano type section (about 10 km away). From here Pillola (1991) described *Proto-*

lenus (*Protolenus*) sp. – later identified as *P.* cf. *pisidianus* (compare Loi et al., 1995) – in the lower part of the section. According to these authors, the occurrence of this taxon (where *Paradoxides* is missing – as in Sardinia) is indicative of the Early/Middle Cambrian boundary in the Mediterranean area. Because of the poor exposures, the basal spiculite facies of the Campo Pisano Formation (occurring in many sections) could not be positively identified in the type section. But there, immediately above the *P.* cf. *pisidianus*-bearing layer, the distinctive echinoderm-rich biofacies, which normally directly overlies the spiculite facies, starts. Thus, it seems that the transition from spiculite facies to echinoderm facies (as an ecostratigraphic boundary) in this local area corresponds with the biostratigraphic Early/Middle Cambrian boundary. Consequently, although *P.* cf. *pisidianus* has not yet been observed in the Su Corovau section, the base of the horizon containing the cambroclaves (which represents the first echinoderm-rich layer) can be roughly correlated with the Early/Middle Cambrian boundary interval. Therefore, the stratigraphic position of the Sardinian cambroclaves is probably lowest Middle Cambrian (early Leonian; Fig. 6).

3.2. Cambroclaves from eastern Germany

Cambrian successions are very rare in Germany. A compilation of the occurrence, faunal content, and biostratigraphy is given in Elicki (1997).

There is one short report on cambroclaves from two German regions (Fig. 1): (1) the Görlitz Syncline area (near the German–Polish boundary) and (2) the Leipzig area (= Doberlug Syncline; Elicki, 1994). Both regions belong to the Mediterranean facies realm of the Cambrian European shelf of western Gondwana (Sdzuy, 1972) and represent the most northerly sites of this realm (Fig. 2).

3.2.1. Görlitz Syncline

The Görlitz section (Lower Cambrian) is characterised by a succession of shallow-water massive dolostones and overlying bedded (and near the top partly nodular) limestones (Ludwigsdorf Member). This carbonate succession is overlain by a suite of claystone and siltstone with some sandstone intercalations (*Lusatiops* Member). The thickness of the whole section is about 250–300 m (Fig. 4). Due to the complex tectonic sit-

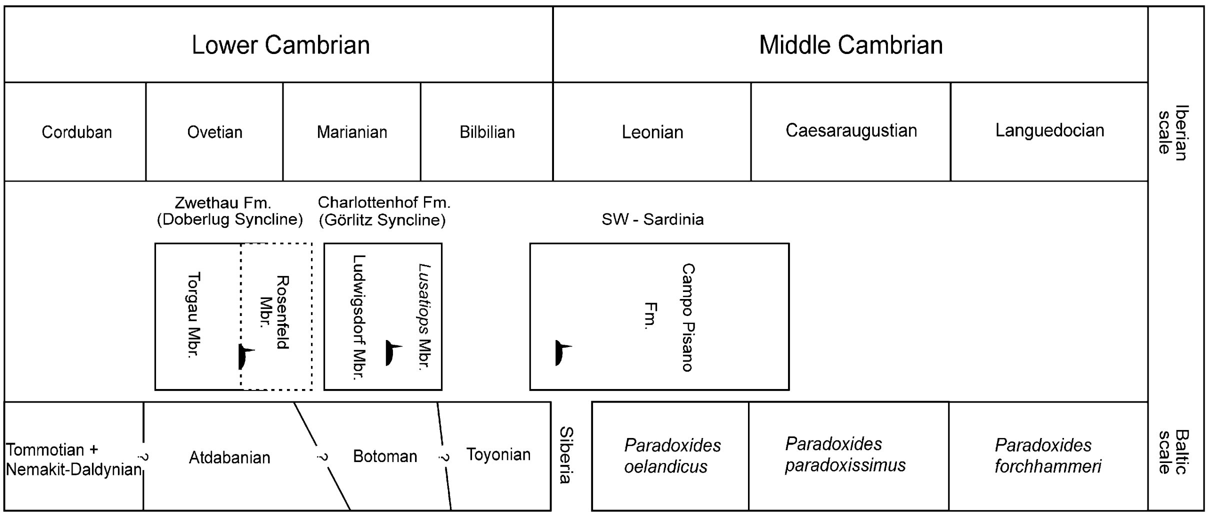


Fig. 6. Sketch of the stratigraphy of the cambroclave-bearing formations and members using the Iberian scale. For comparison, the Siberian scale for the Early Cambrian and the Baltic scale for the Middle Cambrian are also given. The position of cambroclaves is indicated.

uation, the stratigraphic continuations above and below are unknown. The poorly exposed outcrops have been studied for nearly 100 years; the most recent sedimentologic, facies, palaeontologic and stratigraphic work comes from Elicki and Schneider (1992), Elicki (1994, 1998, 2000) and Geyer and Elicki (1995).

A rich microfauna comes from the higher part of the limestone succession. The cambroclaves (*Cambroclavus ludwigsdorfensis* Elicki, 1994 – about 100 cambroclave morphs were recovered; Fig. 7) are restricted here to the horizon with the richest biodiversity. The accompanying fauna consists of echinoderms, hyoliths and chancelloriids, poriferids, trilobites (e.g. *Calodiscus* cf. *lobatus* (Hall, 1847), *Ferralsia saxonica* (Geyer and Elicki, 1995), *Lusatiops* sp.), molluscs (pelagiellids, pelecypods, monoplacophorans) and problematica (e.g. *Coleoloides typicalis* (Walcott, 1890); *Microcoryne cephalata* (Bengtson, 1990); *Aetholicopalla adnata* (Conway Morris, 1990); *Halkieria* sp.).

The litho- and ecostratigraphic level of occurrence of the cambroclaves is remarkable (Fig. 4). They are limited to a layer on top of which the transition from the shallow and open lagoonal carbonate environment to the siliciclastic outer-shelf conditions starts (for details see Elicki, 2000). The sedimentation is characterised by an increase in siliciclastic influx. Small channels filled by phosphatic pebbles, mud pebbles and accumulations of fossil hard-parts may indicate the beginning of the deepening trend. In the immediately overlying stratum the siliciclastic content is much higher, the carbonates decrease, the texture of the carbonates is rather nodular and for the first time *Rhombocorniculum cancellatum* (Cobbold, 1921) occurs. This transition from carbonate to siliciclastic deposition is gradual. The most likely reason for this change is the general transgressive trend of this time interval.

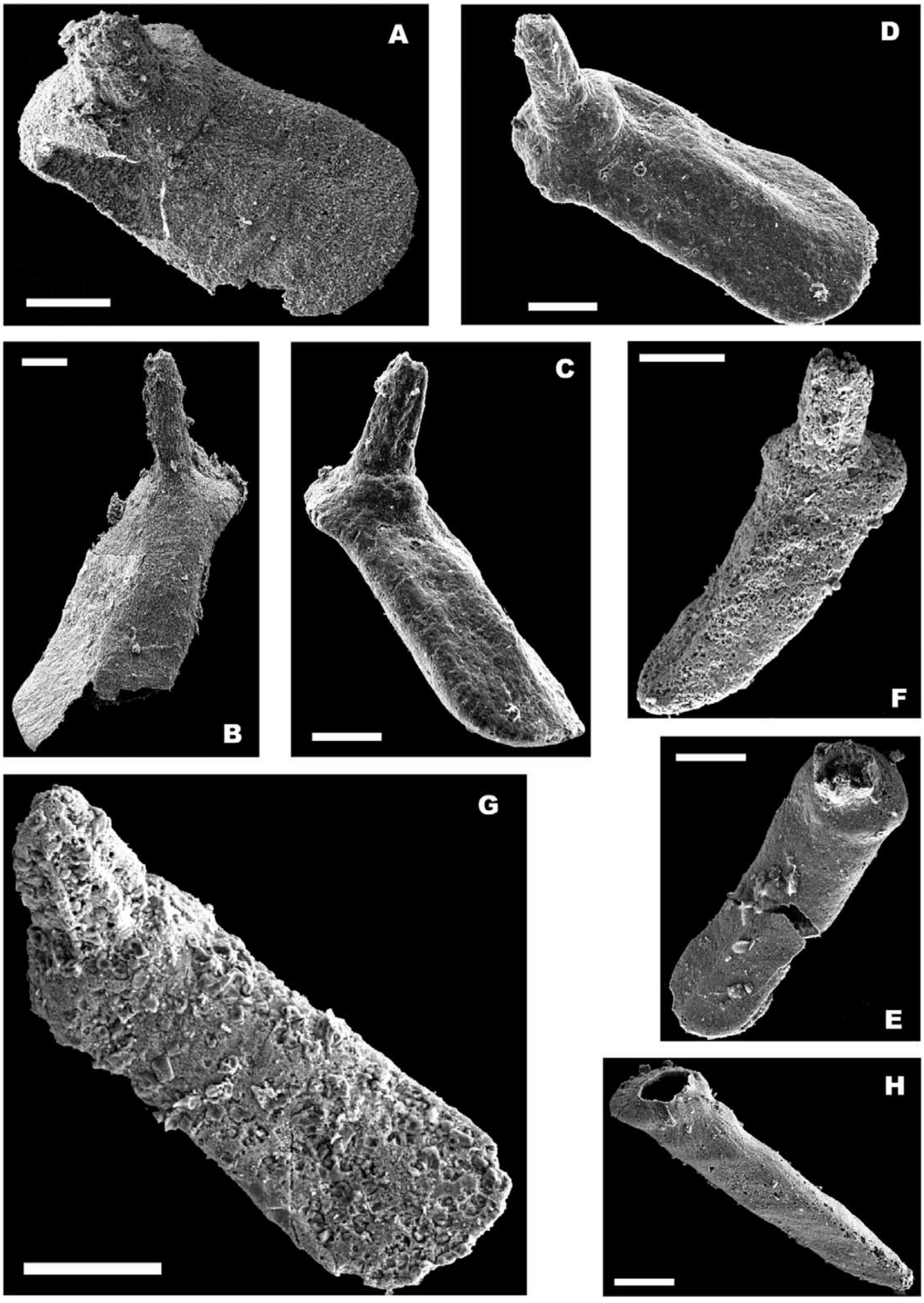
The fauna of the cambroclave-bearing horizon is dominated by suspension feeders and filter feeders (hyoliths, chancelloriids, echinoderms, poriferids, brachiopods, helcionellids). Deposit feeders also occur (pelecypods, trilobites). Grazers and predators (e.g. early gastropods, halkieriids) were rather rare. Archaeocyaths (non-spicular sponges typical of many Early Cambrian carbonate deposits) are absent. The favoured mode of life within this rather eutrophic environment was semi-infaunal (most of the hyoliths, some helcionellids), but includes also infaunal (pelecypods) and sessile and mobile epifaunal elements (poriferids, echinoderms, trilobites, brachiopods, 'small shelly fossils'). The depositional area was a muddy carbonate soft ground. Fossils for which a nektonic behaviour can be assumed (*Rhombocorniculum*) occur firstly directly above the cambroclaves and indicate (together with other faunal and sedimentological data) a deepening trend.

The biostratigraphic position of these cambroclaves is determined by the co-occurrence of *Ferralsia saxonica* (Geyer and Elicki, 1995), which indicates a middle to upper Marianian age (Álvaro et al., 1998) and the onset of the 'small shelly fossil' *R. cancellatum* (Cobbold, 1921) immediately above, which is correlative to the start of the upper Atdabanian *R. cancellatum* zone (Rozanov and Zhuravlev, 1992) and to the Chinese lower Qiongzhusian (Jiang, 1992). The trilobites of the overlying *Lusatiops* Member belong to the early Botoman (*Bergeroniellus micmacciformis* level), which in turn correlates to the *Microcornus parvulus* zone in terms of the small-shelly-based biostratigraphy (Rozanov and Zhuravlev, 1992).

3.2.2. Doberlug Syncline

The subsurface Cambrian succession of the Doberlug Syncline (Leipzig area; Early and Middle Cambrian) is affected by complex tectonics, which have often led to problems in correlation. The Early Cambrian suite (Zwethau Formation) is represented by archaeocyath-bearing shallow marine carbonates and siliciclastics with some thin volcanic intercalations (Fig. 5). The contacts with the underlying Neoproterozoic volcano-sedimentary succession (Buschmann et al., 1995) and probably also the overlying Middle Cambrian siliciclastic succession (Brause, 1970) are disconformable. The thickness of the whole Cambrian is estimated as 1500–2000 m (Lower Cambrian 700–?1000 m).

More recent research (facies, palaeontology, stratigraphy, tectono-facies) has come from Sdzuy (1972), Elicki and Debrenne (1993), Buschmann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et al. (1995), Elicki (1999) and Jonas et al. (2000). The cambroclaves (*Cambroclavus* sp.) have been observed in only a single level of one drilling core (no. 1614/79). They are very rare (only two poorly preserved specimens – one camboclavid and one zhijinitid morph were found), probably reflecting the limited quantity of sample material (diameter of drilling core: 4 cm). The accompanying fauna consists of very frequent tintinnids (*Tintinnoidella praecursa* (Elicki, 1994)), some chancelloriids (*Archiasterella pentactina* (Sdzuy, 1969); *A. hirundo* (Bengtson, 1990); *Allonia tripodophora* (Doré and Reid, 1965); *A. tetrathallis* (Jiang, 1982)), and very rare *Halkieria* sp.

Neither archaeocyaths nor calcimicrobes (usually common in the Doberlug Syncline) were observed. The palaeoecological position of this section is difficult to determine, partly because of the diagenetic overprint. However, regarding the lithologic evolution, and comparing the characteristics of this siliciclastic/carbonate mixed succession with neighbouring and better preserved drilling cores, an open marine, deeper environment (approaching the outer mixed ramp) can be assumed. The cambroclaves occur within bioclastic wackestones dominated by tintinnids (Elicki, 1994). The morphology of the tintinnids points to a floating mode of life in an open marine and a not too strongly agitated environment.

The biostratigraphic position of the cambroclaves (Fig. 6) can also be fixed by comparison with the neighbouring drilling cores, which are dated by archaeocyaths (Elicki and Debrenne, 1993) as early Ovetian (equivalent to lower to middle Atdabanian).

4. Discussion

The biostratigraphic position of the cambroclaves in the different regions of the world is locally more or less well known. The major, and until now unresolved, problem is to correlate these local scales regionally and intercontinentally (for discussion see Palmer, 1998). Cambroclaves occur in Kazakhstan in upper Atdabanian strata (Maly Karatau, Talassky Karatau; Mambetov and Repina, 1979). In China they are known from the Tarim region (North China), from Central (Hubei) and South China, all from beds of comparable age (Bengtson et al., 1990; Jiang, 1992). The South Australian specimens have been reported from the upper Atdabanian Ajax and Parara Limestones (Bengtson et al., 1990). Slightly younger cambroclaves have been reported from Hainan Island (latest Early Cambrian; Jiang and Huang, 1986).

As described above, the cambroclaves from Germany are lower Ovetian, equivalent to lower to middle Atdabanian (based on archaeocyaths, Doberlug Syncline) and middle to upper Marianian, equivalent to upper Atdabanian (Görlitz Syncline). In contrast, the specimens from Sardinia are stratigraphically lowest Middle Cambrian (see above).

So it seems that there are different levels of occurrence of cambroclaves: a first middle Atdabanian level is documented by only one record (Doberlug); a second level is higher Atdabanian (Kazakhstan, North, Central and South China, South Australia, Görlitz area); a third level is slightly younger Lower Cambrian (Hainan), and the highest level is basal Middle Cambrian (Sardinia). Taking into account that the biostratigraphic age determinations have been done on the basis of different taxa and further taking into account the significant problems in intercontinental correlation as mentioned above, the different stratigraphic levels of cambroclaves may only be an artefact of the current state of knowledge. Nevertheless, the very distinct stratigraphic window is remarkable. All cambroclaves on all

Fig. 7. Some representative specimens of the cambroclaves from Sardinia (panels A–D) and Germany (panels E–H). Each scale bar is 100 μm. (A–D) cambroclaves indet.; disarticulated remains from chemical preparation; Su Corovau section (SW Sardinia, Italy); lower Campo Pisano Formation; basal Leonian. (E–H) *Cambroclavus ludwigsdorfensis* (Elicki, 1994); note the hollow interior (e.g. panels E and H) and the star-like cross-section of the vertical spine (panel E). Görlitz Syncline (Germany); Upper Ludwigsdorf Member; upper Marianian.

palaeocontinents occur strictly between middle Atdabanian and most basal Middle Cambrian, a time span of only a few million years. So, this microfossil group represents a good index taxon for this short time interval.

The reconstruction of migration paths of cambroclaves is not yet possible. Jiang (1992) discussed a diachronous migration of this fossil group across central and south Asia, from Kazakhstan through NW China to South China and to Hainan Island. However, the biostratigraphic position of the specimens from Kazakhstan is not as old as assumed by Jiang (the occurrence with *R. cancellatum* in the *R. cancellatum* zone indicates a late Atdabanian age).

Cambroclaves also seem to be very characteristic for a special palaeogeographic region. Their more or less synchronous appearance along the European and the Asian shelf of western Gondwana as well as in South Australia and South China (Fig. 2) points to palaeogeographical connections between these areas (see also Pillola, 1990; Chang, 1998b; Debrenne et al., 1999; Brock et al., 2000; Shergold et al., 2000). This is confirmed for several of these regions by other Cambrian fossils also, such as trilobites, archaeocyaths and small shelly fossils (Kerber, 1988; Brasier, in Cowie and Brasier, 1989; Pillola, 1991; Courjault-Radé et al., 1992; Elicki, 1994; Debrenne et al., 1999; Brock et al., 2000; and others). It may also point to clearer relations of the Gondwana/Perigondwana areas to Kazakhstan (a rather problematic palaeogeographic area in the Cambrian), to the Acado–Baltic region (sensu Sdzuy, 1972), and to Brasier's Palaeotethyan belt (sensu Brasier, in Cowie and Brasier, 1989).

Together with the accompanying fauna, the regional distribution of the cambroclaves has relevance for tectono-sedimentary reconstructions. Based on lithological and geochemical investigations and on the present-day geographical distribution of the Cambrian deposits, the existence of isolated pull-apart basins for this time on the European shelf was suggested by Buschmann et al. (1995). However, the very wide regional distribution of the characteristic Cambrian shelly faunas (e.g. Brasier, in Cowie and Brasier, 1989; Elicki, 1994) clearly indicates a flourishing faunal exchange not only between these 'basins' but also on an intercontinental scale. Further consideration of the palaeontologic and also lithologic data suggests, rather, the existence of a more or less uniform facies belt (which included the whole Mediterranean) in the late Early to early Middle Cambrian, without distinctly separated basins.

The Cambrian faunal characteristics of the German and Sardinian sections do not point to their deposition on terranes, although these areas were terranes later in Palaeozoic time (e.g. Narebski, 1994; Oczlon, 1994; Dallmeyer et al., 1995; Linnemann, 1995; Cymerman et al., 1997; Zulauf et al., 1999; Belka et al., 2000; Cocks, 2000; Linnemann et al., 2000). There are clear relations of the German Early Cambrian archaeocyaths to Morocco and Spain (Elicki and Debrenne, 1993), of the Sardinian archaeocyaths to Spain (but not to Germany because of their younger age) and of Early Cambrian trilobites to Spain and France (Geyer and Elicki, 1995; Pillola, 1991). Nevertheless, Middle Cambrian trilobites from Germany show differences in some time slices. Thus, the German taxa are related to Scandinavian faunas at the beginning of the Middle Cambrian and show Mediterranean affinity only after the middle Middle Cambrian (Sdzuy, 1957, 1966, 1972). The neighbouring Middle Cambrian trilobite fauna in Bohemia (which does not contain basal Middle Cambrian taxa) is consistent with this pattern and indicates that it is a distinct but related depositional area. Further, the small shelly faunas from the German Early Cambrian and from the Sardinian Early and Middle Cambrian (which are both restricted to carbonate environments) indicate clear relations to the Palaeotethyan Belt (sensu Brasier, in Cowie and Brasier, 1989). The seemingly convincing palaeogeographic affinities of the small shelly fossils to regions both near and far may, however, be a further artefact, due to the comparatively poor level of knowledge of such fossils in the Mediterranean.

The existence of a rather continuous, uniform and little-differentiated Cambrian European shelf is strongly supported by the palaeontological data. The model of a terrane-assemblage, including the Armorican terrane-collage [Saxo-Thuringia terrane, Brittany/Normandy terrane = Avalonia sensu stricto, Perunica terrane; Havlíček et al., 1994; Linnemann and Schauer, 1999; Linnemann et al., 2000], southern France/Sardinia and Spain, however, cannot be surely ruled out. If so, these terranes must have been very well connected. All these different regions show distinct similarity in their general sedimentary, biofacies, and structural patterns but also have special regional characteristics. These special differences, however, can be explained e.g. by distinct patterns in palaeooceanographic circulation (e.g. the relations of the Middle Cambrian faunas), by regional faunal endemisms (generally usual for the Cambrian), and by divergent palaeogeographic positions on the shelf. Thus, the palaeontological, biostratigraphic and lithologic data of the Mediterranean Cambrian areas imply that in the Early Cambrian the Normandy and Doberlug regions were situated in a distal position on this structurally uniform shelf, adjacent to the continent including the southern France/Sardinia/Görlitz areas (compare also Courjault-Radé et al., 1991); Bohemia was still terrestrial (fluvial). This distribution pattern persisted more or less into the Middle Cambrian (but Bohemia became marine). During the Late Cambrian/Early Ordovician, exposure and erosion of large areas is assumed by several authors (Chlupáč, 1993; Linnemann et al., 2000). This evolution was succeeded by separation into terranes (e.g. Saxo-Thuringia and Perunica) from the Gondwana European shelf later in the Ordovician (e.g. Matte et al., 1990; Narebski, 1994; Belka et al., 2000; Cocks, 2000; Linnemann et al., 2000; Demange, 2001).

Palaeoecologically, cambroclaves are indicative of shallow, normal marine, eutrophic conditions. They occur in deeper subtidal environments. The specimens from western Gondwana (as well as from Görlitz, Doberlug and Sardinia) mark special palaeogeographic positions: outer ramp deposits during a transgressive phase (Figs. 3–5). Often they occur within horizons with a high biotic diversity (this phenomenon is also observed from South China). The duration of appearance during the deepening process is mostly short, which may suggest that the cambroclave animal was specialised to well defined palaeoecologic conditions and was unable to migrate into neighbouring habitats.

5. Conclusions

(1) Cambroclaves are of still unknown systematic affinity. Their regional distribution is now extended from the northern Gondwana area (Asian shelf and Australia) and Kazakhstan to synchronous sections of western Gondwana (Sardinia/Italy, Germany).

(2) The appearance of this remarkable fossil group is restricted to a small biostratigraphic window (lower Ovetian to lowermost Leonian; equivalent respectively to lower to middle Atdabanian and lowermost Middle Cambrian). Both the oldest (Germany) and youngest (Sardinia) occurrences are on the western Gondwana European shelf. Because of the problems of precise intercontinental correlation for this time interval and because of the use of different groups for biostratigraphy in each region, a more detailed time resolution within this interval of occurrence cannot yet be given. However, cambroclaves seem to be a good stratigraphic index taxon for the late Early to early Middle Cambrian time interval.

(3) The occurrence of this fossil group in Germany and Sardinia points to clear palaeogeographic relations to the Palaeotethyan belt, especially to the Mediterranean region, to China and Australia, and to Kazakhstan. The late Early to early Middle Cambrian palaeogeographic position of Kazakhstan was possibly closer to the western Gondwana margin than previously assumed.

(4) Together with other palaeontological and lithological data, cambroclaves indicate the existence of a rather uniform and continuous facies belt over the whole Mediterranean and so contradict the model of isolated local depositional basins or significantly separated terranes during that time. The palaeontologic data also point to the existence of a little-differentiated shelf or (at least) of an assemblage of very closely related terranes (Avalonia terrane-collage [consisting of Saxothuringia terrane, Brittany/Normandy terrane, Perunica terrane], Spain, southern France/Sardinia) on

or adjacent to the western Gondwana European shelf.

(5) Because of poor biostratigraphic resolution within the time of occurrence of the cambroclaves, the evolutionary migration path of this fossil group cannot yet be reconstructed. Earlier attempts to do this must be rejected because of revision of the biostratigraphical database. There is still no real evidence regarding the location of the centre of origin and distribution.

(6) The palaeoecological position of this fossil group is strongly restricted. Cambroclaves were typical for eutrophic, open normal marine, and rather deeper subtidal carbonate environments without strong agitation. The western Gondwana specimens accompany short transgressive phases during which the depositional area deepened and was distinctly influenced by increased siliciclastic input. These processes were related to a continuous rise of relative sea level, perhaps due to local tectonics and/or climate change, or to movement of the Gondwana landmass to higher southern latitudes.

Further research on Cambrian small shelly fossils in the comparatively poorly investigated Mediterranean will lead to a better understanding of palaeogeographic relations within the western Gondwana shelf areas and to other Cambrian palaeocontinents.

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