

Cryptic relicts from the past: Palaeoecology and taphonomy of encrusting thecideid brachiopods in Paleogene carbonates

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(With 4 figures)

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Abstract

Thecideid brachiopods are poorly known brachiopods of debated phylogenetic relationships which occur from the Late Triassic to the Recent. Although well known in encrusting communities of Jurassic and Cretaceous cryptic habitats, they have received less attention in Cenozoic environments. Extensive thin section analysis of circumalpine Paleogene carbonates (Late Eocene of Austria as well as the Early Oligocene of Slovenia, the Inntal Valley and Northern Italy) has revealed the presence of thecideid brachiopods allowing for the analysis of their taphonomy, component relationships and facies distribution. The complex morphology of the valves enables these brachiopods to be readily identified in thin section, even if highly fragmented or encrusted. Component analyses using semi-quantitative and quantitative methods reveal that these brachiopods are most commonly associated with corals and coralline algae. The brachiopods are often included within complex encrustation sequences. Their palaeoecology thus closely mirrors that of Recent and fossil thecideid species which are characteristics of cryptic habitats in tropical and warm temperate seas. The potential of these minute brachiopods as palaeoecological indicators has been underestimated especially considering their ease of recognition in thin section not only of complete valves, but also of highly fragmented material.

Keywords: Cenozoic, Paleogene, Carbonates, Brachiopods, Thecideida, Palaeoecology, Microfacies

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Introduction

Thecideid brachiopods are ascribed to a separate order (Thecideida) within the Brachiopoda. Their phylogenetic relationships to other brachiopods are highly controversial and origins within the Terebratulida, Spiriferida and Strophomenida have been suggested (see discussions on phylogeny and ontogeny in PAJAUD 1970; WILLIAMS & HURST 1977; JAECKS 2001; JAECKS & CARLSON 2001; BAKER 2006; BAKER & CARLSON 2010; BAKER & LOGAN 2011). Difficulties in their systematic placements have been attributed to their small size, cryptic habitat and complex shell morphology. Complete, isolated skeletons are rare as the free dorsal (“brachial”) valves and cemented ventral “pedicle” valves (n.b. these brachiopods do not have pedicles) can separate after death. Taxonomic identification is hindered by the poor preservation of diagnostic characters including the skeletal supports of the lophophore which, being present in the often separated dorsal valve, are often highly abraded or lost (BAKER 2006). In this paper we aim to describe the presence of thecideid brachiopods in Paleogene carbonate of the circum-alpine area with respect to their taphonomy and facies restrictions and explore their use as palaeoecological indicators in carbonate environments.

The Order Thecideida

The Thecideida are a little known brachiopod order which first appeared in the Triassic and is still extant today. Although the thecideids have hardly changed with respect to their small size and cryptic habitats, they have shown dramatic changes in internal morphologies and shell construction. The Order contains two Superfamilies: the Thecospiroidea restricted to the Late Triassic and the Thecideoidea ranging from the Late Triassic to the Recent. Morphological details are summarized in PAJAUD (1970) and BAKER (2006). In general, they have small thick shells (less than 1 cm in length) with larger, strongly convex, more voluminous ventral valve and a smaller, almost flattened dorsal valve. Recent genera which are also described from Paleogene sediments include *Lacazella* MUNIER-CHALMAS, 1881 (e.g. BITNER & DIENI 2005; BITNER & DULAI 2008) and *Thecidellina* Thomson, 1915 (PAJAUD & TAMBAREAU 1970; PAJAUD & PLAZIAT 1972).

Ecology of thecideid brachiopods through time

Thecideid brachiopods in both fossil and Recent communities show a remarkable ecological continuity as fixo-sessile members of encrusting communities often in cryptic environments. Larger brachiopods as a whole are common in reef communities from the Palaeozoic and Mesozoic (AGER 1965), much less so during the Cenozoic where their presence is restricted to small forms at least in tropical environments. Thecideids form a distinct ecological group of cemented brachiopods (e.g. SURLYK 1972) along with

other micromorphic forms (such as minute terebratulids and rhynchonellides) and macromorphic brachiopods. The success of small brachiopods occupying cryptic habitats in Mesozoic and Cenozoic environments has been attributed to their ability to avoid rasping predators such as camardont echinoids (ASGAARD & STENTOFT 1984). HARPER (2002) notes that the adaption to cryptic environments allows minute brachiopods to survive in relatively shallow water as opposed to larger (exposed) epifaunal forms which inhabit deeper water.

The reported presence of thecideid brachiopods in Mesozoic encrusting communities of both the Jurassic and Cretaceous is higher than that of their Cenozoic counterparts. Thecideid brachiopods from Jurassic hardgrounds are well known along with cryptic encrusting fauna of sponges, serpulids, oysters and bryozoans (see compilation in TAYLOR & WILSON 2003). Encrusted substrates range from single shells such as those of *Plagiostoma* (TAYLOR 1979), hardground surfaces (PALMER & FÜRSICH 1974; FÜRSICH et al. 1992), oncoliths (PALMER & WILSON 1990) to cavity fillings (SCHLÖGL et al. 2008). They are well known as encrusters on the flattened undersides of large demosponges in Upper Jurassic sponge reef environments (e.g. PALMER & FÜRSICH 1981; KRAWCZYNSKI 2008).

The encrusting habitat of thecideid brachiopods is continued throughout to the Cretaceous. A number of studies show thecideid brachiopods as part of diverse encrusting communities together with encrusting foraminifera, sponges, scleractinian corals, serpulids, oyster, rudists, spondylids, cyclostomous and cheilostomes bryozoans and craniid brachiopods (see compilation in TAYLOR & WILSON 2003). Examples include small encrusting thecideid brachiopods along with encrusting bryozoans and various calcareous algae in Hauterivian carbonates of Spain within coral, stromatoporoids and microbial frameworks (ARIAS et al. 1995). MITCHELL (2002) describes unidentified thecideid attached to both rudist and corals as well as in cavities within coral patches in Jamaican Cretaceous coral reefs.

Encrusting thecideids are also described in Cenozoic sediments though mostly in taxonomic overviews. Although often included in general description of brachiopod occurrences, they are mostly vastly outnumbered with respect to specimen numbers. Various Paleogene specimens have been described, for example from an Upper Eocene mobile rockground biota from North Otago, New Zealand (LEE et al. 1997). European localities are also known (e.g. PAJAUD 1970; BITNER 1993; BITNER & DIENI 2005 and BITNER & DULAI 2008). Similar to their Mesozoic counterparts, they are usually described from hardgrounds or structured environments such as coral reefs. In general, thecideids are rare though continuously present throughout the Cenozoic (HARPER 2002).

Recent thecideid brachiopods show a wide distribution in tropical and warm temperate environments with occurrences and new species being continuously discovered (e.g. LÜTER et al. 2003; LOGAN 2005, 2008; BITNER 2008, 2009, 2010; HOFFMANN & LÜTER 2009, 2010; HOFFMANN et al. 2009). In common with their fossil counterparts, these brachiopods occupy cryptic environments, for example *Lacazella mediterranea* (RISSO, 1826), which

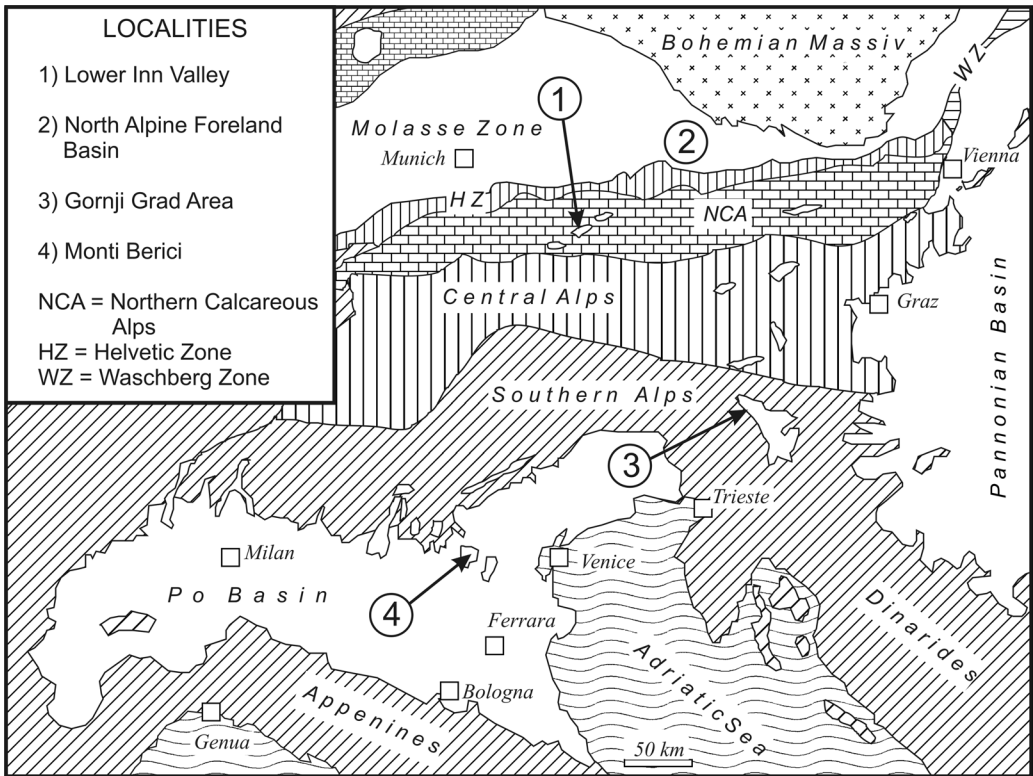


Fig. 1. Localities of studied areas in the circum-alpine area.

resides in crevices within the coralligène of the Mediterranean (LOGAN 1979; LOGAN et al. 2004) or as part of brachiopod faunas inhabiting the undersides of corals in tropical environments (ZUSCHIN & MAYRHOFFER 2009).

Material and Methods

This study is based on detailed microfacies analysis of Upper Eocene and Lower Oligocene carbonates of the circum-alpine area (Fig. 1). The Late Eocene is represented by limestones of the Alpine Foreland Basin in Upper Austria (RASSER 2000; RASSER & PILLER 2004). Lower Oligocene localities are represented by the Gornji Grad Formation of Slovenia (NEBELSICK & BASSI 2000; NEBELSICK et al. 2000), the Lower Inn Valley of Tyrol, Austria (NEBELSICK et al. 2001; RASSER & NEBELSICK 2003) and the Calcarene di Castelmomberto of the Monti Berici in northern Italy (GEISTER & UNGARO 1977; Ungaro 1978). Microfacies analyses serve not only to discern facies relationships in carbonate environments, but also can be used to show component relationships. Thin section analyses also allow aspects of taphonomic processes to be studied which are not readily identifiable in three dimensionally preserved specimens (see NEBELSICK et al. 2011).

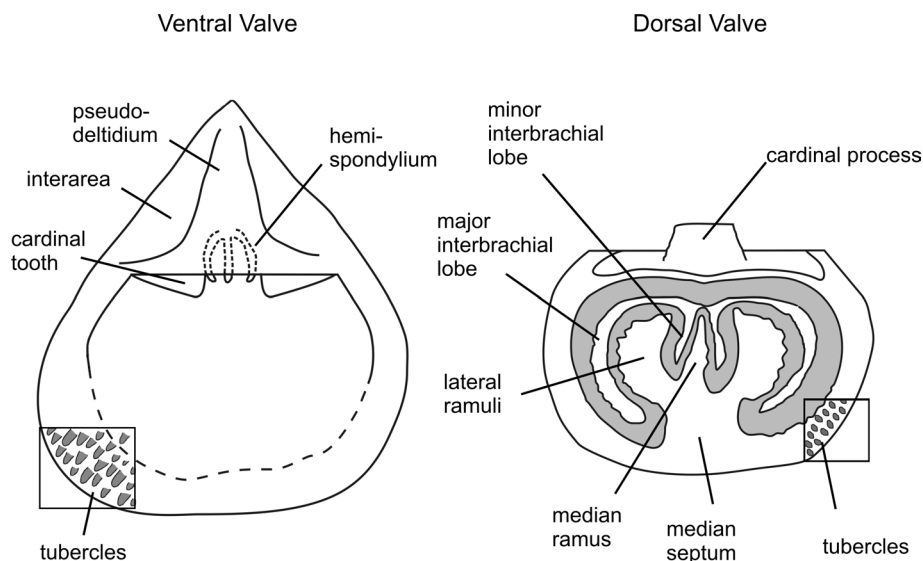
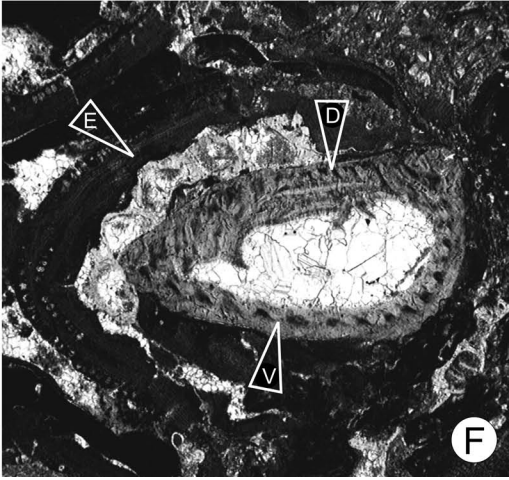
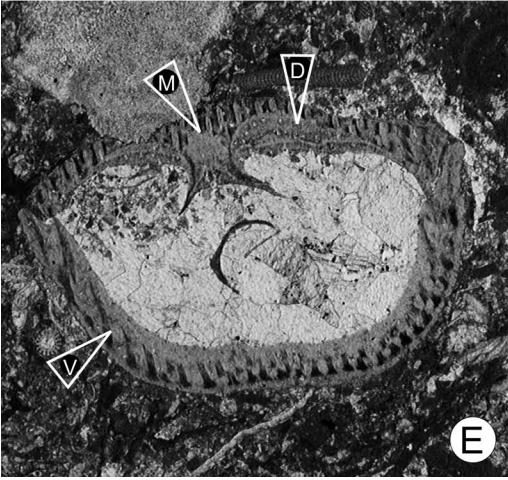
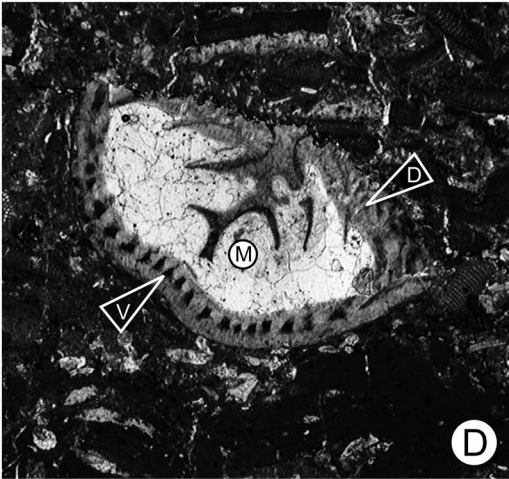
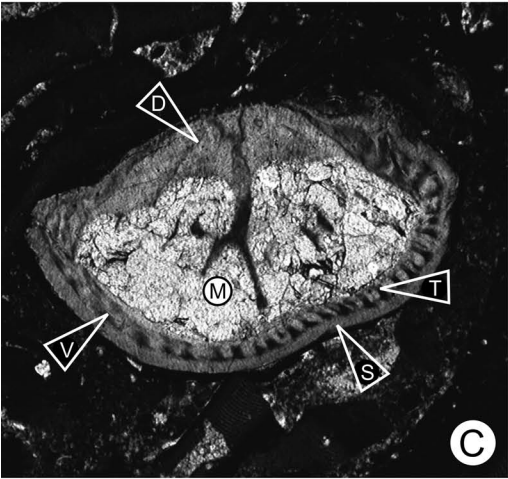
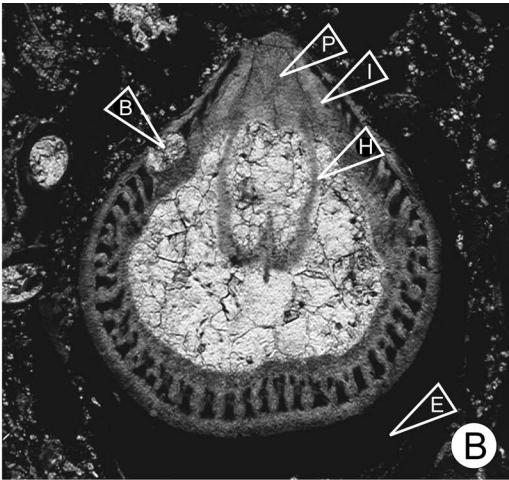
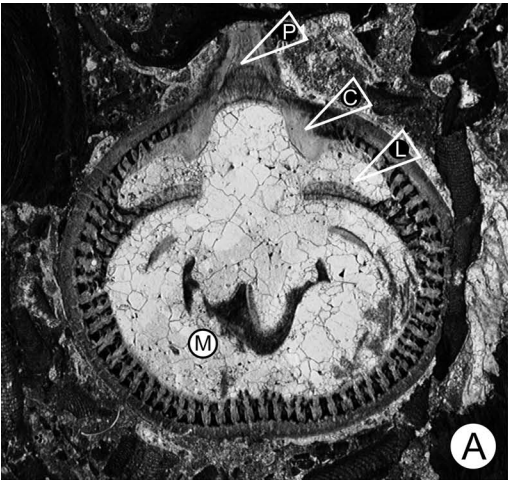


Fig. 2. Schematic depiction of morphological shell features of a thecideid brachiopod (based on *Lacazella*). Internal views of ventral and dorsal valves. Tubercles only depicted in the boxed-in areas. Most of the hemispondylium is hidden (represented by the dashed outline). Drawn after photographs in BAKER (2006). See BITNER (2010) for scanning electron microscopic pictures of the interior morphology of the genus *Lacazella*.

Microfacies analysis is mostly based on numerous thin sections of standard 5 x 5 cm format and larger sections up to 8 x 10 cm in size. The sections were quantified using quantitative (point counting) and semi-quantitative methods which served as the base for various statistical analyses. From the Late Eocene Alpine Foreland Basin of Upper Austria, 120 thin sections were quantified using data from point counting with up to 600 points with the results used for bivariate and multivariate analysis (RASSER 2000; RASSER & PILLER 2004). The carbonates of the Lower Oligocene Gornji Grad Beds were analyzed from 73 thin sections which were point counted (500 points with 1 mm intervals) for cluster and principal component analysis (NEBELSICK et al. 2000). The Lower Oligocene Inn Valley carbonates were studied by treating 28 thin sections to a semi-quantitatively analysis using comparison charts in FLÜGEL (2004). The data were subjected to statistical treatment including bivariate Spearman's rank correlation coefficients and Q-mode hierarchical cluster analysis (NEBELSICK et al. 2001; RASSER & NEBELSICK 2003). Detailed facies analysis of the Early Oligocene of the Monti Berici was carried out by UNGARO (1978) using numerous thin sections of 2 x 4 cm.

The material from the North Alpine Foreland Basin is stored at the Institute of Palaeontology, University of Vienna, material from Slovenia and the Lower Inn Valley at the Institute for Geosciences, University of Tübingen, material from Northern Italy at the Dipartimento di Scienze della Terra, Università degli Studi di Ferrara.



Results

Occurrence and Identification

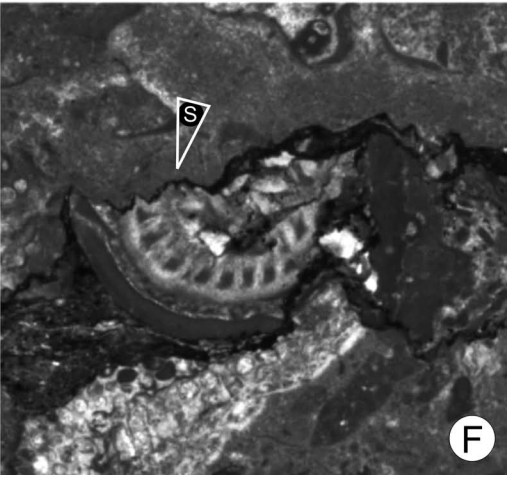
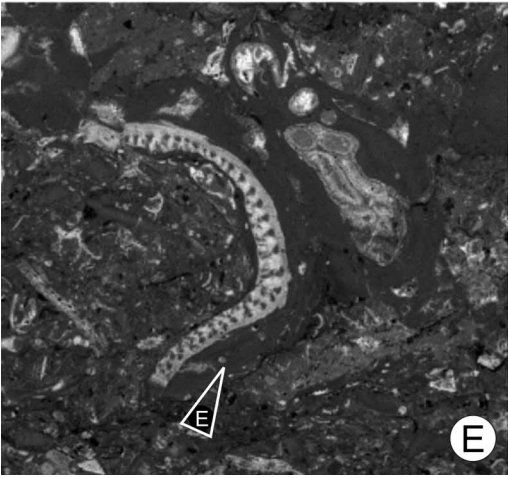
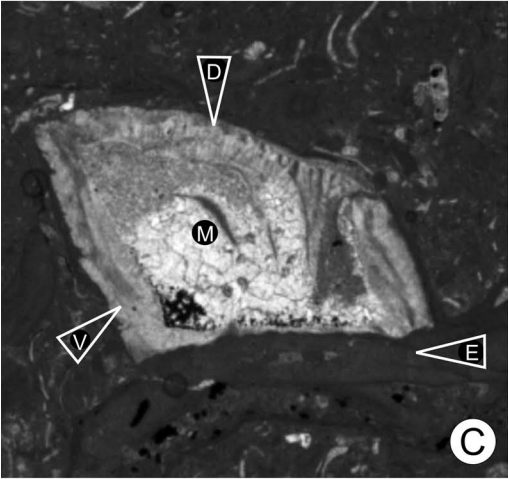
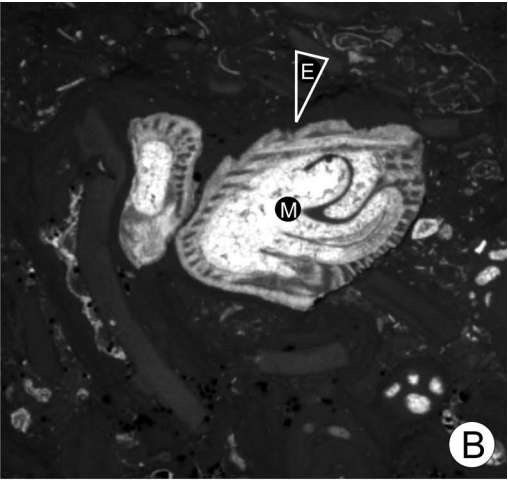
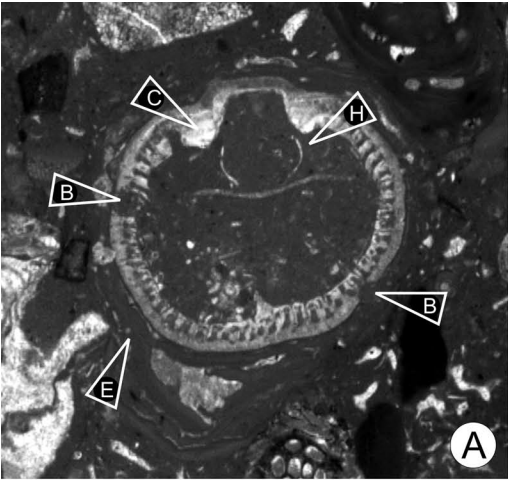
Recognition of thecideid brachiopods in thin section follows the small size (reaching maximum dimensions of ca. 3 mm) and typical features of the shell (Fig. 2) including: 1) tuberculate shells, 2) the often preserved internal features and 3) the fact that the valves often enclose a sparite filled pore space (Figs 3 & 4). It is highly likely that the studied Upper Eocene and Lower Oligocene brachiopods from the circum-alpine area represent the genus *Lacazella* due to the presence of features described below. In fact, one species, *Lacazella mediterranea* which is still extant in the Mediterranean today (LOGAN 1979; LOGAN et al. 2004) has been described from various European Cenozoic sediments from the Paleocene onwards (see BITNER & DIENI 2005; BITNER & DULAI 2008).

A number of morphological features were recognized (Figs. 3 & 4) following PAJAUD (1970), BAKER (2006) and BITNER (2010). Feature readily recognizable in thin section include the tuberculate inner shell wall and smooth outer wall. Recognizable features of the ventral valve include a prominent interarea with a pseudodeltidium, cardinal teeth (Figs. 3A, 4A), as well as the hemispondylium (Figs. 3B, 4A, 4D) within the ventral umbo. The dorsal valves can show a prominent cardinal process. Although the base of the median septum is recognizable (Fig. 3D, 3E, 4E), its subdivisions are difficult to reconstruct due to the sectioning effects. In one section (Fig. 3A), it may be possible distinguish interbrachial lobes from extensions of the median septum. This would fit into the description of *Lacazella* which possesses two major interbrachial lobes and two minor interbrachial lobes. These lobes interdigitate with the trifurcating ramus–ramuli complex consisting of a median ramus and two crescent-shaped lateral ramuli. Furthermore, the median ramus and lateral ramuli can be noticeable trough-shaped leading to sectioning effects (Figs 3D, 3E). To complicate matter even more, especially in thin section, these features are often “offline” and rarely truly bilaterally symmetric in form.

Taphonomy

Both double-valved and disarticulated specimens are found. Double-valved examples can remain empty of matrix and subsequently be filled by sparry calcite. Shells can also

- ◀ Fig. 3. Thin sections of well preserved thecideid brachiopods (?*Lacazella*). All originate from the Upper Eocene of the North Alpine Foreland Basin (Perwang Group). All section show articulated shells filled by blocky sparite cement. **A & B**: section subparallel to commissural plane, **C–E**: Oblique sections, **F**: oblique longitudinal section. A) thin section (ts) = 225, width (w) of picture = 4,3 mm. B) ts = 5912, w = 4.3 mm. C) ts = 534, w = 3.6 mm. D) ts = 234, w = 3.6 mm. E) ts = 236, (w) = 3.2 mm. F) ts = 225, w = 3.4 mm. Abbreviations: D = dorsal valve; I = interarea, P = pseudodeltidium, C = cardinal tooth, H = hemispondylium. V = ventral valve; M = median septum, L = interbrachial lobe; T = tuberculate inner rim, S = smooth outer rim; B = bioerosion, E = encrustation. Material repositied at the Institute of Palaeontology, University of Vienna.



be filled by internal muddy matrix if the valves become disarticulated or fragmented. Disarticulated specimens seem to be dominated by ventral valves. The shell is well preserved being made up of low magnesium calcite. The shells thus do not show diagenetic alterations which affect, for example, the aragonitic skeletons such as corals which are completely replaced by blocky sparitic cements.

The brachiopods encrust hard substrates and are themselves encrusted within multi-taxon encrustation sequences (Figs 3D, 3F). Encrustation by coralline algae is especially common. In one case, two closely spaced thecideid brachiopods probably encrusting the same substrate occur together (Fig. 4B). Bioerosion of the shell in form of small rounded holes can also be observed (Figs 3B, 4A). These holes are not restricted to the brachiopod shell and can include encrusting coralline algae. Isolated double valves as well as single valved specimens also occur within the sediment. These can show high rates of abrasion and fragmentation. Post depositional features include pressure solution along stylolites (Fig. 4F).

Facies distributions

Late Eocene – Alpine Foreland Basin, Upper Austria

Limestones of the Late Eocene Alpine Foreland Basin (from the so called “Lithothamnium Limestones” of the Perwang Group) in Upper Austria (RASSER 2000) show clear facies restriction concerning the occurrence of thecideids. The brachiopods are never common. They show a tight facies restriction to algal dominated sediments often together with branched corals. The thecideids are frequently encrusted by coralline algae and included within rhodoliths. Bivariate analysis (Spearman’s Rank coefficient) show brachiopods positively correlated to coralline algae (RASSER 2000). Multivariate component analysis (cluster analysis, factor analysis) shows the brachiopods being most common in the

- ◀ Fig. 4. Thin sections of both well and poorly preserved thecideid brachiopods. All section from the Early Oligocene: A from the Lower Inn Valley, Austria, B–F from the Gornji Grad Beds, Slovenia. **A** is well preserved though filled with muddy matrix, highly encrusted by coralline algae. **B** shows two individuals most likely encrusting the same substrates; both filled with sparite cement and encrusted by coralline algae. **C** shows articulated brachiopod encrusting coralline algal thalli with the ventral valve. Fragmentation of ventral valve in **D** allows micritic matrix to enter the shell. **E** is highly fragmented along with its encrusting coralline algae. **F** is highly fragmented and shows post-depositional dissolution along a stylolite. A) thin section (ts) = UIT26, width (w) of picture = 3.29 mm. B) ts = KB4.4, w = 6 mm. C) ts = KB4.4, w = 3.5 mm. D) ts = KB4.4, w = 4.8 mm. E) ts = KB6.2, (w) = 5.2 mm. F) ts = SLO94-044, w = 2.8 mm. Abbreviations: D = dorsal valve; C = cardinal tooth, H = hemispondylium, V = ventral valve; M = median septum; B = bioerosion, E = encrustation, S = stylolite. Material from the North Alpine Foreland Basin repositied at the Institute of Palaeontology, University of Vienna; from Slovenia repositied at the Institute for Geosciences, University of Tübingen.

Coralline Detritus – Coral Facies and present in the Coralline Detritus Facies. Factor analysis shows brachiopods positively correlated with coralline algae and corals and negatively correlated with terrigenous components.

Early Oligocene – Gornji Grad Beds, Slovenia

Carbonates of the Lower Oligocene Gornji Grad beds of Slovenia are dominated by coralline algae and corals; larger (*Nummulites*) and smaller benthic foraminifera as well as bivalves can also be common (NEBELSICK et al. 2000; NEBELSICK & BASSI 2000). Encrustation is common and can consist of complex, multitaxon sequences including various coralline algae, encrusting foraminifera (especially *Haddonia*), serpulids, bryozoans and thecideid brachiopods. Facies are dominated by rudstones and packstones mostly in muddy matrix and show excellently preserved, though in part, highly fragmented components.

Thecideid brachiopods are conspicuously present, though always rare in three of seven distinguished facies types. They are most common in the Coralline Algal-Coral facies with 1.64% of the components. The brachiopods are also present in the Coralline Algal Facies (0.86%) where they can be observed directly encrusting the algae (Fig. 4C) and the Coral Facies (0.32%). Brachiopods were not recorded from the Nummulitic, Bivalve, Foraminiferal-Coralline Algal and Grainstone Facies. Principal component analysis shows positive correlation of brachiopod presence to coralline algae.

Early Oligocene – Inn Valley, Tyrol, Austria

Limestones from the Early Oligocene of the Inn Valley are dominated by rudstone and packstones with well preserved components and high amounts of muddy matrix (NEBELSICK et al. 2001; RASSER & NEBELSICK 2003). Major components are coralline algae, corals, larger and smaller foraminifera, corals and bryozoans. Echinoderms, serpulids, bryozoans and brachiopods are subordinate. Five different facies were distinguished: three interpreted from nearshore areas with the Coral-Coralline Algal Facies, Coralline Algal Facies and (Larger) Foraminiferal Facies and then two facies, following a gradient into deeper water, the Coralline Algal – Bryozoan and the Bryozoan Facies. Material from these shallow water facies can be transported within debris flows into deeper water marls.

Thecideids are very rare and restricted to specific facies. They occur with 1% values in the Coral-Coralline Algal Facies and the Larger Foraminiferal Facies and are absent in the other facies types. Bivariate analysis shows brachiopods positively correlated to corals and negatively correlated to bivalves.

Early Oligocene – Monti Berici, northern Italy

Early Oligocene shallow water carbonates in northern Italy are found in the Monti Berici and Monti Lessini. They are collectively known as the Calcareni di Castelgomberto formation and are well known for coral and associated facies (GEISTER & UNGARO 1977; UNGARO 1978; FROST 1981; BOSELLINI & TREVISANI 1992; BASSI et al. 2008). GEISTER &

UNGARO (1977) and UNGARO (1978) distinguished seven facies (massive coral facies, branching coral facies, coralline red algal facies, miliolid facies, small nummulites facies, mollusk facies, echinoid facies). As in the localities described above, thecideids are again very rare and restricted to specific facies. Similar to the results discussed above, they have been found in coralline algal and coral dominated facies types (unpublished data J. LEMPP, J. NEBELSICK, D. BASSI).

Brachiopod presence in Upper Oligocene and Miocene circum-alpine Carbonates

Thecideids were not recorded from the coralline algae (maerl) and larger foraminiferal (miogypsinids) mixed carbonates and siliciclastic facies from the Upper Oligocene of Upper Austria (KAISER et al. 2001). Detailed microfacies analysis of Upper Oligocene coralline algal and larger foraminiferal facies from Northern Italy (BASSI et al. 2007; BASSI & NEBELSICK 2010) also did not reveal these brachiopods.

Similar to the above, thecideid brachiopods were also not found in bryomol carbonates from the Zogelsdorf Formation of the Early Miocene of the Molasse Zone of Lower Austria (NEBELSICK 1989, 1992). Encrusting communities are present in these sediments consisting of bryozoans, barnacles, serpulids and coralline algae on secondary hardgrounds such as echinoids (NEBELSICK et al. 1997). Brachiopods are, however, present in the form of larger terebratulids recognizable through their punctate shells (NEBELSICK 1989). Similarly, thecideids are also not recorded from Lower Miocene brachiopod faunas from the Alpine Foreland Basin of Bavaria (BITNER & SCHNEIDER 2009; SCHNEIDER et al. 2009).

There is little data concerning thecideid brachiopods in the Middle Miocene of the Paratethys (compare BITNER 1990; POPIEL-BARCZYK & BARCZYK 1990; KROH 2003) and other localities from the Paratethys. Investigations dealing with coralline algal and reefal limestones of the Vienna Basin area (DULLO 1983; RIEGL & PILLER 2000) do not mention these brachiopods despite intense thin section and field investigations. Thecideid brachiopods have, however, been recorded from Middle Miocene coral reef facies from Bulgaria (BITNER 1993).

Discussion

The total contribution of brachiopods as a whole to Paleogene circum-alpine carbonates is very small and restricted to specific facies dominated by corals and coralline algae. This paucity of brachiopod remains in carbonate sediments has also been described from Recent environments where the brachiopod fauna is restricted to cryptic and micromorphic and cemented forms (e.g. ZUSCHIN & MAYRHOFER 2009). Nonetheless, the fact that they can be well preserved in encrustation sequences and readily identified in thin sections allows their presence, taphonomy and ecological distribution to be analyzed. The best preserved specimens are those which have been included in complex encrustation sequences which essentially preclude the three-dimensional observations of their morphologies.

Preservation Potentials

A number of these brachiopod specimens are completely preserved with both shells intact and articulated. This allows the preservation of internal shell features. These brachiopods can be preserved in life position encrusting hard substrates. Preservation of double-valved brachiopods is promoted by further encrustation thus cemented the valves together. It is difficult to interpret whether or not the brachiopods encrusted living or dead substrates. Ventral valves predominate over dorsal valves in the thin sections. This is due to the fact that the ventral valves are larger and more robust as well as remaining fixed on the substrate if disarticulation occurs.

The substrates themselves eventually become toppled, fragmented and, in part, transported together the brachiopods. Their shells remain, however, preserved within the encrustation sequences. The original context of encrustation can be preserved, although they, in fact, represent transported components along with their substrates. Isolated double valves as well as single valved specimens occur. Isolated double valved and single valved specimens show that the brachiopods can also be separated from their substrates and committed to the sediment. It is not known if these brachiopods can encrust non-mineralized substrates, which would consequently lead to isolated specimens in the sediment upon decay of these substrates.

Facies Restrictions

Although thecideid brachiopods are never common, they represent characteristic faunal element in distinct facies in all of the studied Upper Eocene and Lower Oligocene carbonates. The consistent presence in coral and coralline algal – coral facies reflects the cryptic habitats provide by the corals. The fact that they are most common in coralline algal-coral facies (as opposed to coral facies *per se*) is that the former represent coral frameworks or rubble with a high degree of encrustation mainly by encrusting coralline algae, but also by the other encrusters including the brachiopods. Their presence in coralline algal facies with low amounts of corals shows that these brachiopods can be present either within rhodolith frameworks, which can also provide cryptic habits, or can directly encrust algal thalli on the sediment surface. The coral and coralline algal – coral dominated facies are interpreted to occur in relatively quiet environments with high amounts of muddy matrix and low sediment accumulation rates allowing for the development of complex multi-taxon encrustation sequences.

The lack of thecideid brachiopods in the other facies dominated by bivalves, larger foraminifera and bivalves is due to the lack of suitable microhabitats with respect to substrates or skeletal frameworks. These facies represent packstones and grainstones with high terrigenous content, from nearer shore, higher energy environments. The fact that these brachiopods seem to be missing in Late Oligocene and Early Miocene carbonates of the circumalpine area is again probably due to the lack of suitable cryptic substrates (for example, colonial corals) in these carbonates. Somewhat surprising is the fact that thecideids have not been reported from the Middle Miocene Carbonates of the Vienna

Basin and associated areas where colonial corals can be common. The fact that thecideid brachiopods have not been reported in these carbonates must, however, be treated with caution as 1) these brachiopods are never common in the first place, 2) they can be destroyed by taphonomic processes, or 3) they may have yet to be recognized in these sediments. More specific studies and surveys, especially on collections of thin sections, are needed in this respect in order to better document the distribution of thecideids in Cenozoic sediments.

Shifts within encrusting communities from the Mesozoic to the Cenozoic

Highly adapted, cryptic encrusting communities have been in existence at least since the Jurassic (WILSON 1998). There have been substantial changes through time with respect to the organisms involved both in terms of the encrusters *per se* or the (often skeletal) substrates which they encrust (see compilation in TAYLOR & WILSON 2003). Their small size and cryptic habitat allow them to continuously avoid predation by rasping organisms such as thecideids as regular echinoids (ASGAARD & STENTOFT 1984). Although thecideid brachiopods were never very common, they managed to survive not only mass extinction events (including that of the Cretaceous – Paleogene boundary), but also substantial changes in available biotic substrates and accompanying shifts in encrusting community make-up. This is an attest to their ability to adapt to different conditions through time. In the Paleogene, carbonate facies are dominated by coralline algal and larger foraminifera (see NEBELSICK et al. 2003, 2005). Corals become increasingly common and it is the corals together with their encrusting coralline algae that provide the habitats most conducive to thecideid brachiopod settlement at least in the studied Upper Eocene and Lower Oligocene carbonates.

Thecideid brachiopods seem to belong to the oldest members of the Paleogene encrusting communities as they first appeared in the Triassic. Other prominent members of Paleogene encrusting communities such as coralline red algae (first appear in the Early Jurassic, but only became common in the Early Cretaceous – AGUIRRE et al. 2000) and cheilostome bryozoans (first appeared in the uppermost Jurassic – TAYLOR 2000) are later additions to the cryptic encrusting communities. Thecideid brachiopods thus truly represent cryptic relicts from the past.

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