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Earliest Ordovician pelmatozoan holdfasts from western Europe: the *Oryctoconus* problem revisited

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Key words: Echinoderms, stratigraphy, palaeoecology, western Europe, Ordovician.
Mots clés: Echinodermes, stratigraphie, paléoécologie, Europe occidentale, Ordovicien.

ABSTRACT

The *Oryctoconus* pelmatozoan holdfasts occur in lower Tremadocian sedimentary rocks of western Europe, with a marked concentration in sandstones and conglomerates and immediate shoal surroundings. They are reported from the Najerilla Formation in the Demanda Mountains, the Valconchán Formation in the Iberian Chains (Spain), the upper part of the Cabitza Formation in south-western Sardinia, and the Leimitz Shales of Frankenwald (Germany). The genus is an amphora-like skeleton prolonged into a crown of anterior, lobate to stellate appendages or radices, regularly spaced. Two species are differentiated: *O. lobatus* (with a flat anterior face) and *O. dorecki* (with a convex anterior face, trapezoidal in cross-section). The anterior face of the holdfasts contains a circular plate that would serve for articulation with the distal end of stems. *Oryctoconus* is associated with early Tremadocian trilobites, graptolites and acritarchs, and is reported as a biostratigraphically significant taxon for correlation in western Europe.

RESUME

Des pédoncules de pelmatozoaires appartenant au genre *Oryctoconus* sont connus dans les sédiments du Trémadocien inférieur de l'Europe occidentale. Ils s'observent accumulés dans des grès et des conglomérats, en relation avec des barrières hydrauliques. Ils sont reconnus dans la Formation de Najerilla de la Sierra de la Demanda, la Formation de Valconchán des Chaînes Ibériques (Espagne), la partie supérieure de la Formation de Cabitza en Sardaigne et les Schistes de Leimitz de Frankenwald (Allemagne). Le genre est décrit comme un squelette en forme d'amphore prolongé dans sa partie antérieure par une couronne d'appendices, espacés régulièrement, à contour lobé à triangulaire. Deux espèces sont ici différenciées: *O. lobatus* (à face antérieure plate) et *O. dorecki* (dont la face antérieure est convexe, à section trapézoïdale). Les faces antérieures des pédoncules possèdent une plaque circulaire qui servirait d'articulation avec la partie distale des tiges. *Oryctoconus* est associé avec des trilobites, graptolites et acritarches du Trémadocien inférieur, et est considéré comme un marqueur biostratigraphique en Europe occidentale.

1. Introduction

Complete and articulated multi-element skeletons (such as arthropods, coeloscleritophorans, echinoderms and sponges) are rarely preserved in the Lower Palaeozoic fossil record of western Europe. Normal, slow to moderate sedimentation rates in platform and deeper water siliciclastic settings, and high-energy conditions favour disarticulation of skeletal elements. As a result, one articulated skeleton can be dissociated into numerous elements, each of them displaying different hydrodynamic behaviours. Their debris will be selectively transported and deposited separately causing biofacies multiplication. In these cases, the identity of original organisms can be broadly inferred on the basis of disarticulated plates, scaly armours, sclerites, spicules, spines, tergites, etc. They are recon-

structed after assuming parallelism with either coeval or modern taxa, but, in most cases, they cannot be assigned to any known species.

The relatively high permeability in coarse-grained siliciclastic sedimentary rocks is another source of taphonomic problems. Fossil remains are commonly dissolved by early diagenetic processes, except under highly specific taphonomic conditions, such as when protected by resistant carbonate or silica nodules and concretions. The complete loss of original skeletal material by solution is frequent because these rocks commonly have pore waters undersaturated with respect to carbonate (Speyer & Brett 1988; Meyer et al. 1989; Martin 1999). In these rocks, disarticulated bioclastic debris is com-

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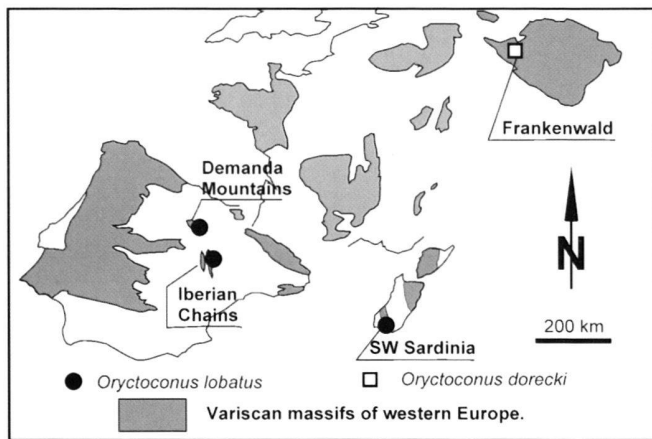


Fig. 1. Geological sketch of the *Oryctoconus* beds in the Variscan massifs of western Europe.

monly preserved as void spaces after solution of the whole skeleton. However, this is easily overcome using one of a range of flexible rubber compounds to cast the specimens of interest (Parsley 1989).

One typical example of the problems reported above is the sudden appearance of the early Tremadocian *Oryctoconus* remains in shell beds of western Europe. The fossil affinity of these coquinas has remained one of the enigmas of the Lower Palaeozoic benthic communities and attempts to identify possible sister groups have been largely problematical (Sdzuy 1955, 1969; Colchen & Ubaghs 1969; Wolf 1980).

The purpose of this paper is to study the type material and new specimens of *Oryctoconus* in order to make a revision of their highly conjectural taxonomic affinities assigned from 1969, which were subsequently accepted and perpetuated. Sdzuy (1969) was convinced that they could be related to 'sponges' (in which the author included the cancelloriids), whereas Colchen & Ubaghs (1969) disagreed with this idea and proposed questionable echinoderm-like affinities. The systematic revision is herewith done with the risk of developing a parataxonomic inflation among pelmatozoans because the *Oryctoconus* skeletons are not associated with crowns and, therefore, cannot be assigned to crown species with certainty. The debris is of biostratigraphical interest for correlation of poorly fossiliferous sedimentary rocks of the Cambrian-Ordovician transition in western Europe.

2. Geological setting and stratigraphy

The Cambrian-Ordovician transition is widely recorded in western Europe as temperate to cold, siliciclastic sedimentary rocks with relatively low-diversity faunas. However, an early Tremadocian colonization event is widely recognized, characterized by a 'bloom' of enigmatic, benthic organisms, commonly reported as *Oryctoconus* remains. The *Oryctoconus* beds are known from the Najerilla Formation of the Demanda Moun-

tains, the Valconchán Formation of the Iberian Chains (north-eastern Spain), the upper part of the Cabitza Formation in south-western Sardinia, and the Leimitz Shales of Germany (Fig. 1).

The Najerilla Formation (about 700 m thick) consists of decimetre- to metre-thick sandstone/shale alternations bearing isolated, centimetre-thick limestone nodules and lenses that have yielded two latest Cambrian-earliest Tremadocian fossil assemblages of trilobites, such as *Maladioidella colcheni* and *Langyashania felixi* in the lower part of the formation, and the pagodiine *Pagodia (Wittekindtia)* sp. in its upper part, as well as brachiopods, hyoliths, ichnofossils and *Oryctoconus* debris (Colchen 1967, 1974; Seilacher 1970; Palacios Medrano 1982; Shergold et al. 1983). The Najerilla Formation is bounded by two thick, sandstone-dominated formations, named the Viniegra and Brieva sandstones (Fig. 2), which are very poor in fossil fauna. The Middle-Upper Cambrian transition has been tentatively located across the boundary between the Viniegra and Najerilla formations (Sdzuy 1958; Colchen & Havlíček 1968).

The *Oryctoconus* beds are abundant in trough cross-stratified sandstones and conglomeratic channels, located within the uppermost part of the Valconchán Formation. The latter consists of quartzites with intercalations of shales and sandstones, and local conglomeratic channels situated at the top. The Valconchán Formation is conformably bounded by two shale-dominated successions: the underlying Upper Cambrian Valtorres Formation (Shergold & Sdzuy 1991; Álvaro & Vennin 1996) and the overlying Borrachón Formation that has yielded a Lower Ordovician trilobite fauna (Wolf 1980; Shergold & Sdzuy 1991). Incomplete biostratigraphical correlations of the Cambrian-Ordovician boundary are mainly based on acritarch and ichnofossil biozonation (Wolf 1976, 1980; Kolb & Wolf 1979) due to the scarcity of trilobites and brachiopods in this critical part of the succession (Schmitz 1971; Havlíček & Josopait 1972; Josopait 1972; Romano 1982; Shergold & Sdzuy 1991). The *Oryctoconus* remains are associated with the occurrence of trilobites (such as *Pagodia (Wittekindtia) alarbaensis*; Shergold & Sdzuy 1991), brachiopods (*Protambonites primigenius*; Villas et al. 1995) and ichnofossils.

The *Oryctoconus* beds also occur in Sardinia in the upper part of the Cabitza Formation, which consists of at least 600 m of silty shales and siltstones with sandstone intercalations and rare carbonate beds and marls at the lowermost part. It is Middle Cambrian to lower Ordovician, and its uppermost trilobite zone (the C6 assemblage of Loi et al. 1995) has yielded the trilobite species *Proteuloma geinitzi*, the graptolite *Rhabdinopora flabelliformis* (Pillola & Leone 1993), and other related acritarchs (Barca et al. 1987).

Finally, the *Oryctoconus*-bearing Leimitz shales occur in Frankenwald (Bavaria, Germany), an area interpreted as a Variscan overthrusting on the autochthonous Thuringian region. The Leimitz Shales are known from some disconnected outcrops, in which they are not in contact with older sedimentary rocks, but with younger Ordovician-Silurian deposits. The

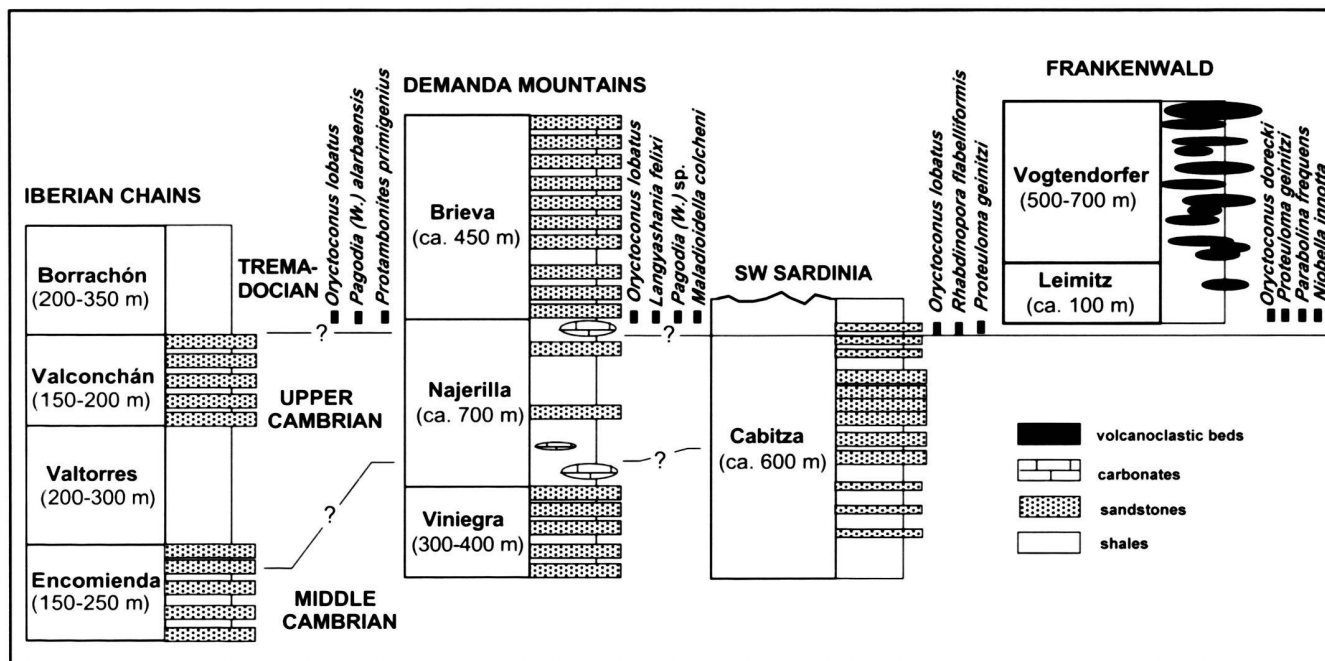


Fig. 2. Stratigraphical setting of the *Oryctoconus* beds and tentative correlation in western Europe.

formation (ca. 100 m thick and early Tremadocian in age) consists of slates, usually indistinctly stratified, with a few thin sandstone intercalations and associated volcanoclastic tuffs. Fossils include the hyolithid *Orthotheca*, the rhombiferan cystoid *Macrocystella*, one species of graptolite (*Aspidograptus* sp.), numerous acritarchs, and several brachiopod and trilobite species, such as *Proteuloma geinitzi*, *Parabolina frequens*, *Niobella innotta*, *Bavarilla hofensis* and *Pharostomina oepiki* (Sdzuy 1955, 1961, 1971; Reitz 1991). The formation is overlain by the Vogtendorfer Beds (Fig. 2), composed of several hundred metres (unmeasured) of volcanic and volcanoclastic rocks and interbedded shales, which have yielded brachiopods, cystoids and trilobites (such as *Euloma ornatum*, *Agerina* sp. and *Pikeia* sp.) of latest Tremadocian age (Sdzuy 1971).

3. Preservation and methods

Different preservation patterns are present in the *Oryctoconus* debris. For instance, the Iberian coquinas are dominated by monotypic concentrations. In cross section, the skeletal orientations are preserved concordant or subparallel with the cross-stratified laminae of the Valconchán sand shoals. On the plane of bedding, the bioclasts are not aligned in any consistent direction and apparently exhibit random embedding features. The debris is discontinuously closely-packed, locally reaching 60% or more hardparts by sandstone volume; in this case, skeletons show a bioclastic-supported fabric. The skeletons are either complete or slightly broken. The specimens described below were selected from these levels, because other debris

occurs as highly broken, conglomeratic channel lags, reworked from lateral sand shoals. By contrast, the *Oryctoconus* debris from the Demanda Mountains occurs as polymictic concentrations in sandstone beds and shoals (associated with linguliformean brachiopods, trilobites and pelmatozoan columnals), displaying biostratinomic characters similar to the Iberian specimens. In summary, the *Oryctoconus* remains are considered as parautochthonous assemblages exhibiting differential preservation as a consequence of post-mortem transport. Skeletal orientation, packing and sorting by size and shape depended on hydrodynamics on bedding planes of shoal pavements. These coquinas represent sedimentological concentrations resulting from hydraulic processes, produced through storm reworking and fair-weather winnowing on immediate shoal surroundings.

During diagenesis, the calcite endoskeletons of *Oryctoconus* were dissolved, producing a secondary porosity in sandstones and conglomerates. In some cases, the secondary porosity was partly or completely filled by quartz fibrous cements. Internal and external moulds could only be studied effectively after their calcite components had been completely removed by acid etching and/or ultrasonic cleaning. Hence, the reconstruction of their morphology is from latex cast preparation.

4. Systematic palaeontology

The illustrated specimens are housed in the Museo Paleontológico of the Zaragoza University (acronym MPZ).

Family uncertain

Genus *Oryctoconus* COLCHEN & UBAGHS 1969

Type species: Oryctoconus lobatus COLCHEN & UBAGHS 1969, by monotypy.

Emended diagnosis: Amphora-shaped skeleton, bearing an anterior circular plate pierced by a straight axial canal (circular in cross section), prolonged into a lobate to stellate crown of anterior appendages or radices, unbranched, unsegmented, irregular in number (3–10), rather regularly spaced, and displaying a radial symmetry.

Remarks: The external morphology of *Oryctoconus* is similar to that of some Devonian crinoidal holdfasts, such as *Ancyrocrinus bulbosus* HALL 1862, *A. armoricanus* MORZADEC 1967, and *Aragonocrinus molinoensis* LE MENN 1988. The discovery of stems and crowns attached to the first species permitted its assignation to the botryocrinids. By contrast, the other two species are rarely associated with their columnals or calyces. *Ancyrocrinus* differs from *Oryctoconus* in the number of radices, the former displaying always a fivefold symmetry, and the star-like transverse section of the axial canal, which shows lateral ramifications. *Aragonocrinus* differs from *Oryctoconus* in its high variability in shape (from fusiform to spheroid in outline), the lack of radices, and the pentalobate transverse section of the axial canal. The special preservation conditions of the *Oryctoconus* type species allow identification of the three-dimensional framework of its axial canal favouring a better understanding of its entire morphology.

***Oryctoconus lobatus* COLCHEN & UBAGHS 1969**

Pl. I/1–12

- 1966 *Calix? dorecki* (SDZUY).– Bartsch, p. 28–29, Pl. 4, figure 5.
1969 *Oryctoconus lobatus* n. gen. n. sp.– Colchen & Ubaghs, p. 649–654, figures 1–9.
1970 “*Calix?*” cf. *dorecki* SDZUY 1955.– Scheuplein, p. 93–94, Pl. 5, figures 2–4.
1971 *Oryctoconus* sp.– Schmitz, p. 48.
1974 *Oryctoconus lobatus* COLCHEN & UBAGHS 1969.– Colchen, p. 178.
1976 *Oryctoconus lobatus*.– Wolf, p. 13, 103–106, Pl. 4, figures 1–6.
1980 *Oryctoconus lobatus*.– Wolf, p. 122–124.
1982 *Oryctoconus* sp.– Mitsche-Collande, p. 45–47, 145, Pl. 5, figures 3–4.
1982 *Oryctoconus*.– Palacios Medrano, p. 25, 48.
1983 *Oryctoconus lobatus*.– Shergold et al., p. 77.
1991 *Oryctoconus lobatus* COLCHEN & UBAGHS 1969.– Shergold & Sdzuy, p. 200.
1995 *Oryctoconus* cf. *O. lobatus*.– Loi et al., p. 70, Pl. 5, figure 14.
1996 *Oryctoconus lobatus*.– Liñán et al., p. 26, figure 8.
2000 *Oryctoconus lobatus*.– Geyer & Shergold, p. 190–191.
2001 *Oryctoconus lobatus*.– Álvaro & Vennin, p. 11.

Holotype: MPZ 17143 (drawing in Text.-pl., fig. 1 in Colchen & Ubaghs 1969; and pl. I/2 in this work).

Material examined: More than 50 specimens preserved as external and internal moulds.

Emended diagnosis: *Oryctoconus* species with height/anterior diameter ratio of 0.4–2 (without appendices), flat anterior face, and axial canal inserted into anterior and posterior, circular plates.

Description: Smooth, amphora-shaped skeleton with convex base, and relative height strongly variable. Stereom microstructure, external sutures and perforations are not visible. Three to six appendages, stout and non-whorled, and ellipsoidal to crescent-shaped in cross-section, grow around the anterior face of the skeleton. The anterior face, subcircular to stellate in cross-section, displays a central circular plate (up to 1.6 mm in diameter) bearing a central orifice (up to 0.2 mm in diameter). The posterior face is concave in external moulds but commonly exhibits a shallow, saddle-like depression whose centre shows the prolongation of the axial canal (in internal moulds), identified as a circular orifice of similar size than the anterior one. The axial canal is more or less straight, simple, circular in cross-section (up to 1.2 mm in diameter), unbranched, crossing the skeleton longitudinally (up to 3.5 mm long), and irregularly subdivided by slight but distinct irregular constrictions, truncate in section, giving convex abaxial expansions; the tips of the axial canal are inserted into the anterior and posterior plates described above, both of them circular in shape.

Intraspecific variability: Three morphological characters are highly variable in *O. lobatus*: the number and shape of the anterior appendages, and the relative height of the amphora-like skeleton. The last two characters allow differentiation into two morphotypes displaying transitional stages between them, which prevent to consider both forms as different species. The first is the lobate morphotype (reported as holotype), found only in the Demanda Mountains, in which the anterior appendages are lobate and short (Pl. I/1–6), and its height/anterior diameter ratio is 0.4–0.6 (so width greater than height). By contrast, the second stellate morphotype (Pl. I/7–12) has a ratio of 0.4–2 and occurs both in the Iberian Chains and the Demanda Mountains. Despite the deformation suffered by these skeletons, some ontogenic trends are recognized (Fig. 3): larger skeletons are relatively thinner than smaller ones, increasing gradually the relative width of the anterior face (in which the appendices are inserted), and their appendices become relatively thinner and longer.

Remarks: Halleck (1973) and Brett (1978) pointed out that pelmatozoans have different radices depending on the firmness of the substrate: the contact with soft substrates may induce production of numerous slender branched rootlets, whereas radices can be limited to short stubby forms on hard substrates. Therefore, the number and geometrical pattern of radices can be associated with substrate consistency, as response to environmental factors. The intraspecific variability both in the number (3 to 6) and shape (relatively thicker smaller forms contrasting with thinner larger forms) of *O. lobatus*

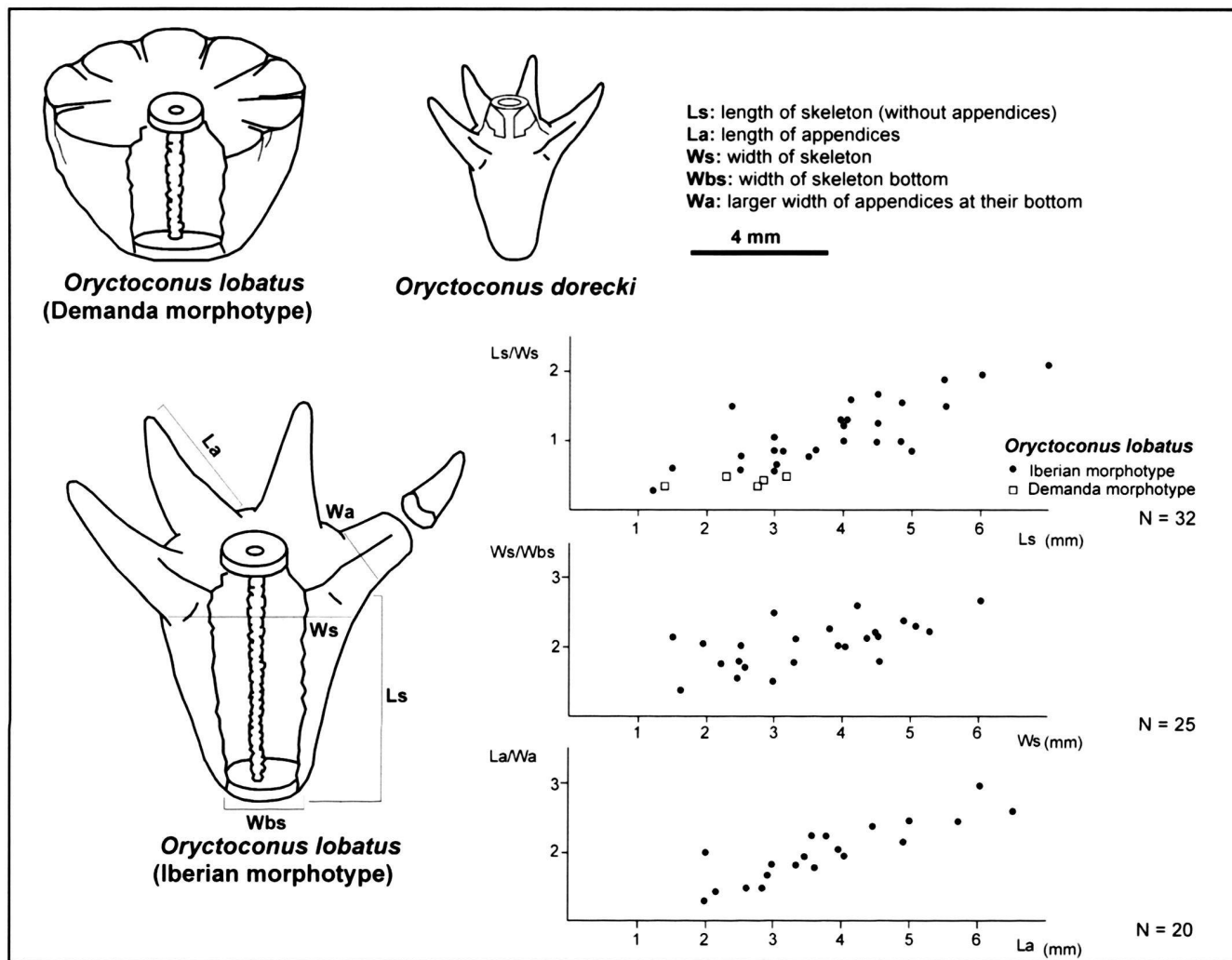


Fig. 3. Reconstruction of the *Oryctoconus* skeletons and biometric patterns.

may indicate ecological conditions. For instance, thinner larger forms would favour supporting functions of a holdfast deeply embedded in the sediment whereas thicker smaller forms would be shallower; the variability in the number of radices could be related to the firmness of mud- to sand-dominated substrates.

Comparisons: Some uncertain, Lower Ordovician fossil debris from Finmark (Norway), described originally by Erdtmann et al. (1984), were assigned to *Oryc(h)toconus* (sic) by Berg-Madsen (1986). These skeletons have close similarities to the Demanda morphotype of *O. lobatus*, are pierced by an axial canal, and their anterior and posterior faces bear a central circular orifice. The presence of an orifice on the posterior face

could be related to preservation as internal moulds; however, external moulds must be studied in order to check the end of the axial canal.

Oryctoconus dorecki (SDZUY 1955)

- 1955 *Calix? dorecki* n. sp.– Sdzuy, p. 274–275, Pl. 1, figures 15–19.
- 1966 non *Calix? dorecki*.– Bartsch, p. 28–29, Pl. 4, figure 5.
- 1969 *Calix? dorecki* (SDZUY).– Sdzuy, p. 128.
- 1969 *Calix? dorecki*.– Colchen & Ubaghs, p. 654.

Holotype: SMF (XXI 51a), Forschungs-Institut Senckenberg (Sdzuy 1955; pl. 1, fig. 17).

Emended diagnosis: *Oryctoconus* species with a height/anterior diameter ratio of 1–2, 5–10 appendages, and anterior face with a convex anterior face, trapezoidal in cross-section, bearing a central funnel-like depression.

Remarks: The skeletons of *O. dorecki* are preserved as external moulds so that their internal structures (e.g. the longitudinal section of the axial canal) are not observable. *O. dorecki* differs from *O. lobatus* in the number of appendages (a character likely related to substrate conditions), the relative height of the skeletons and, which is more important, the upward prolongation of the anterior face and the lack of a central circular plate, changed into a funnel-like depression. Although the general size of *O. dorecki* is slightly smaller than that of *O. lobatus*, these differences do not seem to be associated with ontogenic patterns.

5. Palaeoecological and biostratigraphical significant patterns

The morphological patterns of the skeletons suggest that the holdfasts were oriented with the anterior face upward, lying on the substrate with the amphora-like body partly embedded in the sediment. The proximal appendices would lay on the sediment surface stabilizing the echinoderm. This kind of grapple functioned probably less as a drag and ballast than as an anchor, giving the pelmatozoan a secure and relatively stable base in low- to moderate-energy environments (Ubaghs 1978; Brett 1981). The anterior plate (up to 2 mm in diameter) served for articulation with the distal end of the pelmatozoan stem. The first columnal had a circular outline with a relatively wide epifacet and small articulum. This articulation would be highly vulnerable to breakage and detachment under influence of bottom currents and storm surges, as a result of (i) post-mortem accumulation (after decomposition of the collagenous connective tissues) or (ii) autotomy of the column from the attachments.

Traditionally, *Oryctoconus* is used regionally as a biostratigraphical tool because it is associated with distinct early Tremadocian trilobites (*Proteuloma geinitzi*), brachiopods (genera *Protambonites* and *Poramborthis*), graptolites (*Rhabdinopora flabelliformis*) and acritarchs. However, its first appearance could be latest Cambrian due to its co-occurrence in the Iberian Chains and the Demanda Mountains with the trilobite *Pagodia (Wittekindtia)* sp. and the brachiopod *Billingsella* (Shergold et al. 1983; Villas et al. 1995). An accurate correlation with conodonts is necessary in order to associate its appearance with the Cambrian/Ordovician boundary based on conodonts (Webby 1998).

6. Conclusions

The *Oryctoconus* pelmatozoan meadows flourished episodically in the early Tremadocian, siliciclastic-dominated platforms of western Europe. Their holdfasts display a preference for preservation in sandstone and conglomerate substrates and immediate shoal surroundings. They occur in well-sorted, mono- and polytypic assemblages of skeletal debris, after disarticulation and transport of the stem and calyx ossicles, which were commonly washed away. The densely packed concentrations reported from the Iberian Chains can be as much as 60% hard-parts by volume, in some cases bioclastic supported on the bedding plane and cross-stratified surfaces. As a result of shoal progradation, parautochthonous holdfasts configured shelly pavements on cross-stratified laminae. Conglomerate channels eroded these sandstone sets re-incorporating the holdfasts as broken and incompletely preserved allochthonous debris.

Two species are distinguished in this work, *O. lobatus* and *O. dorecki*, recognized by their amphora-like skeleton prolonged into a crown of anterior appendages or radices. *Oryctoconus lobatus* displays a flat anterior face bearing a circular plate that would serve for articulation with the distal end of the pelmatozoan stem. Its special preservational conditions allow identification of a straight axial canal that crosses the skeleton longitudinally. By contrast, *O. dorecki* has a convex anterior face, trapezoidal in cross-section, bearing a central funnel-like depression. The axial canal of both species (seemingly the prolongation of the axial canal of the stem) is circular in cross section and would contain coelomic and nervous extensions.

Terminal holdfasts bearing well-developed radices (anchor-like grapples *sensu* Ubaghs 1978; Brett 1981) are pelmatozoan attachment structures, lacking carbonate encrustations, and represent permanent or long-term fixation on shale and sand substrates. Major difficulties arise in attempting to associate particular early Tremadocian columns and calyxes to these holdfasts, as discussed by previous authors in the Devonian of the Armorican Massif. Although the crown is preferentially required for taxonomic identification and, therefore, a prerequisite for phylogenetic, palaeoecological and other studies, holdfast elements are by far the most common fossil remains in the *Oryctoconus* beds. The biostratigraphical utility of pelmatozoan holdfasts is demonstrated in this case.

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Plate 1

Debris of *Oryctoconus lobatus* (Demanda and Iberian morphotypes).

1. Inner side of an anterior plate attached to the dissolved prolongation of the skeleton (external mould); MPZ 17142, scale bar = 4 mm.
2. Latex cast of the holotype (h) and stemmed plate (s); MPZ 17143, scale bar = 2 mm.
3. Stemmed plate surrounded by two *Oryctoconus* skeletons; MPZ 17144, scale bar = 5 mm.
4. Inner side of another anterior plate; MPZ 17145, scale = 2 mm.
5. Axial canal piercing one dissolved skeleton; MPZ 17146, scale bar = 1 m.
6. Detail of the posterior end of the axial canal, inserted in a posterior circular plate; MPZ 17147, scale bar = 0.5 mm.
7. External mould of a posterior side exhibiting the convex end of a skeleton bearing four appendices; MPZ 17148, scale bar = 2 mm.
8. Lateral view of two skeletons; MPZ 17149 scale bar = 2 mm.
9. Lateral and oblique view of four skeletons (internal moulds) showing four appendices, the anterior circular plate, and the posterior prolongation of the axial canal; MPZ 17150, scale bar = 4 mm.
10. Two sections of internal moulds, one of them (right) bearing the lower part of the axial canal; MPZ 17151, scale bar = 2 mm.
11. Detail of another internal mould, whose axial canal bears distinct constrictions; MPZ 17152, scale bar = 1 mm.
12. Inner side of an anterior plate and its four prolonged appendices; MPZ 17153, scale bar = 2 mm.

