Journal of Palaeogeography, 2024, 13(4): 939–953 (00362)

Available online at www.sciencedirect.com

ScienceDirect

journal homepage: http://www.journals.elsevier.com/journal-of-palaeogeography/

Palaeobiogeography

Late Ordovician cornulitid tubeworms from high-latitude peri-Gondwana (Sardinia and the Pyrenees) and their palaeobiogeographic significance

Olev Vinn [a,*], *Jorge Colmenar* [b], *Samuel Zamora* [c], *Sofia Pereira* [d], *Gian Luigi Pillola* [e], *Abdullah A. Alkahtane* [f], *Saleh Al Farraj* [f], *Magdy El Hedeny* [g]

[a] *Institute of Ecology and Earth Sciences, University of Tartu, Ravila 14A, 50411 Tartu, Estonia*
[b] *Instituto Geológico y Minero de España-CSIC, La Calera 1, 28760 Tres Cantos, Spain*
[c] *Instituto Geológico y Minero de España-CSIC, Residencia CSIC, Campus Aula Dei, Avenue Montañana 1005, 50006 Zaragoza, Spain*
[d] *Centro de Geociências, Departamento de Ciências da Terra, Universidade de Coimbra, Rua Sílvio Lima, 3030-790 Coimbra, Portugal*
[e] *Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Cagliari, Cittadella Universitaria, Blocco A, 09042 Monserrato, Italy*
[f] *College of Science, King Saud University, Kingdom of Saudi Arabia*
[g] *Geology Department, Faculty of Science, Alexandria University, Egypt*

Abstract Seven *Cornulites* species, including a new one — *Cornulites leonei* n. sp., are described from the Upper Ordovician Portixeddu Formation (Katian, stage slices Ka2–3) of Sardinia and the Cavá (lower Katian, stage slice Ka2) and Estana (upper Katian, stage slices Ka3–4) formations of the Pyrenees. The Sardinian and Pyrenean cornulitids represent an adaptation to live in environments with high sedimentation rates and limited hard substrates availability. Their prominent annuli could have had a stabilizing function in the soft sediment that helped cornulitids to keep a favourable position in the sediment to enable suspension feeding. The known Late Ordovician cornulitid diversity in different Gondwana areas is low, usually ranging from one to three taxa, being higher (seven) in Sardinia. Like other benthic groups during the Late Ordovician, the cornulitid tubeworm faunas within the high-latitude peri-Gondwana Province indicate a certain endemism and share morphological and ecological affinities, such as a small body size and tubes with a strikingly small apical angle. Although essentially endemic, some links with cornulitids from the Late Ordovician of Scotland are revealed.

Keywords Tentaculitid tubeworms, *Cornulites*, Mediterranean, Palaeoecology, Katian

* Corresponding author.
E-mail address: olev.vinn@ut.ee (O. Vinn).
Peer review under responsibility of China University of Petroleum (Beijing).
https://doi.org/10.1016/j.jop.2024.08.009

Received 2 April 2024; revised 6 May 2024; accepted 27 August 2024; available online 7 September 2024

1. Introduction

The order Cornulitida (Bouček, 1964) comprises encrusting tentaculitoid tubeworms that are closely related to free-living tentaculitids (Vinn and Mutvei, 2009). They are found in the carbonate and siliciclastic rocks from the Middle Ordovician (Darriwilian) to the uppermost Carboniferous (Vinn, 2010). Despite uncertainties regarding their biological affinities, cornulitids are thought to belong to the Lophotrochozoa (Vinn and Zatoń, 2012) and may represent precursor forms of phoronids (Taylor *et al.*, 2010). Cornulitids hold significance in palaeoecological studies, due to their tendency to retain their original position on substrates after fossilization as hard substrate encrusters (Taylor and Wilson, 2003). While most cornulitids were simple hard substrate encrusters (Zatoń and Borszcz, 2013; Zatoń *et al.*, 2017), some species lived as endobiotic symbionts in stromatoporoids, tabulates, and bryozoans (Vinn, 2010). Cornulitids exclusively inhabited marine environments with normal salinity, distinguishing them from microconchid tubeworms that dwelled in waters of various salinities (Zatoń *et al.*, 2012, 2016). Commonly found in shallow marine sediments, particularly associated with carbonate platforms, cornulitids also occur in siliciclastic sediments (Zatoń *et al.*, 2017; Musabelliu and Zatoń, 2018).

During the Late Ordovician Epoch, a portion of the Gondwana supercontinent was located in polar latitudes of the southern hemisphere (Colmenar, 2015). Within the high-latitude peri-Gondwana, a faunal province characterized by common brachiopod, trilobites and several other invertebrates extended across mid to high latitudes, ranging from approximately 50°S to 75°S (according to Harper *et al.*, 2013) and from Arabia to most of South America. Presently, remnants of this province are primarily found in the Anti-Atlas, the Armorican Massif, the Iberian Massif, the Montagne Noire, the Iberian Chains, the Pyrenees, the Carnic Alps, Sardinia, and the Bohemian Massif (Colmenar, 2015). During the Middle and early Late Ordovician times, this region was distinguished by low-diversity brachiopod associations, dominated by endemic groups, particularly belonging to the families Heterorthidae and Drabovidae (as detailed by Colmenar, 2015). Like brachiopods, tentaculitoid tubeworms were suspension-feeding benthic organisms, yet their biogeography remains relatively poorly understood compared to that of brachiopods. It prompts a discussion on whether the tentaculitoid tubeworm faunas within this high-latitude peri-Gondwana province shared taxonomic and ecological affinities similarly to those of brachiopods or any other invertebrates.

Although cornulitids became globally distributed during the Late Ordovician (e.g., Fisher, 1962; Richards, 1974; Zhan and Vinn, 2007; Vinn and Gutiérrez-Marco, 2016), their known diversity in the high-latitude peri-Gondwana during this Epoch, mainly represented by shallow siliciclastic environments, is relatively low (Gutiérrez-Marco and Vinn, 2018). This, whether cause or consequence, has led to little attention being paid to the group in this region. Apart from the records from Bohemia (e.g., Barrande, 1867; Prantl, 1948; Bouček, 1964), and, more recently, Morocco (Gutiérrez-Marco and Vinn, 2018), Upper Ordovician cornulitids from other regions of this palaeobiogeographical province are poorly known. They have been reported, often without proper identification, illustration or description, from the Montagne Noire (Dreyfuss, 1948; Colmenar *et al.*, 2013; Álvaro *et al.*, 2016), Spain (e.g., Verneuil and Barrande, 1855) or Portugal (Silvério *et al.*, 2021), Sardinia (Meneghini, 1857; Vinassa de Regny, 1927; Spano, 1974), Saudi Arabia (Gutiérrez-Marco *et al.*, 2017) and Iran (Ghavidel-Syooki *et al.*, 2015).

Here, we describe cornulitid tubeworms from the Upper Ordovician of the Pyrenees and Sardinia, providing a systematic study and discussing the diversity, ecology and palaeobiogeographical distribution of the group during the Late Ordovician in Gondwana.

2. Geological background

During the Ordovician, Sardinia and Iberia (Pyrenees) were peri-Gondwanan terranes located at latitudes of about 60°S—50°S (Harper *et al.*, 2013; Colmenar, 2015). During most of the period, the sedimentation in these high-latitude epicontinental seas was predominantly siliciclastic, but during mid to late

Katian times carbonate sedimentation began to develop (Colmenar, 2015) due to the global Boda warming event (Fortey and Cocks, 2005). This resulted in the migration of lower latitude invertebrates to high-latitude, leading to the increase of diversity and faunal replacements (i.e., Hammann, 1992). The rocks sampled for this work represent the post-Sardic Unconformity (Teichmüller, 1931) sedimentation characteristic in these terranes during Late Ordovician times (Leone *et al.*, 1991; Álvaro *et al.*, 2016; Puddu *et al.*, 2018; Cocco *et al.*, 2023). Siliciclastic sedimentation resumed towards the end of the Ordovician, likely conditioned by the extreme glacial conditions achieved in the region during the Hirnantian glaciation. The Portixeddu Formation (Leone *et al.*, 1991) encompasses most of the Katian deposits of the autochthonous sequence cropping out in southwest Sardinia (Fig. 1A). It consists of an exclusively siliciclastic sequence (Fig. 1B) of greenish-grayish siltstones, claystones and alternating fine to coarse siltstones (Leone *et al.*, 1991) likely deposited in offshore environments, between the fair-weather wave-base and the storm wave-base (Botquelen *et al.*, 2006). Based on the brachiopod and trilobite occurrences, a Katian age (ca. Ka2—3 stage slices; regional late Berounian—early Kralodvorian) was proposed for this unit (Leone *et al.*, 1991; Hammann and Leone, 1997, 2007; Colmenar *et al.*, 2017). In the central Pyrenees, two units — the Cavá and Estana formations (Hartevelt, 1970) — were sampled (Fig. 2A). The Cavá Formation (Fig. 2B) consists of greywackes, slates, siltstones, sandstones and quartzites (Hartevelt, 1970), likely deposited in shoreface environments (Colmenar *et al.*, 2013) and its fossil content suggests an early Katian age (ca. Ka2; regional late Berounian). The Estana Formation (Fig. 2B) represents the Boda event-related carbonate sedimentation in upper offshore environments of high-latitude settings (Colmenar, 2015), and consists of marls and limestones containing the conodont *Amorphognathus ordovicicus* (Hartevelt, 1970; Sarmiento *et al.*, 2011), indicative of the upper Katian (ca. Ka3—4; regional Kralodvorian stage).

3. Localities

3.1. Sardinia

Two Sardinian localities have provided well-preserved cornulitid tubeworms:

1) The Gon1 locality (Fig. 1A) is situated in a small valley west of Sa Siliqua Hill, northeast of Gonnesa and corresponds to the homonymous locality of Hammann and Leone (1997, 2007). Cornulitids were collected from the basalmost Portixeddu Formation, just 1 m above the sandstones of the underlying Monte Orri Formation, represented in this area by a maximum of ten meters of coarse-grained quartzarenites with hummocky cross-stratification ripples (Leone *et al.*, 1991). The co-occurring brachiopods and trilobites suggest an early Katian age (ca. Ka2; regional late Berounian) for this locality.
2) The CR/3 locality (Fig. 1A) is situated at the Punta Pedrona Hill, about 3 km east-northeast of Portixeddu and correspond to locality B of Havlíček *et al.* (1987) and locality Por 7 of Hammann and Leone (1997, 2007). At this site the sampled levels belong to the upper half of the Portixeddu Formation containing characteristic brachiopod taxa of the *Nicolella* Fauna (Colmenar, 2015), which allows correlation with the Katian stage (ca. Ka2—3; regional upper Berounian—lower Kralodvorian). The sampled bed corresponds to the brachiopod horizon BH 4 of Leone *et al.* (1991).

3.2. Pyrenees

Two Pyrenean localities have provided identifiable cornulitid tubeworms:

1) The CP/1 locality (Fig. 2A) is situated near the Andorran/Spanish border on the western slope of Canals de Calm Ramonet peak, approximately 6 km northeast of La Seu d'Urgell, Spain. Cornulitids were collected from the "siltstone member" of the upper half of the Cavá Formation. The shelly fauna indicates an early Katian age (ca. Ka2; regional late Berounian) for this locality.
2) The VS/EST locality (Fig. 2A) is placed approximately 1 km northeast of Alàs village, Spain on the hillside around the km 223 of the road N-260. The material collected comes from decalcified limestones of the lower half of the Estana Formation. The co-occurring fossils indicate a late Katian age (ca. Ka3—4; regional Kralodvorian) for these levels, which is in agreement with conodont data found in this formation (Hartevelt, 1970; Sarmiento *et al.*, 2011).

4. Material and methods

The Sardinian material was collected during several campaigns in the summers of 2013 and 2015. The material from the Pyrenees was collected by Professors N. Spjeldnaes, W. Hammann, and E. Villas in the 1970s and early 1980s and was kindly donated for this study by the latter. Specimens are preserved as external and

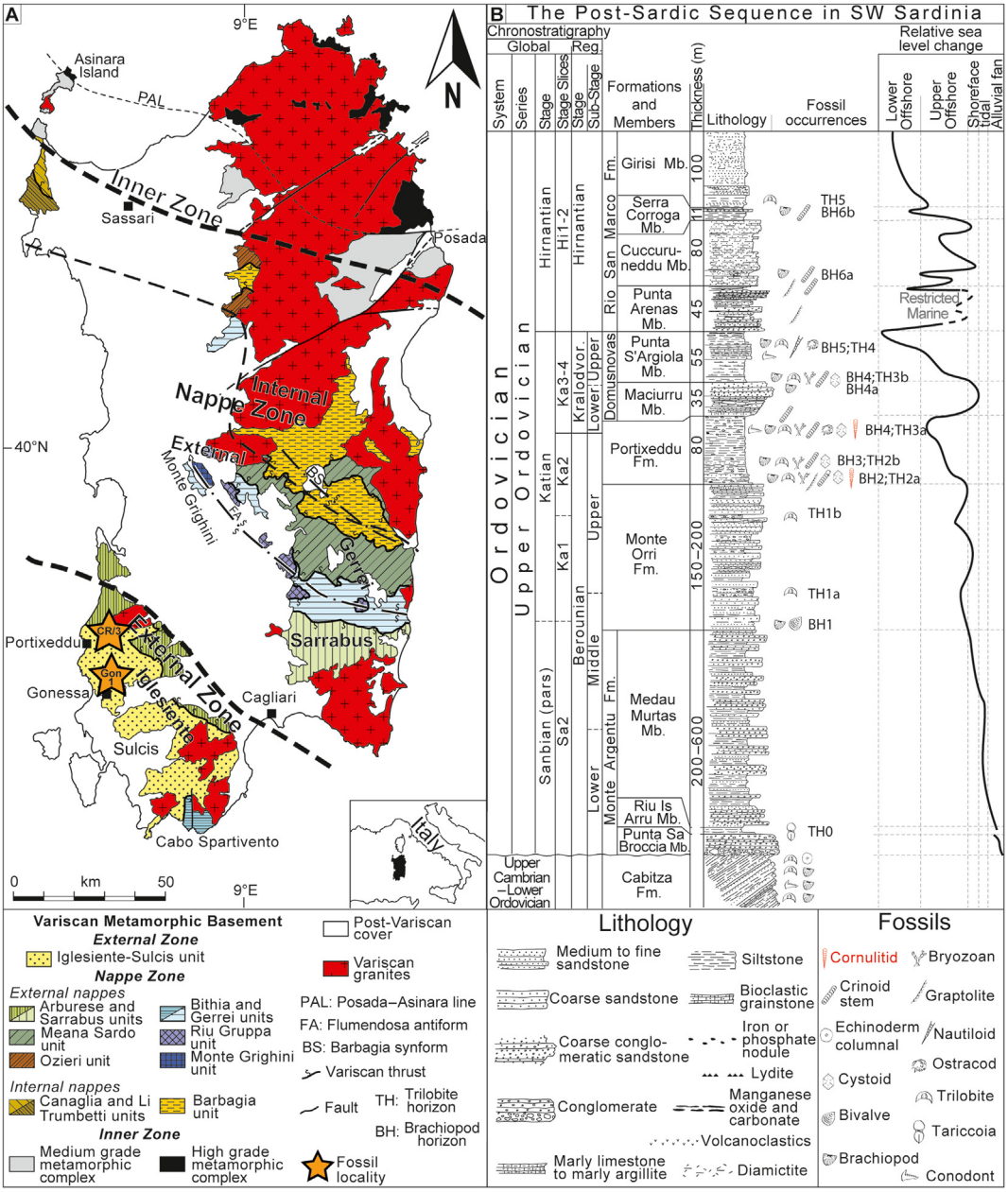

Fig. 1 Geological setting of Sardinian fossil localities. **A)** Tectonic sketch map of the Variscan basement in Sardinia (after Cocco *et al.*, 2023); **B)** Schematic lithostratigraphic succession of the post-Sardic sequences of southwest Sardinia (after Leone *et al.*, 1998 and Cocco *et al.*, 2023). Relative sea-level curve was after Leone *et al.* (1998); Trilobite Horizons (TH) were after Hammann and Leone (1997, 2007); Brachiopod horizons (BH) were after Leone *et al.* (1991, 1998). Abbreviations: SW = Southwest; Reg. = Regional; Kralodvor. = Kralodvorian.

internal moulds in siltstones and marls. Latex casts were made from all of the collected external moulds in order to better compare the specimens with well-preserved material from the Upper Ordovician of Laurentia and Baltica. The latex casts were whitened with ammonium chloride sublimated and photographed with a DSLR camera Nikon D7200 with a 60 mm Nikkor macro lens, mounted on a copystand. Pictures were focus-stacked with Helicon Focus (v4.2.9) software. Figures were compiled using Adobe Photoshop. The original specimens from which latex casts were made, are housed in the collections of the Museo di Geologia e Paleontologia "Domenico Lovisato" (MDLCA) of the University of Cagliari, Sardinia (collection numbers MDLCA 23866 to 23875) and the Museo Geominero, Madrid (collection numbers with MGM).

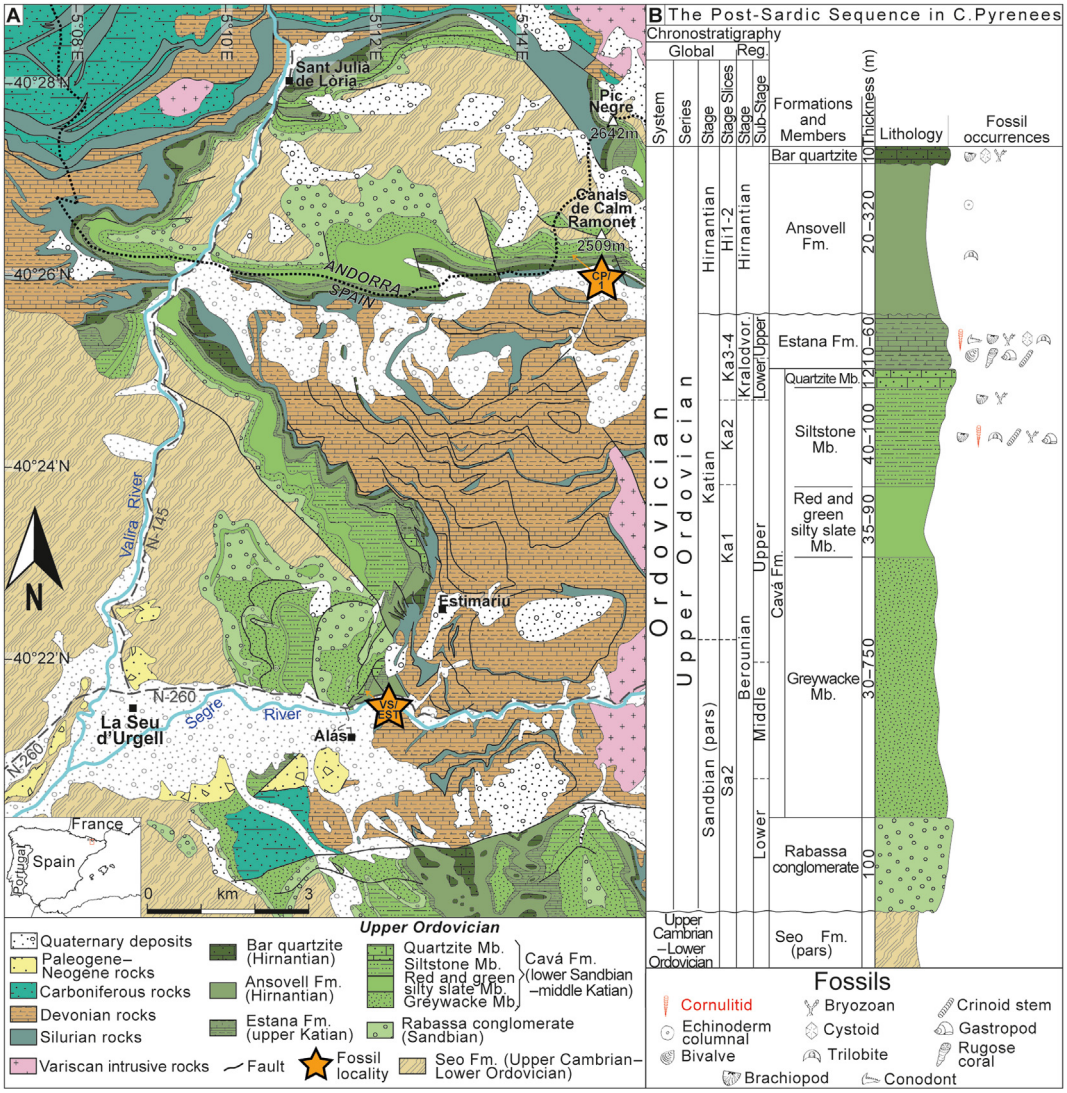

Fig. 2 Geological setting of Pyrenean fossil localities. **A)** Detailed geological map of the upper Segre and Valira Valleys, central Pyrenees; **B)** Schematic lithostratigraphic succession of the post-Sardic sequences of the central Pyrenees (after Hartevelt, 1970). Abbreviations: C. = Central; Reg. = Regional; Kralodvor. = Kralodvorian.

5. Systematic palaeontology

Phylum Incertae sedis.
Class Tentaculitida Bouček, 1964
Order Cornulitida Bouček, 1964
Family Cornulitidae Fisher, 1962.
Genus *Cornulites* Schlotheim, 1820.
Type species. *Cornulites serpularius* Schlotheim (1820), Silurian of Gotland, Sweden.

Cornulites caputaquae Vinassa de Regny, 1927 (Fig. 3A).

1927 *Tentaculites caputaquae* Vinassa de Regny, p. 452, pl. 2, fig. 7.

1974 *Cornulites caputaquae* (Vinassa de Regny, 1927) Spano, pp. 199—200, pl. 1, fig. 1, 1a.

Material. A single, almost complete specimen preserved as a natural mould (MDLCA 23866) but lacking the proximal part.

Locality and stratigraphy. Base of the Portixeddu Formation at locality Gon1, north—north—east (NNE) of Gonnesa, Sardinia, Italy.

Description. Small almost straight tube without any attachment structures. The tube diameter is 3.3 mm. The tube very slowly increases in diameter with an apical angle of 5°. Tube is covered with prominent, almost regular annulation. The annuli are usually perfectly perpendicular to the tube's longitudinal axis and have regular shape, but in some

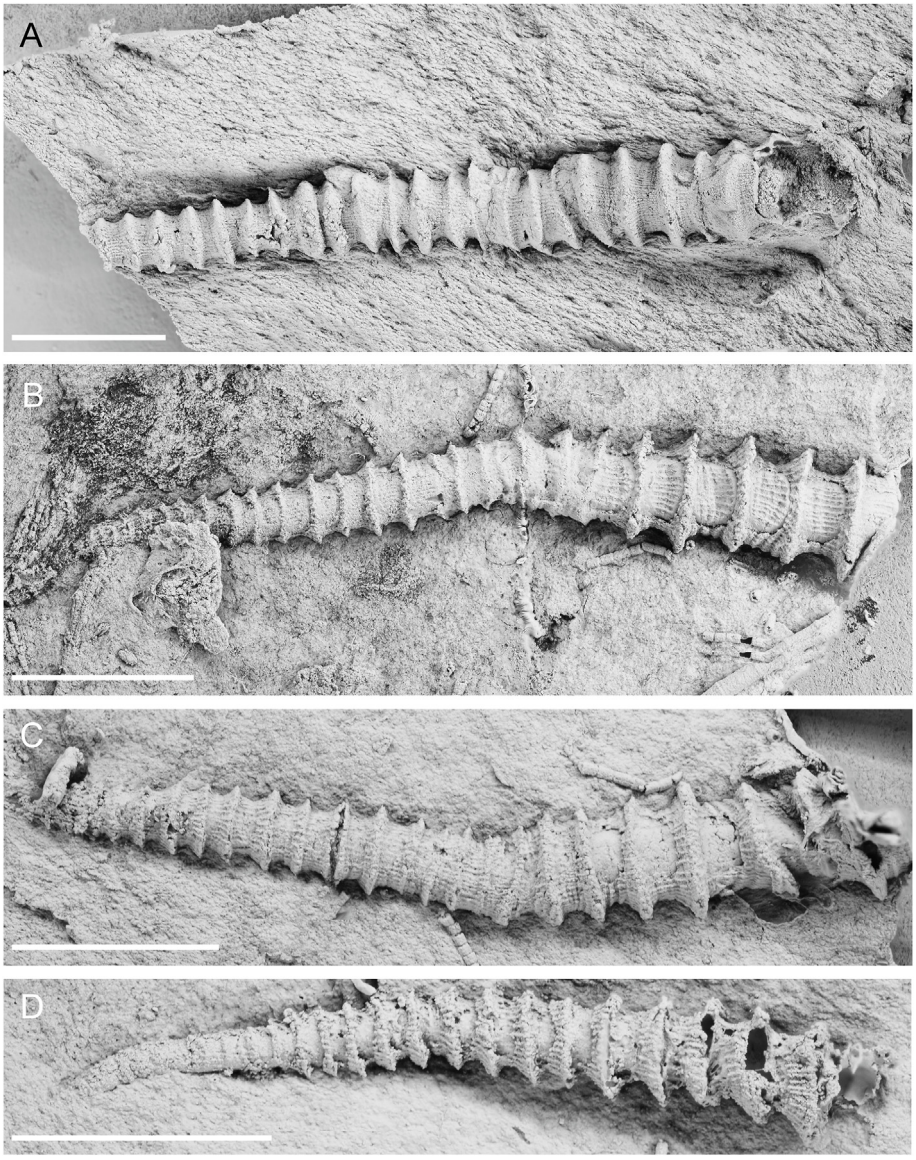

Fig. 3 **A)** *Cornulites caputaquae* Vinassa de Regny, 1927 (MDLCA 23866), base of Portixeddu Formation at locality Gon1, NNE of Gonnesa, Sardinia, Italy; **B)** *Cornulites fluminensis* Spano (1974) (MDLCA 23867), upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Fluminimaggiore, Sardinia, Italy; **C)** *Cornulites fluminensis* Spano (1974) (MDLCA 23868), upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Fluminimaggiore, Sardinia, Italy; **D)** *Cornulites fluminensis* Spano (1974) (MDLCA 23869), upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Fluminimaggiore, Sardinia, Italy. All specimens represent latex casts from original moulds whitened with ammonium chloride sublimated for photography. Scale bars all equal 5 mm.

places they can be slightly tilted or curved and have a somewhat deformed shape. The interspaces between annuli are deep and 1.5—2 times wider than annular crests. The interspaces are flat to slightly concave. The tube exterior is covered with fine, closely spaced longitudinal striae. There are 11—13 striae per 1 mm near the tube aperture. The striae are crossed by variably developed, irregular transverse growth lines. The tube lumen is also covered with annulation.

Remarks. The described specimen is assigned to *Cornulites caputaquae* Vinassa de Regny, 1927 (p. 452, pl. 2, fig. 7) Spano (1974) (pp. 199—200, pl. 1, fig. 1, 1a), a species known from the Portixeddu Formation of the Upper Ordovician (Katian) of Sardinia, because of similar and very small apical angle and very fine closely spaced longitudinal striae. The *Cornulites caputaquae* shares some similarities with *Cornulites fluminensis* in terms of its ornamentation. However, *Cornulites fluminensis* Spano (1974) (pp. 194—195, pl. 2, figs. 3—5, pl. 3, fig. 1) lacks transverse growth lines, and has a smaller apical angle. *Cornulites caputaquae* also shares some similarities with *Cornulites girvanensis* Reed (1923) (pp. 271—272, pl. 12, figs. 1—3), but the

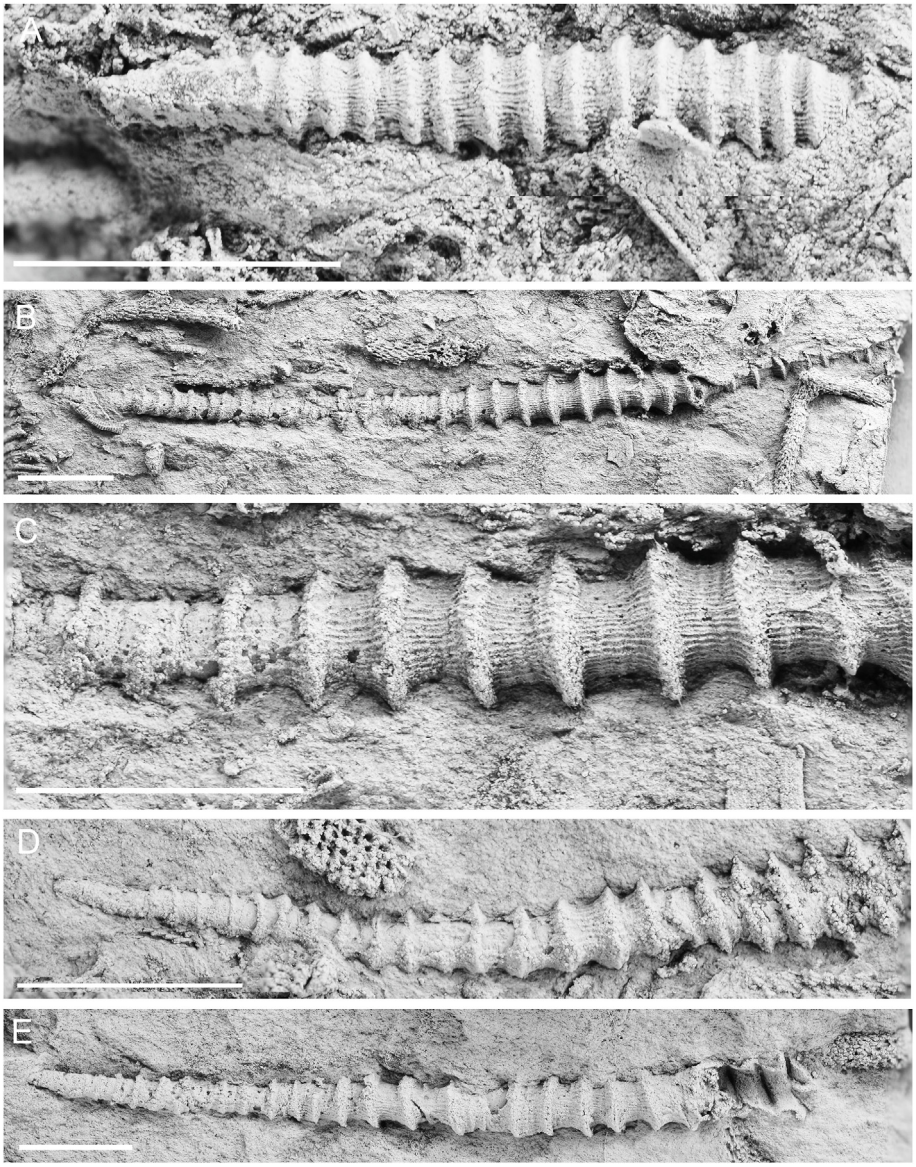

Fig. 4 **A)** *Cornulites sardous* Vinassa de Regny, 1927 (MDLCA 23872), upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Fluminimaggiore, Sardinia, Italy; **B—E)** *Cornulites leonei* sp. nov., upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Fluminimaggiore, Sardinia, Italy. **B** and **C** are holotype specimens (MDLCA 23873); **D** is paratype specimen (MDLCA 23874); **E** is paratype specimen (MDLCA 23875). All specimens represent latex casts from original moulds whitened with ammonium chloride sublimated for photography. Scale bars all equal 5 mm.

latter almost entirely lacks longitudinal striae. *Costatulites kimi* Ghavidel-Syooki *et al.*, 2015 also resembles somewhat *Cornulites caputaquae* but has a larger apical angle.

Occurrence. Besides the studied locality, this species occurs at Ponte Amadori (about 2 km ENE from Portixeddu, Fuminimaggiore), the Portixeddu Formation, Upper Ordovician of Sardinia.

Cornulites fluminensis Spano (1974) (Fig. 3B—D).

1974 *Cornulites fluminensis* n. sp. Spano, pp. 194—195, pl. 2, figs. 3—5, pl. 3, fig. 1.

2015 *Costatulites kimi* sp. n. Ghavidel-Syooki *et al.*, pp. 543—544, fig. 8.

Material. Four complete specimens preserved as moulds (MDLCA 23867—23870) and one mould of a partially preserved tube (MDLCA 23871).

Locality and stratigraphy. Upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Fluminimaggiore, Sardinia, Italy.

Description. Small, almost straight tube without any attachment structures. Tube is 18—22 mm long and 2.3—3.2 mm wide. The tube increases relatively slowly in diameter with an apical angle about 8°. Tube

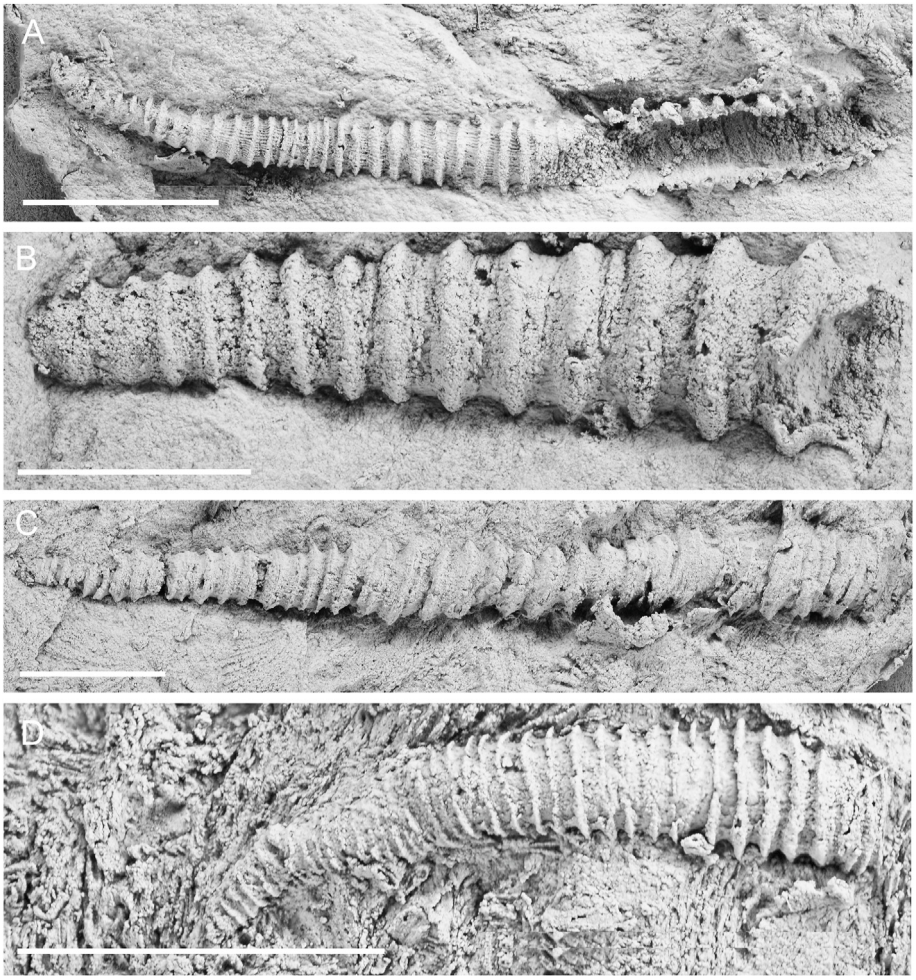

Fig. 5 **A)** *Cornulites* cf. *caputaquae* Vinassa de Regny, 1927 (MGM-8576O), lower half of the Estana Formation at locality VS/EST, about 1 km northeast of Alàs, Pyrenees, Spain; **B)** *Cornulites* cf. *costulatus* Meneghini (1857) (MGM-8577O), lower half of the Estana Formation at locality VS/EST, about 1 km northeast of Alàs, Pyrenees, Spain; **C)** *Cornulites shallochensis* Reed (1923) (MGM-8578O), "siltstone member" of the Cava Formation at locality CP/1, approximately 6 km northeast of La Seu d'Urgell, Pyrenees, Spain; **D)** *Cornulites* sp. A (MGM-8579O), lower half of the Estana Formation at locality VS/EST, about 1 km northeast of Alàs, Pyrenees. All specimens represent latex casts from original moulds whitened with ammonium chloride sublimated for photography. Scale bars all equal 5 mm.

is covered with prominent and regular annulation. The annuli are perpendicular to the tube's longitudinal axis and have regular shape. The annular crests are sharp. The slopes of annular crests are much steeper distally than proximally. The interspaces between annuli are deep and two to three times wider than annular crests. The interspaces are slightly concave. The tube exterior is covered with strong longitudinal striae. There are about eight striae per 1 mm near the tube aperture.

Remarks. Described specimens are assigned to *Cornulites fluminensis* Spano (1974) (pp. 194—195, pl. 2, figs. 3—5, pl. 3, fig. 1), from the Portixeddu Formation of the Upper Ordovician of Sardinia, because of similarly well-developed annuli with sharp crests, similarly long interspaces between annular crests, apical angle and interval of longitudinal striae. *Costatulites kimi* Ghavidel-Syooki *et al.*, (2015) is synonymized with *Cornulites fluminensis* because of similar shape, apical angle and identical external ornamentation. *Cornulites fluminensis* somewhat resembles *C. girvanensis* Reed (1923) (pp. 271—272, pl. 12, figs. 1—3) by its prominent annulation, but it has stronger striae and differs from the latter by the total lack of transverse growth lines and for the considerably smaller dimensions of the tube.

Occurrence. Ponte Amadori (Fluminimaggiore) and Punta Pedrona, the Portixeddu Formation, Upper Ordovician of the Sardinia and Seyahou formations (upper Katian) of Iran.

Cornulites sardous Vinassa de Regny, 1927 (Fig. 4A).

1927 *Tentaculites acuarius* var. *sardous* Vinassa de Regny, p. 425, pl. 2, fig. 10.

1974 *Cornulites sardous* Spano, pp. 191—193, pl. 3, figs. 2—5.

Material. A single partially preserved tube, preserved as a natural mould (MDLCA 23872).

Locality and stratigraphy. Upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Sardinia, Italy.

Description. Small, almost straight tube without any attachment structures. Tube is 1.8 mm wide. The tube is relatively slowly increasing in diameter with an apical angle of 8°. Tube is covered with prominent and almost regular annulation. The annuli are perpendicular to the tube's longitudinal axis and have regular shape. The annular crests are moderately sharp. The slopes of some annular crests are steeper distally than proximally. The interspaces between annuli are moderately deep and 1.5 to two times wider than annular crests. The interspaces are slightly concave. The tube exterior is covered with strong longitudinal striae. There are about ten striae per 1 mm near the tube aperture.

Remarks. The described specimen is assigned to *Cornulites sardous* Vinassa de Regny, 1927 (p. 425, pl. 2, fig. 10) from the Portixeddu Formation of the Upper Ordovician of Sardinia, because of their similar apical angle, similarly shaped annuli with moderately sharp crests, and similar interval of longitudinal striae. The Sardinian specimens resemble *C. camreganensis* Reed (1923) (p. 272, pl. XII, figs. 4, 5, 5a) in having prominent regular annuli, but differs clearly in the absence of fine transverse growth lines in the interspaces of annuli and in having prominent longitudinal striae.

Occurrence. Besides the studied locality this species occurs at Gutturu Mandara (close to Ponte Amadori) and Portixeddu, the Portixeddu Formation, Upper Ordovician of Sardinia.

Cornulites leonei sp. nov (Fig. 4B—E).

Diagnosis. Unattached, small, straight to gently curved tubes with an extremely small apical angle, prominent annuli, and sparse longitudinal striae.

Etymology. Named in honor of Professor Francesco Leone.

Type material. Three complete tubes preserved as a natural mould. Holotype MDLCA 23873 (Fig. 4B and C), paratypes MDLCA 23874 (Fig. 4D) and MDLCA 23875 (Fig. 4E).

Type locality and stratigraphy. Upper half of the Portixeddu Formation at locality CR/3, Punta Pedrona, Fluminimaggiore, Sardinia, Italy.

Description. Small, straight to gently curved tubes without any attachment structures. The tube is 32—37 mm long and with a diameter of 2.5—2.9 mm. The tube increases very slowly in diameter with an apical angle of 5°. The tube is covered with prominent and almost regular annulation. The annuli are usually perpendicular to the tube's longitudinal axis and have regular shape, but in some places, they can be slightly tilted or curved. The interspaces between annuli are deep and two to three times wider than the annular crests. The interspaces are flat to very gently concave. The tube exterior is covered with fine well developed longitudinal striae. There are six to eight striae per 1 mm near the tube aperture. The striae are often crossed by variably developed, irregular transverse growth lines. The tube interior shows strong annulation.

Remarks. The new species most closely resembles *Cornulites caputaquae* Vinassa de Regny, 1927 (p. 452, pl. 2, fig. 7) Spano (1974) (pl. 1, fig. 1, 1a) in its very small apical angle and relatively sparsely spaced annuli. However, it differs in having coarser and more sparsely spaced longitudinal striae and slightly longer distances between annular crests. *Cornulites leonei* sp. nov. also resembles *C. girvanensis* Reed (1923) (pp. 271—272, pl. 12, figs. 1—3) from the Llandovery of Scotland in its sparsely spaced annular crests and small apical angle, but differs in having the less ring-like annular crests.

Cornulites cf. *caputaquae* Vinassa de Regny, 1927 (Fig. 5A).

Material. A single, complete tube preserved as a mould (MGM-8576O).

Locality and stratigraphy. Lower half of the Estana Formation at locality VS/EST, about 1 km northeast of Alàs, Pyrenees, Spain.

Description. Small, straight, but proximally gently curved tube without any attachment structures. The tube is 20 mm long and the diameter of aperture is 2.0 mm. The tube increases very slowly in diameter with an apical angle of 5°. The tube is covered with prominent regular annulation. The annuli are always perpendicular to the tube's longitudinal axis and have regular shape. The slopes of annular crests are uniformly steep. The interspaces between annuli are deep and one to 1.5 times as wide as the annular crests. The interspaces are flat to slightly concave. The tube exterior is covered with well-developed, closely spaced longitudinal striae. There are 14 striae per 1 mm near the tube aperture. The striae are rarely crossed by a few variably developed, irregular transverse growth lines. The tube lumen also features weakly developed annulation.

Remarks. The described specimen is tentatively assigned to *Cornulites caputaquae* Vinassa de Regny, 1927 (p. 452, pl. 2, fig. 7) Spano (1974) (pl. 1, fig. 1, 1a) because of their similarities in very small apical angle and very closely spaced longitudinal striae. It is

only tentatively assigned to the species because it differs from the type material in having more regular and closely spaced annulation and we do not know how variable this character can be.

Cornulites cf. *costulatus* Meneghini (1857) (Fig. 5B).

Material. A single tube fragment (MGM-8577O).

Locality and stratigraphy. Lower half of the Estana Formation (Katian) at locality VS/EST, about 1 km northeast of Alàs, Pyrenees, Spain.

Description. Small, straight tube without any attachment structures. The diameter of the aperture is 4.3 mm. The tube increases moderately in diameter with an apical angle of 10°. The tube is covered with prominent regular ring-like annulation. The annuli are always perpendicular to the tube's longitudinal axis and have regular shape. The slopes of annular crests are uniformly steep. The interspaces between annuli are moderately deep and about 1.5 times as wide as the annular crests. The interspaces are flat.

Remarks. The described specimen is tentatively assigned to *Cornulites* cf. *costulatus* Meneghini (1857) (p. 90, pl. B, fig. 172a—b) from the Portixeddu Formation of the Upper Ordovician at Portixeddu (Marina di Fluminimaggiore), Sardinia, because of their similar apical angle and regular well-developed annulation. The strong longitudinal striae characteristic of *C. costulatus* are, however, lacking, which may be due to the poor state of preservation.

Cornulites shallochensis Reed (1923) (Fig. 5C).

Material. One complete tube preserved as a mould (MGM-8578O).

Locality and stratigraphy. "Siltstone member" of the Cavá Formation at locality CP/1, approximately 6 km northeast of La Seu d'Urgell, in the Pyrenees, Spain.

Description. Small, straight tube, 28 mm long and 3.2 mm wide at the aperture. The tube is covered with prominent, well-developed, and somewhat irregularly shaped annulations. The tube expands moderately in diameter. The apical angle is 9°. The dimensions of annuli increase somewhat irregularly with the growth of the tube. The crests of annuli are sharp and the interspaces between the annular crests are deep and slightly to strongly concave. The tube does not show attachment scars or widened tube base.

Remarks. The described specimen is assigned to *Cornulites shallochensis* Reed (1923) (p. 18, pl. 12, fig. 8, 8a) from the Whitehouse Group (Katian, Upper Ordovician) of Scotland, because of their similarly shaped annuli and a similar apical angle. The specimen also resembles *Cornulites* aff. *shallochensis* from the Hirnantian of Morocco (Gutiérrez-Marco and Vinn, 2018, p. 64, fig. 4D) in the shape of annuli but differs in its smaller size and slightly larger apical angle.

Occurrence. Besides the Pyrenean locality, this species occurs at Shalloch Mill the Whitehouse Group of Scotland and Portixeddu (Marina di Fluminimaggiore), the Portixeddu Formation, Upper Ordovician of Sardinia.

Cornulites sp. A (Fig. 5D).

Material. Single mould of almost complete tube (MGM-8579O).

Locality and stratigraphy. Lower half of the Estana Formation at locality VS/EST, about 1 km northeast of Alàs, Pyrenees, Spain.

Description. Small, slightly curved tube without any attachment structures. The tube is 11 mm long and the diameter of aperture is 1.9 mm. The tube increases moderately in diameter with an apical angle of about 10°. The tube is covered with fine regular annulation with sharp annular crests. The annuli are always perpendicular to the tube's longitudinal axis and have regular shape. The slopes of annular crests are uniformly steep. The interspaces between annuli are deep and about 1.5 times as wide as the annular crests. The interspaces are flat.

Remarks. The described specimen differs from all other Ordovician species of *Cornulites* by having very closely spaced annuli. There is a possibility that the specimen could have been compressed along its longitudinal axis.

6. Discussion

6.1. Palaeoecology

Seven distinct adaptive strategies have been described in the encrusting tentaculitoid tubeworm (Vinn, 2010). The Sardinian and Pyrenean cornulitids are best classified as secondary free solitary soft-bottom dwellers that have a stratigraphic range from the Upper Ordovician to Lower Devonian (Vinn, 2010). They presumably represent an adaptation for living in environments with high sedimentation rates and limited availability of hard substrates. Their prominent annuli could have had a stabilizing function in the soft sediment that helped cornulitids to maintain a favorable position in the sediment to enable suspension feeding. It is possible that most members of Sardinian and Pyrenean cornulitid fauna were growing partially embedded in the soft sediment subperpendicular to the seafloor similarly to the recent polychaete serpulid *Ditrupa arietina* (ten Hove and Smith, 1990). The relatively small size of all Sardinian and Pyrenean

cornulitids could indicate that they were members of a phylogenetic lineage with small body size prevailing on the northern margin of Gondwana.

6.2. Diversity

The known Late Ordovician cornulitid diversity in Gondwana sectors ranges from two to seven species, all belonging to the genus *Cornulites* as similar *Conchicolites* does not have longitudinal striae. However, the genus *Cornulites* needs a revision, and it is possible that the Gondwanan cornulitids belong to a separate genus, or that there is more than one genus in the Upper Ordovician of Gondwana. Three species are known from Iberia (Verneuil and Barrande, 1855; this study) and a single cornulitid species "*Tentaculites anglicus*" has been described from Katian strata (Glauzy Formation, upper Berounian) of the Montagne Noire region of southeastern France (Dreyfuss, 1948). More recently, additional cornulitids from southeastern France were illustrated from the Montagne Noire (Glauzy Formation) by Colmenar *et al.* (2013, fig. 6S—6T) and from the Mouthoumet Massif (Gascagne Formation) by Álvaro *et al.* (2016, fig. 7i) in association with lower Katian (ca. Kal-2) brachiopods. The Late Ordovician cornulitids of the Czech Republic (Bohemia) are represented by two species, *Cornulites confertus* Barrande (1867) and *C. mescai* Prantl (1948) that were reported from different Sandbian to Katian formations, such as the Letná Formation (lower Berounian, upper Sandbian) and the Bohdalec Formation (upper Berounian, lower Katian) respectively. A single species *C. kimi* (= *C. fluminensis* Spano, 1974), occurs in the upper Katian of Iran (Ghavidel-Syooki *et al.*, 2015). There are two described species in the Upper Ordovician of Peru (Calapuja Formation, upper Sandbian; Vinn and Gutiérrez-Marco, 2016) and Morocco (Lower Second Bani Formation, Hirnantian; Gutiérrez-Marco and Vinn, 2018). In contrast, the Sardinian part of the Gondwana has a higher cornulitid diversity with seven species described from the Katian (upper Berounian to Kralodvorian) of Sardinia (Meneghini, 1857; Vinassa de Regny, 1927; Spano, 1974; this study). However, there is a possibility that some Sardinian species could represent morphotypes of a single morphologically variable species. The possibility of a study bias should also be considered, which could partially explain the higher diversity in the Upper Ordovician of Sardinia. Alternatively, unusually nutrient-rich waters may have supported the high diversity of suspension feeding cornulitids in that particular region, turning it into a hot spot for the group. On the one hand, the increase in diversity could be related to the Boda event, which allowed taxa typical from lower latitudes to expand

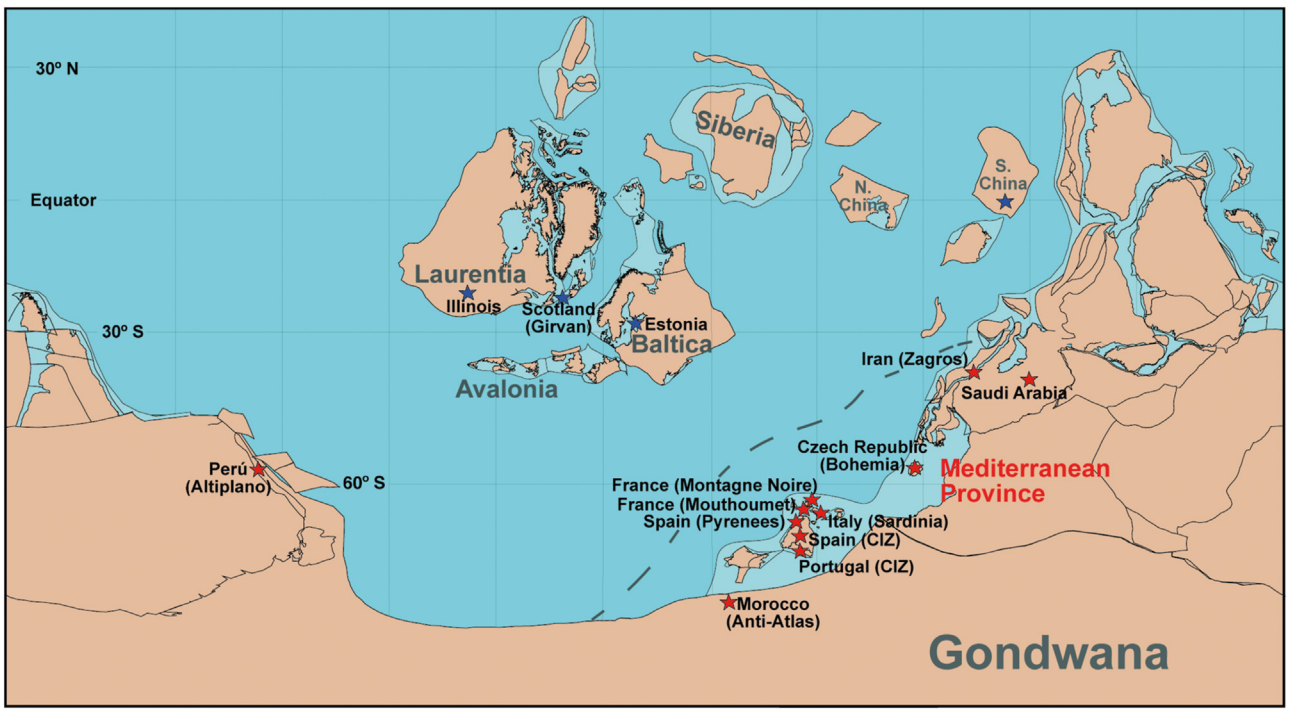

Fig. 6 Palaeogeography of Late Ordovician cornulitids. Red stars represent high-latitude fauna. Blue stars represent low-latitude fauna. Modified after Harper *et al.* (2013) and Colmenar (2015) and performed with BugPlates, using a Mollweide projection. Present-day outlines of lands and seas are shown on each continent to aid recognition. CIZ = Central Iberian Zone; N. China = North China; S. China = South China.

their geographical distribution to peri-Gondwana. On the other hand, the cornulitids in the Ordovician of Sardinia do not resemble any species known from the lower latitudes, such as in Baltica and Laurentia, and the "Boda event" corresponds to the carbonate levels higher in the succession, represented by the Punta S'Argiola Member of the Domusnovas Formation. There are mudstones in the Kralodvorian and sandstones in the upper Berounian, which more likely indicates the environmental preference of cornulitids rather than the evolution of the fauna. The diversity of cornulitids is unusually high only in the Kralodvorian (upper Katian), but in the Berounian of Sardinia, cornulitids are as diverse as or less diverse than in any other peri-Gondwanan sector. Nevertheless, it seems that diversity of cornulitids in Gondwana and related terranes during the Late Ordovician was predominantly low compared to the Laurentian (Hall, 1847, 1888) and Baltic records (Vinn, 2013; Vinn and Madison, 2017; Vinn *et al.*, 2023).

6.3. *Palaeobiogeography*

Fossil localities on the Mediterranean region, including those in Sardinia and Pyrenees, were located in high-latitude peri-Gondwana during the Late Ordovician (Harper *et al.*, 2013). The genus *Cornulites* had a relatively wide distribution in this realm, with records from Morocco, Spain (Verneuil and Barrande, 1855), Bohemia (Barrande, 1867), France (Dreyfuss, 1948), Sardinia (Spano, 1974), and Iran (Ghavidel-Syooki *et al.*, 2015). There are also listed occurrences in Saudi Arabia (Gutiérrez-Marco *et al.*, 2017) and Portugal (Silvério *et al.*, 2021) that potentially correspond to *Cornulites* (Fig. 6). A single record of the genus is known from the temperate region (Peru) of Gondwana (Vinn and Gutiérrez-Marco, 2016). Late Ordovician cornulitids from Sardinia and the Pyrenees do not resemble those from Laurentia (North America) (Hall, 1847, 1888; Meek and Worthen, 1865) and Baltica (Estonia) (Vinn, 2013; Vinn and Madison, 2017; Vinn *et al.*, 2023, 2024), likely due to a different palaeogeographic setting. On the contrary, there are strong taxonomic similarities between the cornulitid faunas of the high-latitude peri-Gondwana terranes. In addition to taxonomic similarities, cornulitids in high-latitude peri-Gondwana also shared ecological and morphological characteristics, such as domination by secondary free solitary soft-bottom dwellers and small body size, in addition to developing tubes with strikingly small apical angle. These demonstrate a certain degree of endemism for the group within this province, which is in line with what has been observed in other benthic groups (Gutiérrez-Marco *et al.*, 2017).

In Mediterranean localities, cornulitids never appear attached to strophomenids as commonly happen in Laurentia, which is remarkable, considering that similar strophomenids commonly occur in the same beds. There could be combined physiological and environmental factors behind this pattern. Seawater temperature, influenced by latitude and seasonal variations, plays a crucial role in shaping marine communities, including the composition of encrusting organisms (Vinagre *et al.*, 2020). It affects various aspects such as spawning, settlement, growth, and reproduction of organisms. Typically, encrustation rate rises with increasing temperature, leading to less encrustation in polar regions due to their lower temperatures (<5 °C). In these polar areas, encrustation primarily occurs during midsummer when temperatures are higher (Vinagre *et al.*, 2020). Conversely, in tropical to sub-tropical regions, encrustation tends to be more pronounced, as the warmer temperatures (>20 °C) support continuous reproduction throughout the year, fostering accelerated growth of encrusting organisms (Vinagre *et al.*, 2020), explaining the common cornulitid encrustation in Laurentia. Thus, the cold waters of high-latitude peri-Gondwana province may have inhibited encrustation. Moreover, encrusting life mode could have been energetically more costly for cornulitids than unattached life mode. In the latter case, cold waters of this province presumably did not provide cornulitids with enough energy for an encrusting life mode.

The Sandbian *Cornulites vilcae* Vinn and Gutiérrez-Marco, 2016 from Peru resembles *Cornulites shallochensis* Reed (1923) from the Pyrenees, which may indicate a palaeobiogeographic link along west-east peri-Gondwanan migration routes operating from intermediate to high palaeolatitudes during the Ordovician (Gutiérrez-Marco *et al.*, 1999). The cornulitid faunas of the Pyrenees and Sardinia also show some similarity to species described from the Upper Ordovician of Scotland (Reed, 1923), sharing the species *Cornulites shallochensis,* suggesting a palaeobiogeographic link between these two regions, perhaps related to the Late Ordovician 'provincial breakdown' (Fortey, 1984; Gutiérrez-Marco and Vinn, 2018), the reduction of endemism that culminated during the Boda event.

7. Conclusions

The Sardinian and Pyrenean cornulitids are best classified as secondary free solitary soft-bottom dwellers. Their prominent annuli could have had a stabilizing function in the soft sediment that helped cornulitids to maintain a preferred position in the sediment to enable suspension feeding. The known

Late Ordovician cornulitid diversity in Gondwanan sectors is lower compared to that in low-latitude faunas, represented by seven species of the single genus *Cornulites*. In most of the sectors there is only one to three species known, while in Sardinia the genus shows the greatest diversity, with seven species occurring. This can be related to a sampling bias, but some ecological advantage of this sector, like unusually nutrient-rich waters, cannot be excluded. The same endemism that characterizes other benthic groups during the Late Ordovician in this province can also be observed in the cornulitids. There is clearly a group of species restricted to the high-latitude peri-Gondwana province and they are characterized by occupying similar ecological niches. These species were dominated by secondary free solitary soft-bottom dwellers and also exhibit several morphological characteristics, such as a small body size and tubes with a strikingly small apical angle.

Funding

The financial supported was provided by a Sepkoski Grant from the Paleontological Society; King Saud University, Riyadh, Saudi Arabia, Researchers Supporting Project Number RSP 2024R140; and Project PDI 2021-125585NB-100 of the Spanish Ministry for Science Innovation (MICINN).

Availability of data and materials

Data supporting the findings of this study are available upon request from the corresponding author.

Author's contributions

All the authors have actively participated in the preparation of this manuscript. OV and JC conceived the conceptualization of the manuscript, and OV and JC wrote original draft. SZ, SP, GLP collected and organized the data. SZ, SP, GLP, AAA, SF and MH finished and revised the original version of the manuscript. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Authors want to acknowledge Prof. E. Villas for kindly providing the Pyrenean specimens. This is a contribution to Project PDI 2021-125585NB-100 of the Spanish MICINN.

References

Álvaro, J.J., Colmenar, J., Monceret, E., Pouclet, A., Vizcaïno, D., 2016. Late Ordovician (post-Sardic) rifting branches in the North Gondwanan Montagne Noire and Mouthoumet massifs of southern France. *Tectonophysics*, 681, 111—123.

Barrande, J., 1867. Système Silurien du Centre de la Bohême, 1ére Partie: Recherches Paléontologiques. *Texte et 16 Planches. Classe des Mollusques. Ordre des Ptéropodes. Chez l'auteur et éditeur, Prague*, III, 1—179.

Botquelen, A., Gourvennec, R., Loi, A., Pillola, G.L., Leone, F., 2006. Replacements of benthic associations in a sequence stratigraphic framework, examples from Upper Ordovician of Sardinia and Lower Devonian of the Massif Armoricain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239, 286—310.

Bouček, B., 1964. *The Tentaculites of Bohemia*. Published by the Czechoslovakian Academy of Sciences, Prague, pp. 1—125.

Cocco, F., Loi, A., Funedda, A., Casini, L., Ghienne, J.F., Pillola, G.L., Vidal, M., Meloni, M.A., Oggiano, G., 2023. Ordovician tectonics of the South European Variscan Realm: new insights from Sardinia. *International Journal of Earth Sciences*, 112(1), 321—344.

Colmenar, J., 2015. The arrival of brachiopods of the *Nicolella* Community to the Mediterranean margin of Gondwana during the Late Ordovician: palaeogeographical and palaeoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 428, 12—20.

Colmenar, J., Pereira, S., Pires, M., da Silva, C.M., Sá, A.A., Young, T.P., 2017. A Kralodvorian (upper Katian, Upper Ordovician) benthic association from the Ferradosa Formation (Central Portugal) and its significance for the redefinition and subdivision of the Kralodvorian Stage. *Bulletin of Geosciences*, 92, 443—464.

Colmenar, J., Villas, E., Vizcaïno, D., 2013. Upper Ordovician brachiopods from the Montagne Noire (France): endemic Gondwanan predecessors of prehirnantian low-latitude immigrants. *Bulletin of Geosciences*, 88, 153—174.

Dreyfuss, M., 1948. Contribution a l'étude géologique et paléontologique de l'Ordovicien Supérieur de la Montagne Noire. *Memoires de la Societe Geologique de France*, 58, 1—63.

Fisher, D.W., 1962. Small conoidal shells of uncertain affinities. In: Moore, C.D. (Ed.), *Treatise on Invertebrate*

Paleontology, Pt. W Miscellanea. Geological Society of America and University of Kansas Press, Lawrence, Kansas, pp. 130—143.
Fortey, R.A., 1984. Global earlier Ordovician transgressions and regressions and their biological implications. In: Bruton, D.L. (Ed.), *Aspects of the Ordovician System*, 295. Palaeontological Contributions from the University of Oslo, pp. 37—50.
Fortey, R.A., Cocks, L.R.M., 2005. Late Ordovician global warming — the Boda event. *Geology*, 33, 405—408.
Ghavidel-Syooki, M., Evans, D.H., Ghobadi Pour, M., Popov, L.E., Álvaro, J.J., Rakhmonov, U., Klishevich, I.A., Ehsani, M.H., 2015. Late Ordovician cephalopods, tentaculitides, machaeridians and echinoderms from Kuh-e Faraghan, High Zagros, Iran. *Alcheringa*, 39, 530—549.
Gutiérrez-Marco, J.C., Sá, A.A., García-Bellido, D., Rábano, I., 2017. The Bohemo—Iberian regional chronostratigraphic scale for the Ordovician System and palaeontological correlations within South Gondwana. *Lethaia*, 50, 258—295.
Gutiérrez-Marco, J.C., Vinn, O., 2018. Cornulitids (tubeworms) from the Late Ordovician Hirnantia fauna of Morocco. *Journal of African Earth Sciences*, 137, 61—68.
Gutiérrez-Marco, J.C., Rábano, I., Sarmiento, G.N., Aceñolaza, G., San José, M.A., Pieren, A.P., Couto, H.M., Picarra, J.M., 1999. Faunal dynamics between Iberia and Bohemia during the Oretanian and Drobotivian (late Middle—earliest Upper Ordovician), and biogeographic relations with Avalonia and Baltica. *Acta Universitas Carolinae, Geologica*, 43, 487—491.
Hall, J., 1847. Palaeontology of New York. In: *Containing Descriptions of the Organic Remains of the Lower Division of the New York System*, 1. Van Benthuysen, Albany, p. 338.
Hall, J., 1888. *Tubicolar Annelida. Natural History of New York, Palaeontology*, 7. Geological Survey, New York, pp. 1—278.
Hammann, W., 1992. The Ordovician trilobites from the Iberian Chains in the province of Aragón, NE Spain. The trilobites of the Cystoid Limestone (Ashgill Series). *Beringeria*, 6, 1—219.
Hammann, W., Leone, F., 1997. Trilobites of the post Sardic (Upper Ordovician) sequence of southern Sardinia Part 1. *Beringeria*, 20, 1—217.
Hamman, W., Leone, F., 2007. The trilobites from the 'post-Sardic' (Upper Ordovician) sequence of the Iglesiente, Arburese and Sarrabus region, southern Sardinia, Italy. Part II. *Beringeria*, 38, 1—138.
Harper, D.A.T., Rasmussen, C.M.Ø., Liljeroth, M., Blodgett, R.B., Candela, Y., Jin, J., Percival, I.G., Rong, J.Y., Villas, E., Zhan, R.B., 2013. Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods. In: Harper, D.A.T., Servais, T. (Eds.), *Early Palaeozoic Biogeography and Palaeogeography*, 38. Geological Society of London, Memoirs, pp. 127—144.
Hartevelt, J.J.A., 1970. Geology of the Upper Segre and Valira valleys, Central Pyrenees, Andorra/Spain. *Leidse Geologische Mededelingen*, 45, 167—236.
Havlíček, V., Kříž, J., Serpagli, E., 1987. Upper Ordovician Brachiopod Assemblages of the Carnic Alps, Middle Carinthia and Sardinia. *Bollettino della Società Paleontologica Italiana*, 25, 277—311.
Leone, F., Hammann, W., Serpagli, E., Villas, E., 1991. Lithostratigraphic units and biostratigraphy of the post-sardic Ordovician sequence in south-west Sardinia. *Bollettino della Società Paleontologica Italiana*, 30, 201—235.
Leone, F., Ferretti, A., Hammann, W., Loi, A., Pillola, G.L., Serpagli, E., 1998. Outline of the post-Sardic Ordovician sequence in south-western Sardinia. *Giornale di Geologia*, 60, 39—56.
Meek, F.B., Worthen, A.H., 1865. Descriptions of New Crinoidea, etc., from the Paleozoic Rocks of Illinois and some adjoining States. *Proceedings of Philadelphia Academy of Natural Sciences*, pp. 1—155.
Meneghini, G., 1857. *Paleontologie dell'île de Sardaigne ou description des fossils recueillis dans cette contrée par le Général A.* De Lamarmora. *Suite à la III partie du "Voyage en Sardaigne". de la Marmora, Paris* 1—90.
Musabelliu, S., Zatoń, M., 2018. Patterns of cornulitid encrustation on the Late Devonian brachiopod shells from Russia. *Proceedings of the Geologists' Association*, 129, 227—234.
Prantl, F., 1948. The genus *Conchicolites* Nicholson, 1872 (Serpulimorpha) in the Ordovician of Bohemia. *Věstník Královské české Společnosti nauk, Třída Matematicko-Přírodovědecká*, 1948—9, 1—7.
Puddu, C., Álvaro, J.J., Casas, J.M., 2018. The Sardic unconformity and the Upper Ordovician successions of the Ribes de Freser area, Eastern Pyrenees. *Journal of Iberian Geology*, 44, 603—617.
Reed, F.R.C., 1923. New fossils from Girvan. *Geological Magazine*, 60, 268—276.
Richards, P.R., 1974. Ecology of the Cornulitidae. *Journal of Paleontology*, 48, 514—523.
Sarmiento, G.N., Gutiérrez-Marco, J.C., Rodríguez-Cañero, R., Algarra, A.M., Navas-Parejo, P., 2011. A brief summary of Ordovician conodont faunas from the Iberian Peninsula. In: Gutiérrez-Marco, J.C., Rábano, I., García-Bellido, D. (Eds.), *Ordovician of the World*. Cuadernos del Museo Geominero, 14. Instituto Geológico y Minero de España, Madrid, pp. 505—514.
Schlotheim, E.F., 1820. *Die Petrefaktenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner sammlung versteinerter und fossiler Überreste des I- und Planzenreichs erläutert*. Becker'sche Buchhandlung, Gotha, pp. 1—437.
Silvério, G., Pereira, S., Moreira, N., Piçarra, J., Machado, G., 2021. Tentaculites e cornulitídeos de Portugal: revisão bibliográfica e museulógica. *Comunicações Geológicas*, 108, 153—158.
Spano, C., 1974. Tentaculita dell'Ordoviciano della Sardegna. *Rendiconti del Seminario della Facoltà di Scienze dell'Università di Cagliari*, 44, 187—204.
Taylor, P.D., Wilson, M.A., 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, 62, 1—103.
Taylor, P.D., Vinn, O., Wilson, M.A., 2010. Evolution of biomineralization in 'lophophorates'. *Special Papers in Palaeontology*, 84, 317—333.
Teichmüller, R., 1931. Alte und junge Krustenbewegungen im südlichen Sardinien (Zur Geologie des

Thyrrhenisgebietes). *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen, Mathematisch-Physikalische Klasse Folge*, 3, 857—950.

ten Hove, H.A., Smith, R.S., 1990. A re-description of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a discussion of the genus. *Records of the Australian Museum*, 42, 101—118.

Verneuil, E. de, Barrande, J., 1855. Descriptions des fossiles trouvés dans les terrains Silurien et Dévonien d'Almaden, d'une partie de la Sierra Morena et des Montagnes de Tolède. *Bulletin de la Societe Geologique de France*, 12, 964—1025.

Vinagre, P.A., Simas, T., Cruz, E., Pinori, E., Svenson, J., 2020. Marine biofouling: A European database for the marine renewable energy sector. *Journal of Marine Science and Engineering*, 8(7), 495. https://doi.org/10.3390/jmse8070495.

Vinassa de Regny, P., 1927. Fossili Ordoviciani Sardi, Parte I. *Memoire della Regia Accademia Nazionale dei Lincei, Classe di Scienze Fisiche*, 2, 437—496.

Vinn, O., 2010. Adaptive strategies in the evolution of encrusting tentaculitoid tubeworms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 211—221.

Vinn, O., 2013. Cornulitid tubeworms from the Ordovician of eastern Baltic. *Carnets de Géologie*, 13, 107—114.

Vinn, O., Gutiérrez-Marco, J.C., 2016. New Late Ordovician cornulitids from Peru. *Bulletin of Geosciences*, 91, 89—95.

Vinn, O., Madison, A., 2017. Cornulitids from the Upper Ordovician of northwestern Russia. *Carnets de Géologie*, 17, 235—241.

Vinn, O., Mutvei, H., 2009. The calcareous tubeworms of the Phanerozoic. *Estonian Journal of Earth Sciences*, 58, 286—296.

Vinn, O., Zatoń, M., 2012. Phenetic phylogenetics of tentaculitoids — extinct problematic calcareous tube-forming organisms. *GFF*, 134, 145—156.

Vinn, O., Madison, A., Wilson, M.A., Toom, U., 2023. Cornulitid tubeworms and other calcareous tubicolous organisms from the Hirmuse Formation (Katian, Upper Ordovician) of northern Estonia. *Journal of Paleontology*, 97, 38—46.

Vinn, O., Wilson, M.A., Madison, A., Toom, U., 2024. Small cornulitids from the Upper Ordovician (Katian) of Estonia. *Palaeoworld*, 33, 57—64.

Zhan, R., Vinn, O., 2007. Cornulitid epibionts on brachiopod shells from the Late Ordovician (middle Ashgill) of East China. *Estonian Journal of Earth Sciences*, 56(2), 101—108.

Zatoń, M., Borszcz, T., 2013. Encrustation patterns on post-extinction early Famennian (Late Devonian) brachiopods from Russia. *Historical Biology*, 25, 1—12.

Zatoń, M., Vinn, O., Tomescu, M., 2012. Invasion of freshwater and variable marginal marine habitats by microconchid tubeworms — an evolutionary perspective. *Geobios*, 45, 603—610.

Zatoń, M., Wilson, M.A., Vinn, O., 2016. Comment on the paper of Gierlowski-Kordesch and Cassle "The '*Spirorbis*' problem revisited: sedimentology and biology of microconchids in marine—nonmarine transitions". *Earth-Science Reviews*, 152, 198—200.

Zatoń, M., Borszcz, T., Rakociński, M., 2017. Temporal dynamics of encrusting communities during the Late Devonian: a case study from the Central Devonian Field, Russia. *Paleobiology*, 43, 550—568.