

Conulariids from the Lower Ordovician of the southern Montagne Noire, France

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The Tremadocian–Floian (Lower Ordovician) Saint-Chinian, La Maurerie, and Landeyran formations of the southern Montagne Noire (France) collectively contain at least two species of conulariids, namely *Archaeoconularia* cf. *insignis* and *Conularia azaisi*, the latter herein designated as the type species of the new genus, *Galliconularia*. *Archaeoconularia insignis* may also occur in the Lower Ordovician Fezouata Shale of southern Morocco, and an indeterminate species of this genus probably occurs in the Lower Ordovician Tonggao Formation of South China. *Galliconularia azaisi* differs from all other conulariids in having a raised facial midline and very fine, trochoidal transverse ribs which cross the midline ridge without interruption or diminution. In specimens preserving the outermost peridermal lamellae, the transverse ribs bear sub-microscopic nodes, and the broad interspaces are crossed by very slender interspace ridges. Finally, even though the Montagne Noire was part of the western Gondwanan passive margin during Cambro-Ordovician times, *G. azaisi* remains unknown outside of France.

Key words: Cnidaria, Scyphozoa, Conulariida, Paleozoic, Gondwana, Europe.

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Introduction

Current knowledge of the fossil record of conulariids, coupled with the results of cladistic analyses of the phylogenetic relationships among genera within this extinct group of medusozoan cnidarians, imply that at least some of these genera diverged from each other during the Neoproterozoic Era (Van Iten et al. 2014, 2016a, b). However, the first appearance of diverse conulariids occurs within strata of the Lower Ordovician Series. In contrast to the underlying Cambrian System, which thus far has yielded only one genus of definite conulariid (Hughes et al. 2000; Van Iten et al. 2006; see however Guo et al. 2020 for a mention of *Conulariella* Bouček, 1928 from the Cambrian Fortunian Stage of China), Tremadocian–Floian strata collectively contain at least five genera, namely *Archaeoconularia* Bouček, 1928 (= *Exoconularia* Sinclair, 1952; Van Iten et al. 2020), *Conularia* Miller in Sowerby, 1821, *Conulariella*, *Eoconularia* Sinclair, 1943, and *Teresconularia* Leme, Heredia, Rodrigues, Simões, Aceñolaza, and Milana, 2003 (Van Iten et al. 2016b). Most of the currently known occurrences of these genera are in Core Gondwana (Argentina

and Morocco) or in peri-Gondwanan areas (Bohemia, South China, and Wales). Additionally, Lower Ordovician strata in the southern Montagne Noire (France; Fig. 1), which was then part of the Gondwanan passive margin at high southern latitudes (Matte 2001; Nysaether et al. 2002; Ballèvre et al. 2009; Álvaro et al. 2013), have yielded rare specimens of a conulariid originally named *Conularia azaisi* Thoral, 1935. Subsequently, this species was variously assigned to the genera *Eoconularia* (e.g., Capéra et al. 1978; Vizcaíno et al. 2001) or *Paraconularia* Sinclair, 1940 (Leme et al. 2003). Most recently, Van Iten et al. (2016b) argued that *C. azaisi* probably belongs to a separate yet undescribed genus.

In the present paper we erect the new, monotypic genus, *Galliconularia*, with the type species *Conularia azaisi*, to accommodate specimens previously named *C. azaisi*, *Eoconularia azaisi*, or *Paraconularia azaisi*. Along with this material our paradigm also includes specimens originally labelled as *Conularia* sp. indeterminate or ?*Eoconularia* sp. and reposed in the palaeontological collections of Lyon and Montpellier universities, France (see below). In addition to erecting a new taxon, we describe *Archaeoconularia* cf. *insignis* (Barrande, 1867) from the late Floian Landeyran

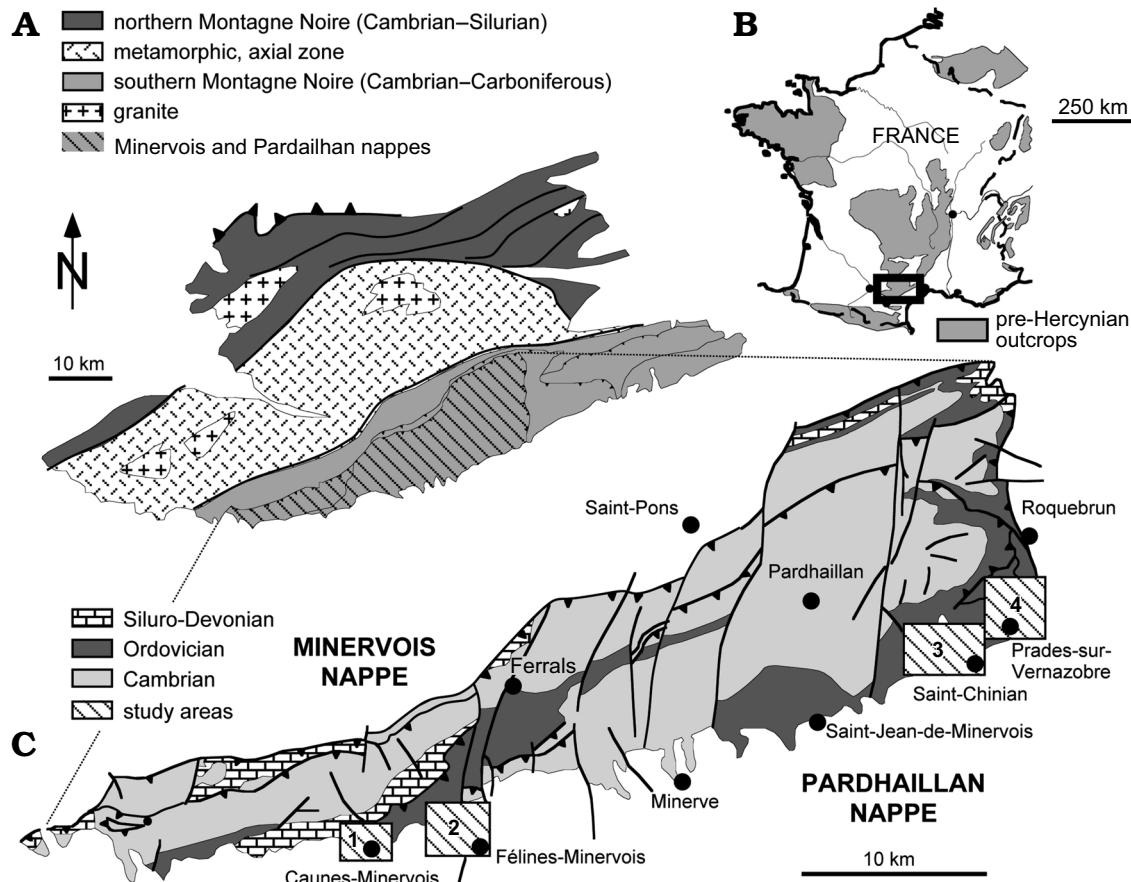


Fig. 1. Geology of the Montagne Noire with conulariid localities. **A.** Geologic sketch of the Montagne Noire. **B.** Geologic sketch of France showing the pre-Hercynian rocks and the location of the Montagne Noire (rectangle). **C.** Simplified geological map of the Minervois and Pardailhan nappes, southern Montagne Noire, with the four main areas yielding Lower Ordovician conulariids (dashed square boxes); 1, western Minervois area, Aude (ruisseau des Lavandières, vallée de l'Ourdiveille); 2, eastern Minervois area, Aude (Brama, vallée du Merlaux); 3, western Saint-Chinianais area, Hérault (Canimalis, Donnadieu, Saint-Cels); 4, eastern Saint-Chinianais area, Hérault (Pech Tavernier, les Rocs Nègres, la Rouvelane, les Sources du Foulon). Maps redrawn and modified from Guérangé-Lozes and Burg (1990) and Álvaro and Vizcaíno (2001).

Formation, which has also yielded the medusozoan genus *Sphenothonthallus* (Van Iten et al. 2016b). This is the first report of *Archaeoconularia* in the Montagne Noire. This genus was previously known from the Lower Ordovician of Core Gondwana, Avalonia, and Perunica (Van Iten et al. 2016b).

Institutional abbreviations.—MNHN, Muséum National d'Histoire Naturelle, Paris, France; UCBL-FSL, Lyon 1 University, Villeurbanne, France; UM.ACI, Montpellier University, France.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:D166F2F7-BAFB-4F13-A8D7-5E971383B610

Geological setting

The small amount of available material of *Galliconularia azaisi* (just 32 specimens collected since the mid 19th century) suggests that it is a relatively rare fossil in the Lower

Ordovician of the Montagne Noire. The locality details and stratigraphic positions of most specimens collected between 1850 and 1930 (Azaïs, Lignières, and Villebrun collections) are not known precisely (“Lower Ordovician of Saint-Chinian area”; see Appendix 1). However, the lithologic features of the rocks in which they are preserved make it possible to assign all of them relatively confidently either to the late Tremadocian Saint-Chinian Formation or to the lower part of the early Floian La Maurerie Formation (i.e., the *Euloma filacovi* and *Taihungshania miqueli* trilobite zones; Fig. 2). In contrast, the localities and stratigraphic positions of all specimens of *G. azaisi* collected between 1980 and 2015 (Monceret and Vizcaíno collections) are known precisely (see Appendix 1; Fig. 1). This new material confirms that *G. azaisi* occurs mainly in the Saint-Chinian Formation (mostly in the *Euloma filacovi* Zone) and that it is far less common in the overlying La Maurerie Formation (Fig. 2). In both rock units, specimens of *G. azaisi* are preserved in dark shale or siliceous concretions.

The stratigraphy and palaeontology of the two formations yielding *G. azaisi* have been thoroughly investigated and regularly updated since the early 20th century (see e.g.,

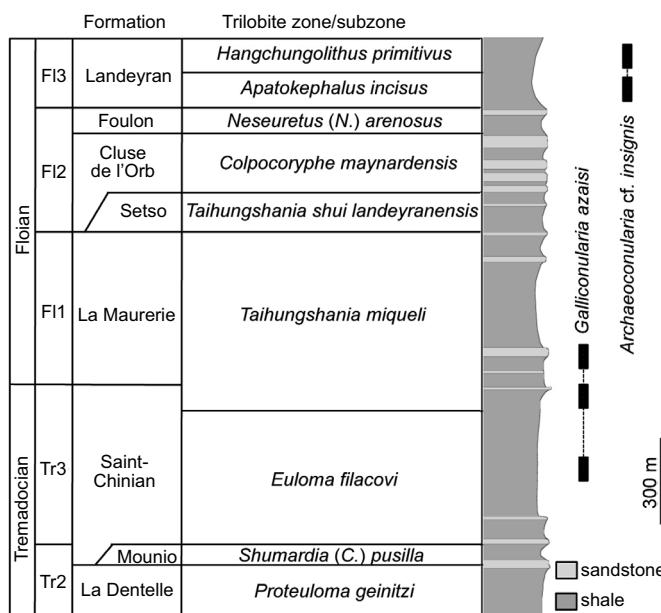


Fig. 2. Stratigraphic range of conulariids in the Lower Ordovician of the southern Montagne Noire. Stratigraphic column redrawn and modified from Courteille et al. (1983). Stratigraphy based on Vizcaíno et al. (2001), Álvaro and Vizcaíno (2003), Tortello et al. (2006), and Serpagli et al. (2007).

Miquel 1912; Thoral 1935; Capéra et al. 1978; Courteille et al. 1981, 1983, 1985; Vizcaíno et al. 2001; Vizcaíno and Álvaro 2003; Tortello et al. 2006; Serpagli et al. 2007). The Saint-Chinian Formation is ~600 m thick and consists mostly of claystone and siltstone with thin beds of sandstone, abundant trace fossils, and numerous fossiliferous concretions. This formation has yielded particularly abundant and diverse invertebrate assemblages dominated by trilobites but also containing various brachiopods, echinoderms, graptolites, hyolithids, machaeridians, and molluscs (Thoral 1935; Capéra et al. 1978; Babin et al. 1982; Courteille et al. 1983; Vidal 1996; Vizcaíno and Lefebvre 1999; Vizcaíno et al. 2001; Vizcaíno and Álvaro 2003; Kröger and Evans 2011). The Saint-Chinian Formation is generally interpreted as consisting of relatively deep shelf deposits that were formed at or slightly below storm-wave base (Vidal 1996; Vizcaíno and Lefebvre 1999; Vizcaíno et al. 2001; Lefebvre 2007).

The overlying La Maurerie Formation is ~400 m thick and consists of numerous thick sandstone beds intercalated within shales bearing fossiliferous concretions. This unit has yielded abundant fossil remains, though these are less diverse than those in the Saint-Chinian Formation. Assemblages are dominated by molluscs and trilobites associated with various brachiopods, echinoderms, graptolites, and machaeridians (Thoral 1935; Capéra et al. 1978; Babin et al. 1982; Courteille et al. 1983; Vizcaíno et al. 2001; Vizcaíno and Álvaro 2003; Kröger and Evans 2011). Strata of the La Maurerie Formation are generally interpreted as shallower in origin than those of the Saint-Chinian Formation, having been deposited at or slightly above storm-wave base (Noffke and Nitsch 1994; Vizcaíno and Lefebvre 1999; Vizcaíno et al. 2001; Vizcaíno and Álvaro 2003; Kröger and Evans

2011). No conulariid remains have been reported so far from the overlying Setso, Cluse de l'Orb, and Foulon formations (Fig. 2; Vizcaíno et al. 2001), all characterized by shallower, storm-dominated deposits (Courteille et al. 1985).

The occurrence of conulariids referred to *Conularia* cf. *azaisi* in the lower part of the Landeyran Formation (*Apatokephalus incisus* Zone, late Floian) has been regularly mentioned in the literature since its first report by Dean (1966) in a faunal list (see e.g., Capéra et al. 1978; Vizcaíno et al. 2001; Van Iten et al. 2016b). New specimens collected in the 2000s (Kundura collection) confirm the occurrence of conulariids in the lower part of the Landeyran Formation and also extend their stratigraphic range into the upper part of the same unit (*Hangchungolithus primitivus* Zone, late Floian). Their geographic origin and stratigraphic position are known precisely (see Appendix 1). However, all specimens collected in the Landeyran Formation are assigned herein to *Archaeoconularia* cf. *insignis*. Their limited number, in spite of intensive quarrying in Dean's original sections during the past 50 years, suggests that they were originally relatively uncommon members of the faunal assemblages.

The Landeyran Formation is a 200–400 m thick lithostratigraphic unit consisting of concretion-bearing dark shale conformably overlying the sandstone and shaly sandstone of the underlying Foulon Formation (Capéra et al. 1978; Vizcaíno et al. 2001). The Landeyran Formation has yielded particularly abundant and diverse faunal assemblages dominated by trilobites but also comprising annelids, brachiopods, echinoderms, graptolites, hyolithids, molluscs, and ostracods (Dean 1966; Capéra et al. 1978; Babin et al. 1982; Courteille et al. 1983; Vizcaíno and Lefebvre 1999; Vizcaíno et al. 2001; Vizcaíno and Álvaro 2003). These assemblages are characterized by the re-occurrence of various taxa (e.g., raphiophorid trilobites and stylophoran echinoderms) which are absent in the underlying Cluse de l'Orb and Foulon formations but are present in the Saint-Chinian and La Maurerie formations (Courteille et al. 1991; Henry and Vizcaíno 1996; Vizcaíno and Lefebvre 1999). This pattern, which is also exhibited by the conulariids, is in good agreement with the interpretation of the Landeyran Formation as a transgressive unit consisting of relatively distal facies deposited at or below storm-wave base and thus comparable in origin to the Saint-Chinian and La Maurerie formations (Vizcaíno et al. 2001; Vizcaíno and Álvaro 2003; Bonin et al. 2007).

Material and methods

The present report is based on examination of 32 specimens of *Galliconularia azaisi* and four specimens of *Archaeoconularia* cf. *insignis* collectively reposited in the palaeontological collections of Lyon 1 University (France), Montpellier University (France), and the Muséum National d'Histoire Naturelle, Paris (France). The Montpellier spec-

imens were collected in the late 19th and early 20th centuries (Azaïs and Villebrun collections) and correspond to the original material described by Thoral (1935). The Lyon material includes some samples from “old” collections (Lignières and Villebrun collections) but is mostly composed of specimens collected in the late 20th and early 21st centuries (Monceret and Vizcaïno collections). The Paris material consists entirely of specimens collected in the 2000s (Kundura collection).

All of the specimen photographs in this paper are of high-resolution latex casts whitened with ammonium chloride. The photographs were taken with a Canon 5DSR camera mounted with an MP-E 65 mm or 100 mm macro lens.

In addition to examining the material from the southern Montagne Noire, the senior author also examined specimens of *Archaeoconularia* from the Ordovician of Bohemia and reposed in the paleontological collections of the National Museum of Natural History of the Czech Republic in Prague.

Systematic palaeontology

Phylum Cnidaria Verrill, 1865

Subphylum Medusozoa Peterson, 1979

Class Scyphozoa Götte, 1887

Order Conulariida Miller and Gurley, 1896

Genus *Archaeoconularia* Bouček, 1939

Type species: *Archaeoconularia insignis* (Barrande, 1867), Bohemia (Czech Republic), Lower–Upper Ordovician.

Archaeoconularia cf. *insignis* (Barrande, 1867)

Fig. 3.

1966 *Eoconularia?* cf. *azaisi* (Thoral, 1935); Dean 1966: 271.

1978 *Eoconularia* cf. *azaisi* (Thoral, 1935); Capéra et al. 1978: 75.

2001 *Eoconularia* cf. *azaisi* (Thoral, 1935); Vizcaïno et al. 2001: 219, fig. 3.

2016 *Conularia* cf. *azaisi* Thoral, 1935; Van Iten et al. 2016b: 171, table 1.

Material.—Four specimens from the late Floian Landeyran Formation: NHN.F.A71848a, b, A71849, and A71850 from the *Apatokephalus incisus* Zone; les Sources du Foulon, Cessenon, Hérault; MNHN.F.A71851a, b, from the *Hang-chungolithus primitivus* Zone; les Rocs Nègres, Causses-et-Veyran, Hérault. All Montagne Noire, France.

Description.—Most complete specimen (MNHN.F.A71851a, b; Fig. 3A, 3B, respectively) flattened, lacking the apertural margin but terminating at the apical end in a crumpled schott (apical wall; Fig. 3A₂), measuring approximately 31 mm in length, with a maximum single face width of approximately 10 mm and a minimum single face width of approximately 0.5 mm. Faces approximately equal in width, with the corners bounding a given face diverging from each other at approximately 20°. Midline sulcus appears to be deeper than

the corner sulcus; both the midline sulcus and the corner sulcus simple (without internal carina or other thickening). Minute, circular to subcircular nodes (Fig. 3B₂) on the faces arranged in gently arching, bell-curve-shaped transverse rows and less distinct longitudinal files, with approximately 15–20 transverse rows per mm and approximately 15 longitudinal files per mm.

Remarks.—Of all previously described species of *Archaeoconularia* (Barrande 1867; Slater 1907; Bouček 1928, 1939; Reed 1933; Sinclair 1943; Sayar 1964; Van Iten et al. 2020), the four incomplete specimens here described from the Landeyran Formation appear to be most similar to *A. insignis*, a species with relatively small nodes (12–30 per mm; Bouček 1928) that occurs in the late Tremadocian (Lower Ordovician) Mílina Formation of Perunica (Czech Republic; Van Iten et al. 2016b). Both the French specimens and *A. insignis* are also similar to specimens identified as *Archaeoconularia* sp. from the late Tremadocian–middle Floian (Lower Ordovician) Fezouata Shale of southern Morocco (Van Iten et al. 2016b) and may be conspecific with them. Like the material from the Landeyran Formation, the Fezouata Shale specimens occur in pale green-brown or pale gray-green mudstone. Additionally, a single specimen illustrated by Van Iten et al. (2013: fig. 3b) from pale green-grey shale in the early Floian (Lower Ordovician) Tonggao Formation of South China, and identified by these authors as “Conulariid sp. and gen. indeterminate” (Van Iten et al. 2013: 719), closely resembles deeply exfoliated specimens of *A. exquisita* from the Middle or Upper Ordovician of Bohemia (see in particular Bouček 1928: pl. 2: 7); therefore it is probably a specimen of *Archaeoconularia*. In sum, then, *A. insignis* or a species closely related to it appears to be present both in the Lower Ordovician of Morocco and the southern Montagne Noire (Gondwana), and *Archaeoconularia* is also present in the Lower Ordovician of Perunica, Avalonia, and, probably, South China. Collectively, these five Early Ordovician areas spanned a broad range of palaeolatitudes extending from near the South Pole to the southern subtropics (see Van Iten et al. 2013: fig. 5).

Genus *Galliconularia* nov.

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Type species: *Conularia azaisi* Thoral, 1935, by monotypy see below.

Etymology: From the Latin *gallicus*, meaning of or pertaining to Gaul or France, and *Conularia*.

Diagnosis.—As for the type species by monotypy.

Remarks.—*Galliconularia* is a highly distinctive genus, the most conspicuous characteristic of which is the presence of a broadly elevated facial midline together with very fine, trochoidal transverse ribs which are continuous across this feature. Additional notable features of the new genus are the presence on or within the faces of accessory longitudinal furrows or ridges (“filets”; Thoral 1935: 160) and (at least in some specimens) minute nodes and interspace ridges.

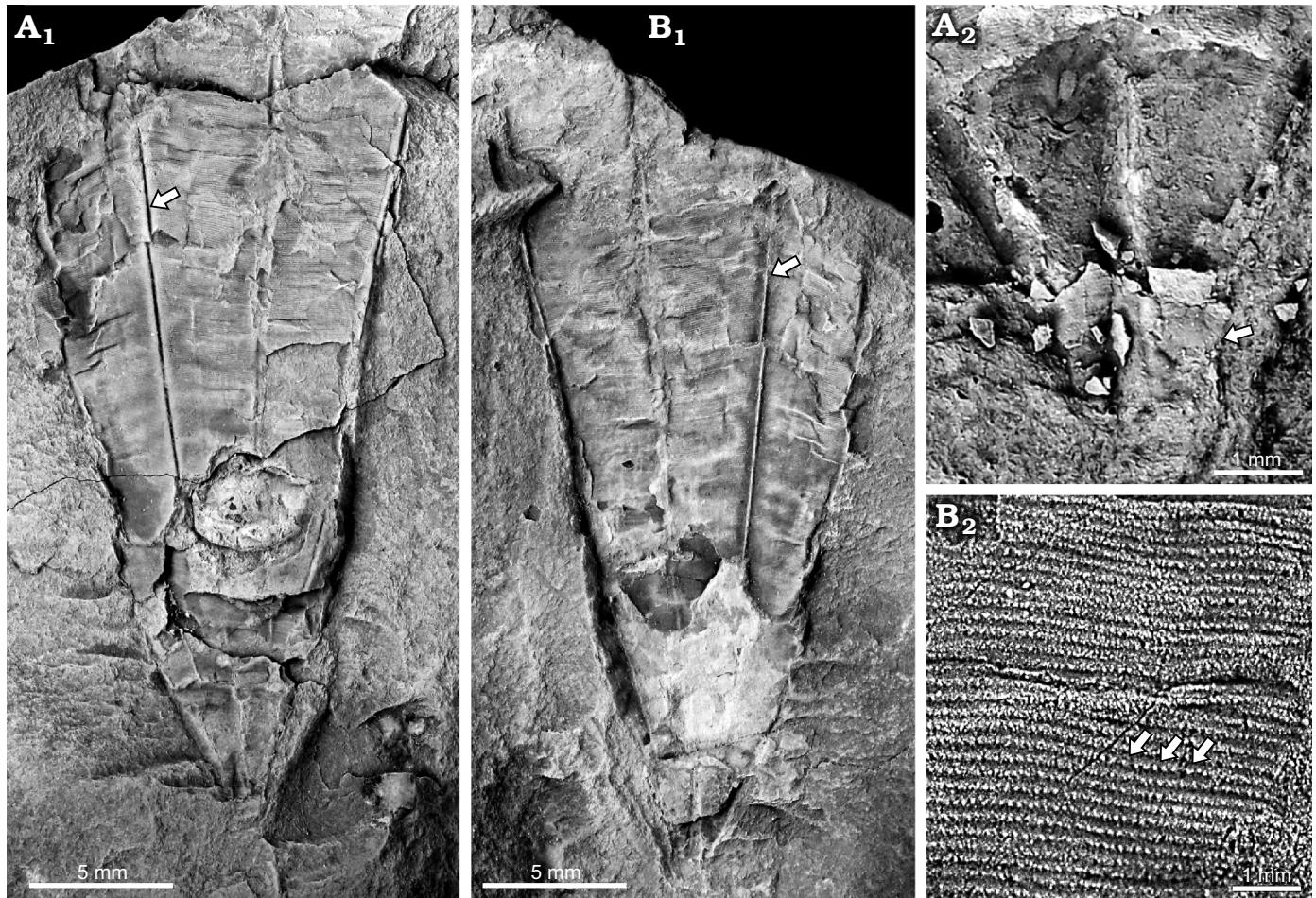


Fig. 3. Conulariid scyphozoan *Archaeoconularia* cf. *insignis* (Barrande, 1867), Landeyran Formation, upper Floian, Lower Ordovician; southern Montagne Noire, France. Specimens oriented with the apertural end directed toward the top of the page; arrows in A₁ and B₁ point to a facial midline. A. The two exposed faces of the part of the most complete specimen (MNHN.F.A71851a), which terminates in a crumpled schott (A₁). Detail of the part, arrow pointing to the crumpled terminal schott (A₂). B. The counterpart of the specimen in A (MNHN.F.A71851b) (B₁). Detail of the apertural region of the counterpart, showing the fine ornament including some of the most clearly defined nodes (arrows) (B₂).

Only three previously described genera, *Climacoconus* Sinclair, 1942, *Pseudoconularia* Bouček, 1928, and *Reticulaconularia* Babcock and Feldmann, 1986, share with *Galliconularia* the presence of an external midline ridge (see e.g., Van Iten et al. 2000, 2020). Unlike *Galliconularia*, however, *Pseudoconularia* lacks transverse ribs and its nodes are elongate and coarse, and the transverse ribs of *Climacoconus* and *Reticulaconularia* are coarse and usually alternate along the facial midline (see e.g., Sinclair 1942: pl. 3: 7). Moreover, no other genus or species exhibits trochoidal transverse ribs as fine as those of *Galliconularia*, though the pattern of arrangement of its tiny nodes and interspace ridges is similar to that of certain species in *Conularia* and *Paraconularia*. Superficially, specimens of *G. azaisi* exhibiting narrow longitudinal ridges or furrows coupled with adapical recurvature (scalloping) of the transverse ribs (Fig. 4E) resemble the faces of *Glyptoconularia* Sinclair, 1952, which bears a distinctive ornament consisting of longitudinal files of short, straight, or adaperturally arching transverse ridges collectively resembling chain mail (Van Iten 1994). The

fine longitudinal ridges are also similar to the “accessory longitudinal lines” (Sinclair 1952: 139) commonly seen in specimens in the genus *Archaeoconularia*. Owing in part to deformation of available specimens of *Galliconularia*, it is difficult to discern details of the anatomy of the corner sulcus. Nevertheless, it appears that like *Conularia* Sinclair, 1942, *Eoconularia*, and *Glyptoconularia*, *Galliconularia* exhibits termination or severe diminution of the transverse facial ornament in or near the corner sulcus. Importantly, Van Iten et al. (2016b: 1) interpreted this similarity as a non-homoplasic synapomorphy uniting these four taxa in a single, monophyletic group that excludes other conulariids. *G. azaisi* (shown in the cladogram of Van Iten et al. 2016b as “*Eoconularia*” *azaisi*) is the basalmost taxon of this fully resolved clade. According to the phylogenetic analysis of Van Iten et al. (2016b), the midline ridge was derived independently in *Galliconularia* (coded as *Conularia azaisi*), *Pseudoconularia*, and the minor clade consisting of *Climacoconus* and *Reticulaconularia*. Trochoidal transverse ribs, a primitive feature present in *Galliconularia*,

Conulariella, and many other conulariids, were lost in at least two lineages, including the lineage leading to the most recent common ancestor of *Conularina* and *Eoconularia*. However, Van Iten et al. (2016b) also scored *G. azaisi* as lacking nodes and interspace ridges, features which were detected in two specimens assigned to this species in the present study. Therefore, the phylogenetic relationships of *G. azaisi* to other conulariids should be reanalyzed based on the new anatomical data revealed by the present study.

Galliconularia azaisi (Thoral, 1935) comb. nov.

Fig. 4.

1912 *Conularia* nova sp.; Miquel 1912: 20.

1935 *Conularia azaisi* Thoral, 1935; Thoral 1935: 159, pl. 11: 7–9, pl. 15: 11a, b.

not 1966 *Eoconularia?* cf. *azaisi* (Thoral, 1935); Dean 1966: 271.

1978 *Eoconularia azaisi* (Thoral, 1935); Capéra et al. 1978: 73.

not 1978 *Eoconularia* cf. *azaisi* (Thoral, 1935); Capéra et al. 1978: 75.

2001 *Eoconularia azaisi* (Thoral, 1935); Vizcaíno et al. 2001: 219, fig. 3.

not 2001 *Eoconularia* cf. *azaisi* (Thoral, 1935); Vizcaíno et al. 2001: 219, fig. 3.

not 2001 *Eoconularia azaisi* (Thoral, 1935); Álvaro et al. 2001: 228.

2004 *Eoconularia azaisi* (Thoral, 1935); Van Iten and Vhylasová 2004: 122.

2003 *Paraconularia azaisi* (Thoral, 1935); Leme et al. 2003: 270, fig. 5.

2016 *Conularia azaisi* Thoral, 1935; Van Iten et al. 2016b: 171, table 1.

not 2016 *Conularia* cf. *azaisi* Thoral, 1935; Van Iten et al. 2016b: 171, table 1.

Type material: Thoral's (1935) four syntypes: UM.ACI.416 (Thoral 1935: pl. 15: 11a, b), UM.ACI.645 (Thoral 1935: pl. 11: 7), UM.ACI.646 (Thoral 1935: pl. 11: 9), and UM.ACI.647 (Thoral 1935: pl. 11: 8). A specimen deposited in the palaeontological collections of western Brittany, Brest, France (LPB 10777) was erroneously mentioned as the holotype of *Eoconularia azaisi* by Álvaro et al. (2001). This specimen is instead a bivalve (*Eopteria crassa* [Thoral, 1935]) from the Lower Ordovician of the Montagne Noire (Muriel Vidal, personal communication 2018).

Type locality: Saint-Chinian, Hérault, France.

Type horizon: *Euloma filacovi* Trilobite Zone, Saint-Chinian Formation, upper Tremadocian, Lower Ordovician.

Material.—28 specimens: UM.ACI.654–656 and 658; UCBL-FSL 133604–133610, 712799, and 713214–713229; from Lower Ordovician of Montagne Noire, France, for details see Appendix 1.

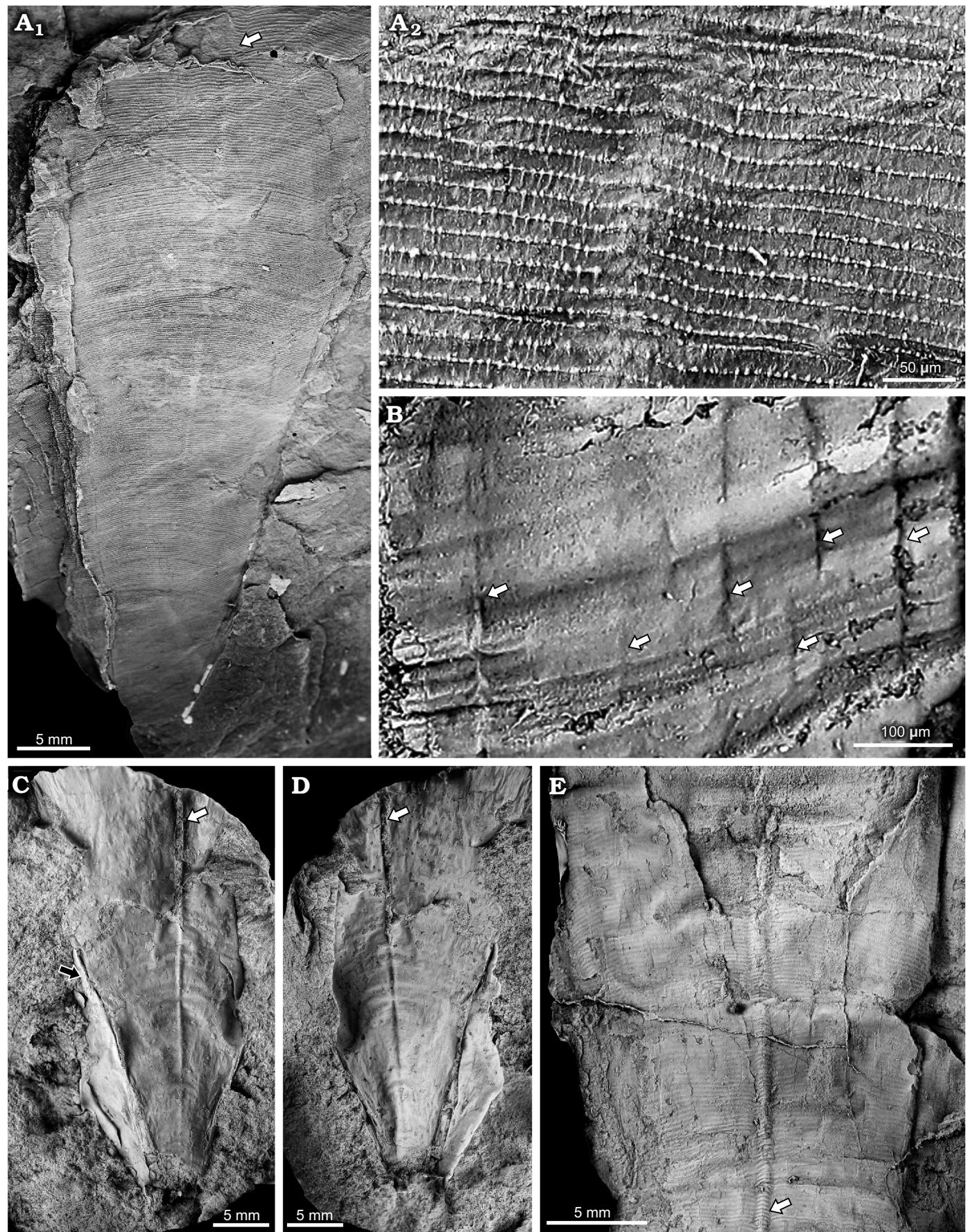
Diagnosis.—Raised facial midline marked by a low, rounded (transversely), continuous external ridge. Exterior-

most lamellae of the faces exhibit very fine, adaperturally gently arching, trochoidal (longitudinally) transverse ribs bearing submicroscopic, circular to sub-circular nodes; transverse ribs cross the midline ridge without interruption or diminution, terminating or greatly diminished in height in the narrow corner sulcus. Exterior-most lamellae of the interspaces exhibit very slender interspace ridges that terminate at their apertural end in a node. Deeper lamellae exhibit fine longitudinal ridges or grooves.

Description.—Specimens incomplete, variably deformed and exfoliated, with the largest specimen measuring approximately 58 mm in length; apex unknown, schott (apical wall) not observed, apertural margin gently arcuate but without evidence of inward folding (apertural lappets). Transverse cross section slightly rectangular; corners and facial midline un-thickened and lacking internal carina(e). Angle of divergence of the corners bounding a given face ranges from approximately 10–50°. Corners sulcate; corner sulcus narrow (Fig. 4A₁, C). Periderm along the facial midline outwardly folded to form a low, rounded (transversely), continuous ridge that is wider than the corner sulcus (Fig. 4A, C–E). On the faces, the exterior-most lamellae exhibit very fine, gently arched (adaperturally), trochoidal (longitudinally) transverse ribs, 2–11 per mm, which parallel the apertural margin; in two specimens, the transverse ribs exhibit closely spaced, sub-microscopic nodes (approximately 14–18 per mm; Fig. 4A₂); transverse ribs cross the midline ridge without interruption or diminution (Fig. 4A₂), terminating or greatly diminished in height in the corner sulcus. Interspaces wider than the transverse ribs, in the two node-bearing specimens exhibiting very slender interspace ridges that extend from a node on the transverse rib nearest the aperture to the gap between two nodes on the transverse rib nearest the apex (Fig. 4A₂). Faces of many specimens exhibit coarse, irregular folds and/or broadly sinusoidal, gently arched transverse folds that may be artifacts of deformation (Fig. 4C, D). Transverse ribs may be scalloped or jagged, especially in completely flattened specimens preserved in shale (Fig. 4E). Many specimens show multiple fine, commonly discontinuous, longitudinal folds or grooves (“filets”; Thoral 1935: 160) that number about 2 per mm (transversely) and along which the transverse ribs may be recurved adapically.

Remarks.—The foregoing description is based on Thoral's (1935) original material (total of 12 specimens) plus 20 ad-

Fig. 4. Conulariid scyphozoan *Galliconularia azaisi* (Thoral, 1935), Saint Chinian and La Maurerie formations, upper Tremadocian–lower Floian, Lower → Ordovician; southern Montagne Noire, France. Specimens oriented with the apertural end directed toward the top of the page. **A.** The exterior surface of a single face of a relatively large specimen, parts of which preserve the sub-microscopic nodes and interspace ridges (UCBL-FSL 713229; midline ridge indicated by the arrow) (A₁). Detail of the apertural region, showing some of the sub-microscopic nodes and interspace ridges, which cross the broad midline ridge (central part of the photograph) without diminution or disruption (A₂). **B.** Close-up view of the central portion of a single face (corners bounding the face missing) (UM.ACI.645), showing at least six discontinuous, narrow longitudinal folds and furrows (arrows). **C.** Overall view of the exterior surface of the single fully exposed face and bounding corners of one of the most complete specimens, which is preserved in a siliceous concretion (UCBL-FSL 712799A; midline ridge indicated by the white arrow, corner sulcus by the black arrow). **D.** View of the counterpart of the specimen in D (UCBL-FSL 712799B; midline ridge indicated by the arrow). **E.** View of the exterior surface of part of a single face of a flattened specimen, the very fine transverse ribs of which are slightly wavy (scalloped) owing, probably, to tectonic shearing and deformation (UM.ACI.646; midline ridge indicated by the arrow; specimen also figured in Thoral 1935: pl. 11: 9). Scale bars: A₁, C, D, E, 10 mm; A₂, B, 0.1 mm.



ditional specimens. Though longer and more complete than that of Thoral (1935), the present description is generally in close agreement with equivalent portions of Thoral's (1935) text. The most significant difference between the two descriptions is that Thoral (1935) did not note the presence of minute nodes and interspace ridges. Such features appear to be absent in Thoral's (1935) material (e.g., Fig. 4C, D), but they are present in at least two of the additional specimens (UCBL-FSL 713215 and 713229) examined by the present authors. In all other respects, the node-bearing specimens are similar to those examined by Thoral (1935), exhibiting for example the same broadly rounded midline ridge and thread-like transverse ribs which cross the midline ridge without diminution or disruption.

As is true for many other conulariids, the appearance of a given specimen of *G. azaisi* depends in part on the depth or level within the finely lamellar periderm at which the specimen is being examined. This in turn depends on the preservation of the periderm (whether complete or exfoliated) as well as on whether the periderm was split along one or more internal lamellae during extraction from the host rock matrix. The very fine, nodose transverse ribs and interspace ridges appear to be restricted to the outermost lamellae, which in many specimens are either missing (owing, we believe, to exfoliation) or covered by rock matrix, which can only be removed through mechanical preparation (which may destroy delicate external surface features). The fine longitudinal ridges or furrows, which are similar to and possible homologous with those which occur within the periderm of many specimens of *Archaeoconularia* (see e.g., Bouček 1928: pl. 1: 17), occur in lamellae beneath those bearing the very fine transverse ornament and interspace ridges. In short, then, we do not believe that the two node-bearing specimens and the more numerous specimens that do not exhibit nodes should be assigned to separate species in the new genus. However, if future discoveries should prove this conclusion to be incorrect, then the diagnosis of *Galliconularia* will have to be emended accordingly.

Another factor affecting the appearance of specimens of *G. azaisi* is tectonic deformation, more specifically shearing of flattened specimens preserved in shale (Fig. 4E). In addition to being strongly compressed, such specimens differ from more or less three-dimensional specimens preserved in siliceous nodules in having the transverse ribs scalloped or jagged. But even in specimens preserved in siliceous nodules, deformation expressed as very fine wrinkling of the periderm may be present in the interspaces (Fig. 4A₂).

Subsequent to the publication of Thoral's (1935) description, Vizcaíno et al. (2001) listed *G. azaisi* as *Eoconularia azaisi*. This assignment apparently was based on the presence in certain specimens of relatively coarse, sinusoidal transverse folds that follow the course of the very fine, adaperturally arching transverse ribs. Such folds resemble the sinusoidal transverse ribs of species such as *Eoconularia amoena* Sinclair, 1944 and *Eoconularia loculata* (Wiman, 1895). However, because most specimens of *G. azaisi* are

deformed, we are inclined to agree with Thoral's (1935) suggestion that the transverse folds in this conulariid are artifacts of directed stress sustained after final burial. In this connection it should be noted that Thoral (1935: 160) grouped the 12 specimens of *G. azaisi* he examined in two "distinct series". The first series consisted of specimens having broad faces, large apical angles, poorly defined transverse ribs, and numerous, clearly defined, narrow longitudinal furrows or ridges ("filets"). Thoral did not list the registration numbers of these specimens. The second series consisted of larger and narrower specimens, again unspecified, that were further characterized by well-defined transverse ribs but only a few, widely spaced and discontinuous longitudinal lines. Thoral (1935) provisionally interpreted his two series as consisting, respectively, of the apical (first series) and more distal regions (second series) of an originally more elongate periderm having high apical angles in the apical region and much lower apical angles closer to the apertural end of the periderm. Owing to distortion and incomplete preservation of the faces, we think that determination of apical angles in *G. azaisi* is more difficult than implied by Thoral (1935); however, at this point we cannot rule out his hypothesis that the two series represent different portions of the periderm of a single species.

Stratigraphic and geographic range.—Late Tremadocian Saint Chinian Formation and early Floian La Maurerie Formation, Lower Ordovician of the southern Montagne Noire, France. See Appendix for detailed geographic and stratigraphic information on each specimen.

Concluding remarks

Archaeoconularia, previously known from the Lower Ordovician of Avalonia (Wales) and Perunica, is now documented from two distinct regions of Core Gondwana: the Anti-Atlas (Morocco) and the southern Montagne Noire (France). The same genus probably also occurs in the Lower Ordovician of South China. The new, monospecific genus *Galliconularia* is currently known only from the Lower Ordovician of the Montagne Noire. This fact is interesting given that during this time interval, this region was part of the passive margin of Gondwana and, based on palaeogeographic reconstructions (see e.g., Fortey and Cocks 2003; Torsvik and Cocks 2013), was situated close to several other peri-Gondwanan areas from which conulariids have been described (e.g., the Anti-Atlas, Argentina, Bohemia, and Wales; Leme et al. 2003; Van Iten and Vhylasová 2004; Van Iten et al. 2016a).

The diversity pattern observed for conulariids in the Montagne Noire (Fig. 2) is identical to those described for most other invertebrates, in particular echinoderms and trilobites (Vizcaíno and Lefebvre 1999; Vizcaíno et al. 2001; Vizcaíno and Álvaro 2003): thus, diversity peaks in the late Tremadocian (Saint-Chinian Formation) before decreasing in the early Floian (La Maurerie Formation) and even more

dramatically during the middle Floian (Cluse de l'Orb and Foulon formations). This diversity trend mostly follows large-scale environmental changes, with the Saint-Chinian Formation corresponding to deeper settings (transgressive interval) and the early–middle Floian units recording shallowing conditions (regressive interval).

Not surprisingly, endemicity is particularly reduced during the late Tremadocian transgressive interval, with most invertebrate taxa reported from the Saint-Chinian Formation also occurring in other peri-Gondwanan areas, in particular Argentina and Morocco (Vizcaïno and Lefebvre 1999; Vizcaïno et al. 2001; Vizcaïno and Álvaro 2003; Lefebvre et al. 2016; Martin et al. 2016). In short, then, we predict that the genus *Galliconularia* probably also occurs in other peri-Gondwanan areas, possibly as one or more new species distinct from *G. azaisi*.

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Appendix 1

Locality and stratigraphic information for all available specimens of conulariids registered in the collections of Lyon 1 University (UCBL-FSL), Montpellier University (UM), and the Muséum National d'Histoire Naturelle, Paris (MNHN), France:

Saint-Chinian Formation (trilobite zone unknown, upper Tremadocian); locality unknown, Saint-Chinian area (Hérault): UM.ACI.416, 645, 658 (Azaïs coll.), and UM.ACI.646–647, 654–656, UCBL-FSL 133605–133606 (Villebrun coll.).

Saint-Chinian Formation (*Euloma filacovi* Zone, upper Tremadocian); Donnadieu, Babeau-Bouldoux (Hérault): UCBL-FSL 713218 (Monceret coll.), and UCBL-FSL 713224–713225 (Vizcaïno coll.); locality unknown, Félines-Minervois area (Hérault): UCBL-FSL 133609 (Lignières coll.); vallée du Merlaux, Félines-Minervois (Hérault): UCBL-FSL 133610 (Lignières coll.); Pech Tavernier, Prades-sur-Vernazobre (Hérault): UCBL-FSL 713216–713217, 713220 (Monceret coll.), and UCBL-FSL 713221, 713228 (Vizcaïno coll.); SW of Prades-sur-Vernazobre (Hérault): UCBL-FSL 713222 (Vizcaïno coll.); locality unknown, Saint-Chinian area (Hérault): UCBL-FSL 133608 (Villebrun coll.); Canimals, Saint-Chinian (Hérault): UCBL-FSL 133604 (Villebrun coll.), and UCBL-FSL 712799, 713219 (Monceret coll.); Brama, Trausse (Aude): UCBL-FSL 713223 (Vizcaïno coll.).

Saint-Chinian Formation (lower part of the *Taihungshania miqueli* Zone, late Tremadocian); ruisseau des Lavandières, Caunes-Minervois (Aude): UCBL-FSL 713226 (Vizcaïno coll.); vallée de l'Ourdiveille, Caunes-Minervois (Aude): UCBL-FSL 713227 (Vizcaïno coll.).

La Maurerie Formation (upper part of the *Taihungshania miqueli* Zone, lower Floian); la Rouvelane, Prades-sur-Vernazobre (Hérault): UCBL-FSL 713214 and 713215 (Monceret coll.), and UCBL-FSL 713229 (Vizcaïno coll.); Saint-Cels, Saint-Chinian (Hérault): UCBL-FSL 133607 (Villebrun coll.).

Landeyran Formation (*Apatocephalus incisus* Zone, upper Floian); les sources du Foulon, Cessenon (Hérault): MNHN.F.A71848–A71850 (Kundura coll.).

Landeyran Formation (*Hangchunolithus primitivus* Zone, upper Floian); les Rocs Nègres, Causses-et-Veyran (Hérault): MNHN.F.A71851 (Kundura coll.).