

***Metaconularia? pyramidata* (Bronn, 1837): a scyphozoan from the Ordovician of Normandy, France, recorded for the first time as a reworked fossil in the Triassic of Devon, England**

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ABSTRACT

A conulariid originally figured by Deslongchamps (1825) from the Grès de May (Caradoc) of Normandy as “Conulaire ondulée (var.)” is revised. It is one of the first conulariids to have been figured in the literature. This large species, preserved as sandstone steinkerns, has usually been referred to as *Conularia pyramidata* Hoeninghaus, 1830. However, Hoeninghaus’ publication does not satisfy criteria of availability and the species should instead be attributed to Bronn, as *Metaconularia? pyramidata* (Bronn, 1837). A lectotype is chosen from the Bronn Collection. *Metaconularia? pyramidata* is recorded for the first time reworked into the Triassic Budleigh Salterton Pebble Beds Formation of Devon, England.

KEY WORDS

Cnidaria,
Conulariida,
Ordovician,
Triassic,
reworked fossils,
lectotypification,
taxonomy.

RÉSUMÉ

Metaconularia? *pyramidata* (Bronn, 1837): un scyphozoaire de l'Ordovicien de la Normandie, France, signalé pour la première fois comme remanié du Trias de Devon, Angleterre.

Un conulaire du Grès de May (Caradoc) en Normandie, initialement figuré par Deslongchamps (1825) comme « Conulaire ondulée (var.) », est révisé. C'est l'un des premiers conulaires à avoir été figuré dans la littérature. Cette grande espèce, conservée sous forme de moulages de grès, a souvent été décrite comme *Conularia pyramidata* Hoeninghaus, 1830. Toutefois, la publication de Hoeninghaus, qui ne satisfait pas aux critères de disponibilité de l'espèce, doit être attribuée à Bronn, comme *Metaconularia?* *pyramidata* (Bronn, 1837). Un lectotype est désigné dans la collection Bronn. *Metaconularia?* *pyramidata* est signalé pour la première fois comme remanié du Trias Budleigh Salterton dans la Pebble Beds Formation du Devon, en Angleterre.

MOTS CLÉS

Cnidaria,
Conulariida,
Ordovician,
Triassic,
fossiles remaniés,
lectotypification,
taxonomie.

INTRODUCTION

Conulariids are a group of Vendian to Late Triassic scyphozoan cnidarians (Van Iten *et al.* 2006a). They have potential for use in biostratigraphy because of their cosmopolitan distribution, most species being geographically widespread (Sendino & Domínguez 2006). Although rare in most deposits (Holm 1893), more than 52 genera and 357 species of conulariids are now known from around the world (Sendino Lara & Domínguez Alonso 2007). Recent literature on conulariids has focused on affinities and phylogeny (e.g., Van Iten *et al.* 2006b; Leme *et al.* 2008a), palaeoecology (e.g., Rodrigues *et al.* 2006), taphonomy (e.g., Van Iten *et al.* 1996, 2006b; Simões *et al.* 2000, 2003; Rodrigues *et al.* 2003; John *et al.* 2010), palaeobiogeography (e.g., Weldon & Shi 2003; Van Iten & Vhylasová 2004), and history of study (e.g., Leme *et al.* 2008b; Sendino & Darrell 2009a, b).

The most striking feature of conulariids is their four-sided pyramidal shape. Individuals range in length from about 2 to 50 cm, although most are 3 to 10 cm long when measured from the pointed closed end to the aperture at the wider open end (Sendino & Domínguez 2006). Transverse banding typifies conulariids. The bands, often defined by ridges or lines of nodes, according to Babcock & Feldmann (1986) represent strips of skeleton added

around the aperture during growth. Longitudinal banding may also be developed, in this case formed by nodes or crests aligned parallel to growth direction. Other important features are the facial midlines, in many cases marked by deviations in the ornament, which divide each face of the pyramid into two or four equal parts, and the four corners at the edges of the pyramid. When preserved in its original state, the thin, delicate skeleton of conulariids is composed of calcium phosphate (apatite) and varies from light pink to white, or from light blue to black in colour. Skeletal microstructure is lamellar. In many instances the skeleton is not preserved, and the fossil conulariid is represented by an internal cast or steinkern, as it is the case with the conulariids described here.

Among the first conulariids to have been illustrated in the scientific literature are fossils from the famous locality of May-sur-Orne, south of Caen in Normandy. They were figured by Jacques-Amand Eudes-Deslongchamps (1794-1867) in a paper published in 1825 (Deslongchamps 1825: pl. 20, figs 6a-c; 7a, b; 8). Deslongchamps' plate is reproduced here as Figure 1. Although not mentioned in Deslongchamps' text, the large species (Deslongchamps 1825: figs 6a-c; 7a, b) was labelled "Conulaire ondulée (var.)" in the figure caption, alluding to the undulating surface of the steinkerns, whereas the smaller one (Deslongchamps

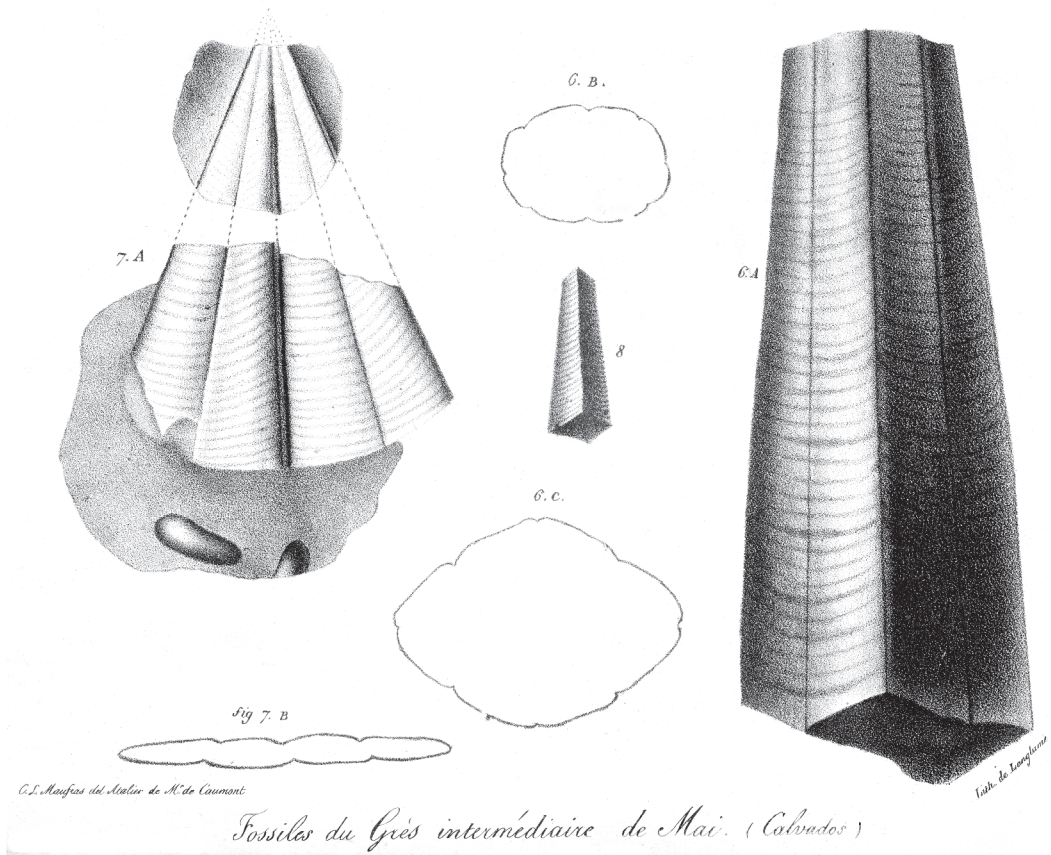


FIG. 1. — Reproduction of a part of plate 20 of Deslongchamps (1825), showing conulariids referred to as “Conulaire ondulée (var.)” (figs 6a-c; 7a, b) and “Conulaire acutangle” (fig. 8). The former is the large conulariid characteristic of the Ordovician Grand May Formation of May-sur-Orne, here revised as *Metaconularia?* *pyramidata* (Bronn, 1837).

1825; fig. 8) was labelled “Conulaire acutangle”. Subsequently, the large species was formally named *Conularia pyramidata* by Hoeninghaus (1830) but, as argued below, the introduction of this species name by Hoeninghaus does not satisfy the rules of nomenclatural availability, and thus the species should instead be attributed to Heinrich Georg Bronn (1837). The aims of the present paper are to revise *Metaconularia?* *pyramidata* (Bronn, 1837), choose a lectotype for the species, and describe material from the type locality as well as specimens occurring as reworked fossils in the Budleigh Salterton Pebble Beds Formation (BSPBF) of Devon, England, the first record of conulariids in this Early Triassic deposit.

MATERIAL AND METHODS

Syntypic specimen of *M.?* *pyramidata* from the Bronn Collection, Museum of Comparative Zoology, Harvard (MCZ) and topotypes from the d’Orbigny Collection, Muséum national d’Histoire naturelle, Paris (MNHN) were studied using photographs provided by Dr Jessica D. Cundiff and Dr Didier Merle. Other specimens of this species came from the conulariid collection of the Natural History Museum, London (NHM). These comprise topotypes from May-sur-Orne, as well as reworked fossils from the Triassic Budleigh Salterton Pebble Beds Formation of Devon bequeathed by W. Vicary in November 1903.

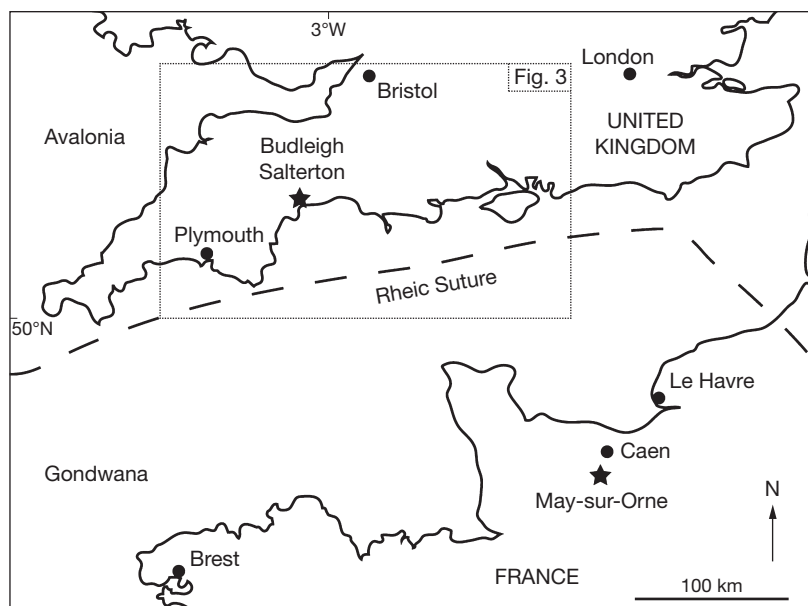


FIG. 2. — Locations of Budleigh Salterton (Devon) and May-sur-Orne (Normandy), with the approximate position of the Rheic Suture between the palaeocontinents of Avalonia and Gondwana. Both localities yield *Metaconularia? pyramidata* (Bronn, 1837): indigenous examples occur in the Upper Ordovician Grès de May of May-sur-Orne, while reworked fossils occur in the Triassic Budleigh Salterton Pebble Beds Formation of Budleigh Salterton.

Conulariids were previously unknown in the BSPBF; this is the first time that conulariids, and indeed cnidarians of any kind, have been reported and described from this formation. There are nine incomplete specimens preserved as steinkerns in the NHM Collections. Three can be assigned with confidence to *Metaconularia? pyramidata*, four additional specimens may be juveniles of this species, and the final two are indeterminate. Along with France and the Czech Republic, Devon becomes the third region in the world to have yielded the Ordovician conulariid *M.? pyramidata*.

GEOLOGICAL SETTING

MAY-SUR-ORNE, NORMANDY

Quarrying for iron at May-sur-Orne in Calvados, Normandy (Fig. 2) began in the Middle Ages (Tritsch & Delaunay 2004). Here, Ordovician and Silurian sediments form the core of a syncline, surrounded by the Cambrian Grès Feldspethiques

and Briovérien (Upper Proterozoic) rocks of the Saint-Malo Nappe. The Ordovician succession comprises Schistes à Calymènes (Llandeilo = Darrivilian), overlain by the Grès de May and the Schistes gréseux à *Trinucleus* et *Calliops*.

Three subdivisions of the Grès de May are recognized: Grès ferrugineuse, Petit May and Grand May. Iron-rich oolitic sandstones occur in the Grès ferrugineuse, while the Petit May contains ripple marks. The Grand May Formation (Grès du Grand May) has a thickness of 127 m and consists of quartzose sandstones with a shaly member 9 m thick which near the top contains trace fossils. The base of the Grès de May belongs to the *Laufeldochitina clavata* Biozone of Llandeilo [Darrivilian] age (Paris 1990; Young 1992), but most of the formation is regarded as Caradocian in age, including the Grand May Formation. Due to problems with global correlation of Ordovician stages (R. A. Fortey pers comm., February 2009), we use the Gondwanan regional stage name herein (i.e. Caradocian) instead of the approximate equivalents Sandbian and Katian.

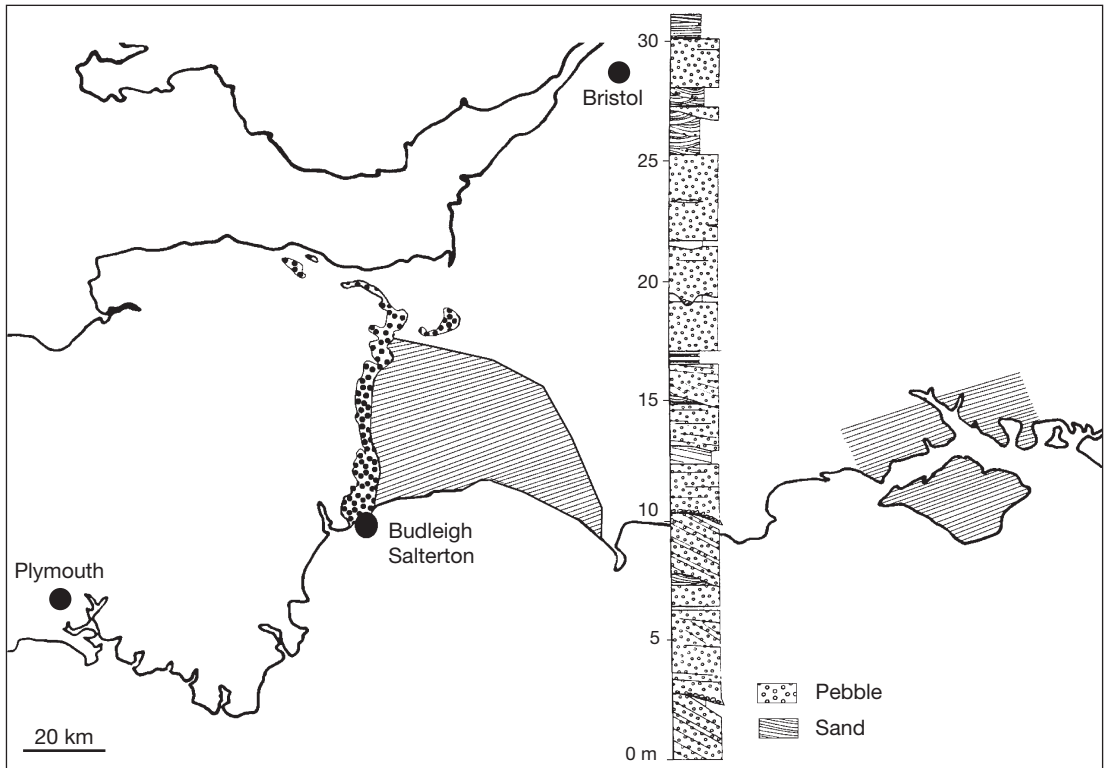


FIG. 3. — Outcrop (stippled) and subcrop (hatched) of the Sherwood Sandstone Group, including the Budleigh Salterton Pebble Bed Formation, in southern England, with sedimentary column of the BSPBF at its type locality (after Smith & Edwards 1991).

Parts of the Grand May Formation are ripple-marked (Vossmerbaeumer 1969), and the formation was deposited in the littoral zone, intertidally in some places (Doré *et al.* 1977). Aside from conulariids, the large trilobite *Eohomalonotus* and various bivalves occur in the formation.

BUDLEIGH SALTERTON, DEVON

The Budleigh Salterton Pebble Beds Formation (BSPBF) of Devon, England (Fig. 2) is of early Triassic age. It is about 28–34 m in thickness (Woodward & Ussher 1911; Edwards 1999), and consists of red and purplish brown, sandy to very sandy, poorly sorted, fine to coarse gravels with occasional fine silty-sand horizons. The pebbles and cobbles are rounded and consist predominantly of metaquartzite in a matrix of silty sand (Edwards 1999). Arid conditions at the time of deposition account for the red colour of the deposit.

The BSPBF and the overlying Otter Sandstone together form the Sherwood Sandstone Group, the middle group of the British New Red Sandstone. The formation has a small outcrop in the southwest of Budleigh Salterton but is known more extensively from the subsurface as far east as Hampshire and the Isle of Wight (Fig. 3). Smith (1989, 1990), Smith & Edwards (1991) and Edwards (1999) described the type section in the cliff west of Budleigh Salterton (Fig. 3). Here 30 m of sediment are visible, of which the bottom 16 m comprises three stacked sequences of cross-bedded gravel overlain by horizontally-bedded gravel. Whereas the lowermost sequence fines upwards from a coarse cobble layer, the other two coarsen upwards. Cross-bedding indicates currents flowing from the southwest. Thin sand lenses are intercalated with the horizontally-bedded gravels. A bed of reddish brown clay- and silt-rich sand, approximately 0.3 m thick, capped

by a layer of wind-faceted pebbles, occurs at the top of the BSPBF (Edwards 1999).

Although the BSPBF was first named more than 140 years ago, the palaeontology of the formation is not well known, despite the publications of Vicary & Salter (1864), Davidson (1870, 1880), Cocks & Lockley (1981) and Cocks (1989, 1993). The fauna is composed of brachiopods, bivalves and trilobites, plus the conulariids described here. More than 25 species of reworked Ordovician fossils have been recorded (Shrubsole 1903), all of which occur as indigenous fossils in the Grès de May and Grès Armorican of Normandy (Jukes-Browne 1911). The reworked fossils contained in the clasts can be matched sources in northwestern France, sharing taxonomical composition, age, and preservational style, as in the case of the conulariid described below.

Vicary & Salter (1864) were the first to discover reworked Ordovician fossils near the town of Budleigh Salterton in south Devon (Fig. 1). Their work, along with that of Thomas (1902, 1909) and Davidson (1870, 1880), has made the BSPBF a reference horizon for studying fossils equivalent to French Ordovician faunas and reflecting the history of Avalonia as it drifted away from Gondwana during Ordovician times (Cocks 2000). According to Cocks & Lockley (1981), brachiopods from the BSPBF are very similar to fossils found *in situ* in the Grès Armorican and Grès de May formations of Brittany and Normandy respectively, and in the Gorran Quartzites of south Cornwall (Sadler 1974; Edwards 1999). The BSPBF contains more exotic clasts that have travelled a greater distance, seemingly from Armorica (Benton *et al.* 2002).

The fauna of the BSPBF is richest towards Newton Abbott in the southwest (Woodward & Ussher 1911). The NHM conulariid specimens described were probably collected from Anstis Cove (Davidson 1870) or other outcrops near the road to Lypmston, Saint John's Cottage, Withycombe Raleigh Knowle Hill or Hayes Barton (Ussher 1913). The nine conulariids come from the W. Vicary Collection, and were likely picked up together with the brachiopods that were described by Cocks & Lockley (1981). Davidson (1870) noted that the extensive collection of Mr Vicary came from near Exmouth. Vicary & Salter (1864) described the sites as follows: "A quarter of a

mile west of Budleigh Salterton, and for about a mile and a half further on in the same direction, is a bed containing pebbles in large quantities, varying from a small size to that of a man's head," and "the beach from the River Exe on the west to the River Otter on the east is mainly composed of the pebbles from this bed, and they may be found sparingly for three or four miles beyond Sidmouth".

SYSTEMATIC PALAEOLOGY

Class SCYPHOZOA Götte, 1887

Subclass CONULATA

Moore & Harrington, 1956

Order CONULARIIDA Miller & Gurley, 1896
in Moore & Harrington (1956)

Suborder CONULARIINA Miller & Gurley, 1896
in Moore & Harrington (1956)

Family CONULARIIDAE Walcott, 1886

Genus *Metaconularia* Sinclair, 1952

Metaconularia? *pyramidata* (Bronn, 1837)

(Figs 4; 5; 6A, B, E-K, M-O)

Conulaire ondulée (var.) – Deslongchamps 1825: pl. 20, figs 6a-c, 7a-b.

"*Conularia pyramidata*" – Bronn 1830: 228. — De la Beche 1832: 535.

Conularia pyramidata Bronn, 1835-1838: 1284, pl. 1, fig. 12. — d'Orbigny 1850: 10. — Roemer 1857: 437, pl. 1, fig. 12a, b. — Barrande 1867: 50, pl. 2, figs 1-6. — Tromelin 1877: 29. — Lapparent 1886: pl. 3, fig. 9. — Lamouche 1925: 13, pl. 4, fig. 3.1a, b. — Bouček 1928: 79, 80, pl. 4, figs 11, 12.

Conularia curvata – Sandberger 1847: 23, pl. 1, fig. 14.

Conularia pyramidata Hoeninghaus [*n.n.*] – Sherborn 1930: 5335.

Conularia pyramidata Hoeninghaus – Kowalski 1935: pl. 12, figs 3-6. — Kiderlen 1937: 119, figs 2, 3. — Termier & Termier 1953: 1006, fig. 1.

Exoconularia pyramidata (Hoeninghaus) – Moore & Harrington 1956: F62, fig. 24.1. — Fischer 1980: 19, pl. 2, fig. 1.

Metaconularia pyramidata (Hoeninghaus) – Pillet & Beaulieu 1998: 35, 36, figs 1-5.

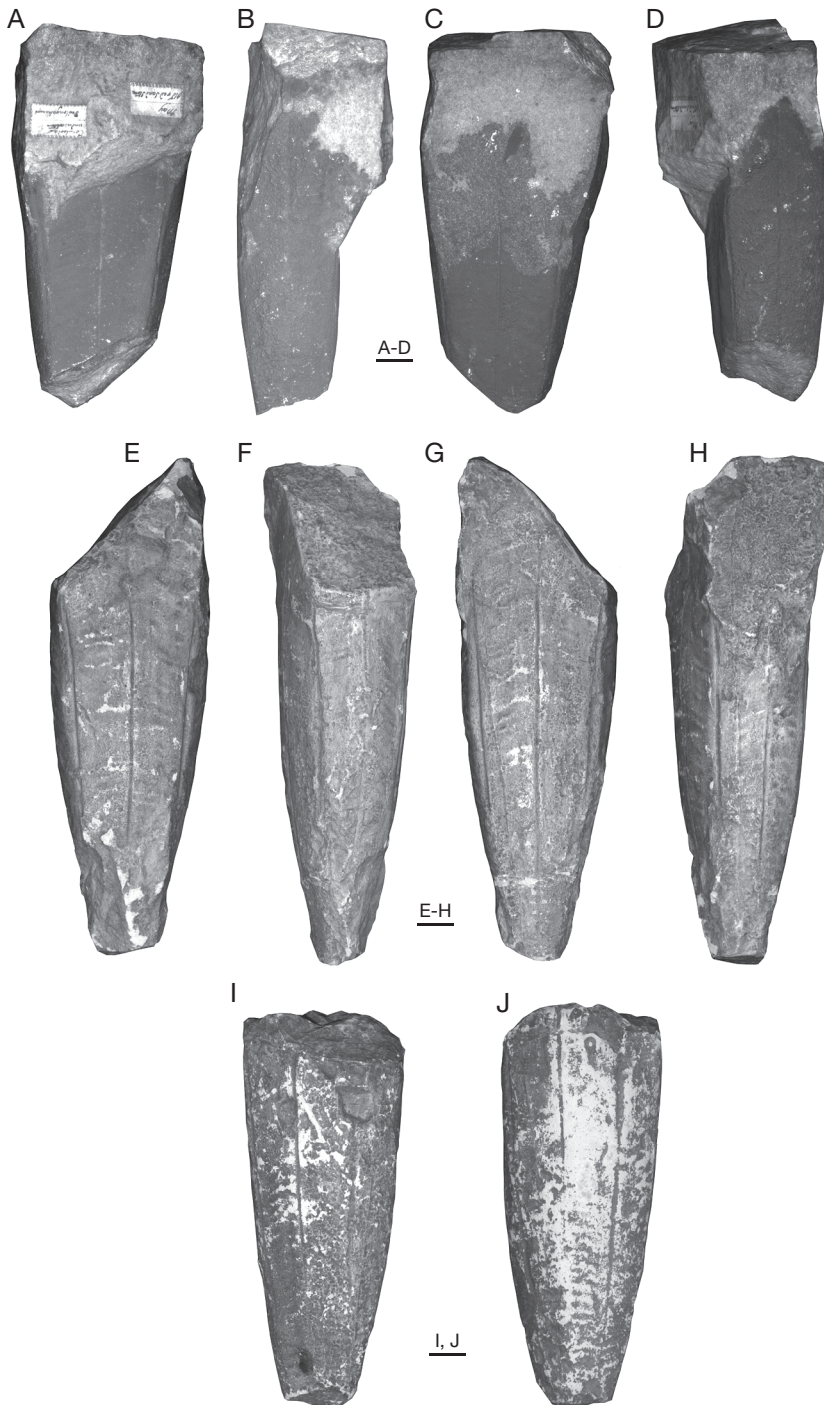


FIG. 4. — *Metaconularia?* *pyramidata* (Bronn, 1837) from the Upper Ordovician Grès de May of May-sur-Orne, Normandy: Harvard, Bronn collection: **A-D**, lectotype, MCZ16028; **E-H**, plaster cast, MCZ16029; **I, J**, plaster cast MCZ (no number). Scale bars: 10 mm.

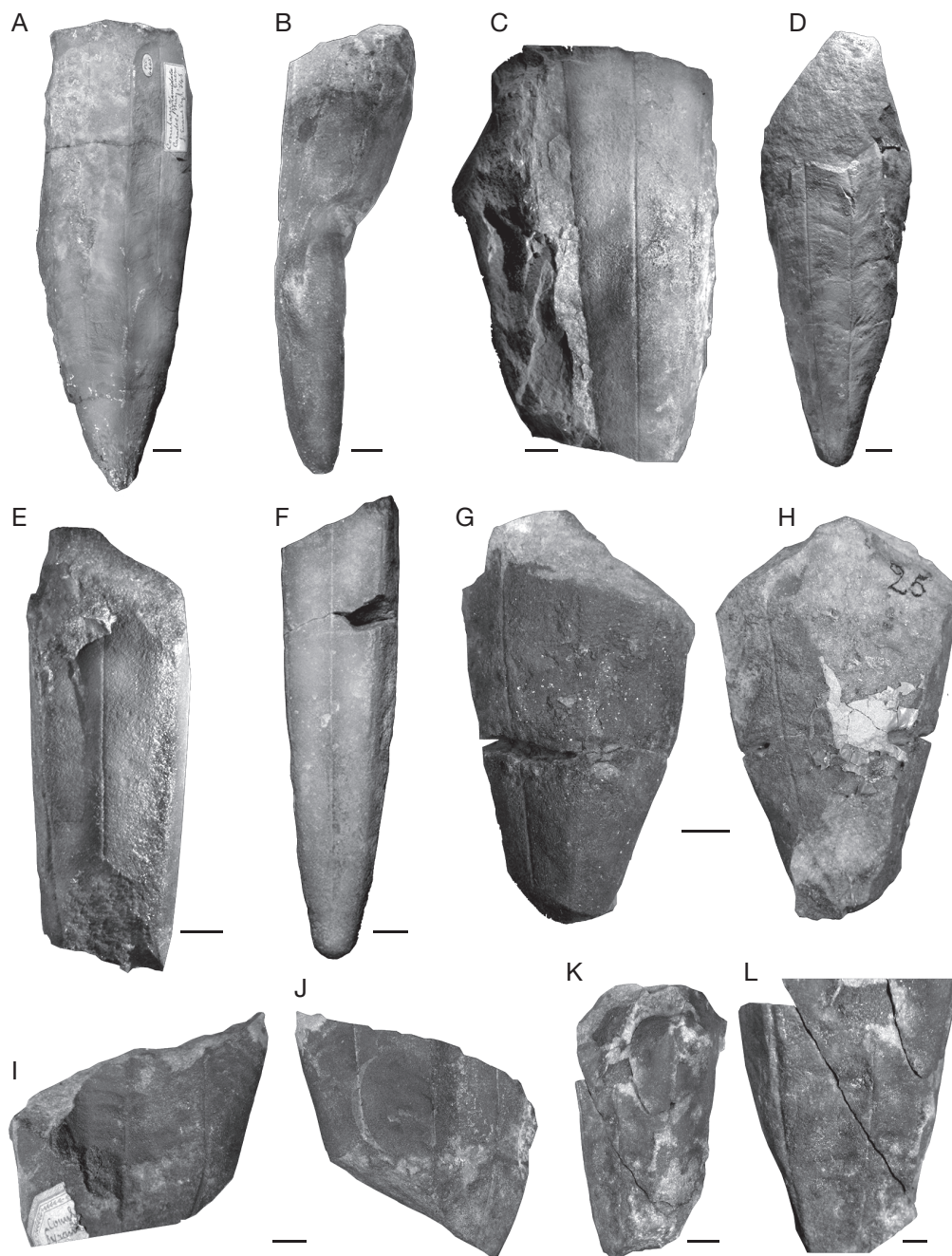


FIG. 5. — *Metaconularia? pyramidata* (Bronn, 1837) from the Upper Ordovician Grès de May of May-sur-Orne, Normandy: **A**, NHMUK PI PG4465; **B**, NHMUK PI C3409a; **C**, NHMUK PI CL1000; **D**, NHMUK PI C3408d; **E**, NHMUK PI C3407; **F**, NHMUK PI 3408b; **G-L**, MNHN.F. d'Orbigny collection no. 25; **G**, **H**, specimen [MNHN.FA00023](#) (a); **I**, **J**, specimen [MNHN.FA00023](#) (b); **K**, **L**, specimen [MNHN.FA00023](#) (c). Scale bars: 10 mm.

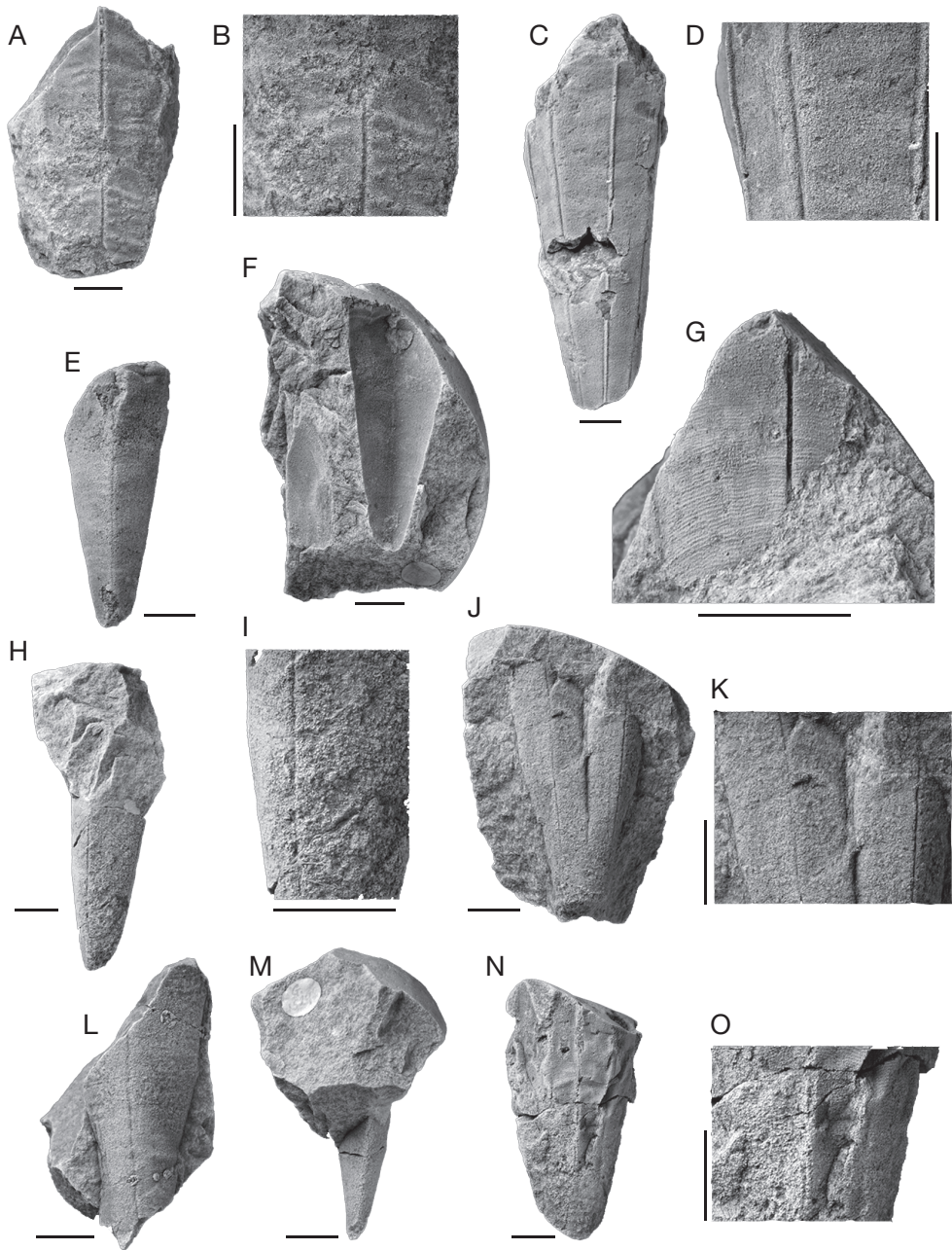


FIG. 6. — Reworked Ordovician conulariids from the Triassic Budleigh Salterton Pebble Beds Formation, Devon: **A, B**, *Metaconularia?* *pyramidata* (Bronn, 1837) (NHMUK PI G15294); **C, D**, conulariid indet. (NHMUK PI G15295); **E, F**, part and counterpart of conulariid indet., probably a juvenile individual of *M.?* *pyramidata* (NHMUK PI G15287); **G**, fragment of *M.?* *pyramidata* (NHMUK PI G15288); **H, I**, conulariid indet., probably a juvenile individual of *M.?* *pyramidata* (NHMUK PI G15289); **J, K**, conulariid indet., probably a juvenile individual of *M.?* *pyramidata* (NHMUK PI G15290); **L**, conulariid indet. (NHMUK PI G15291); **M**, conulariid indet., probably a juvenile individual of *M.?* *pyramidata* (NHMUK PI G15292); **N, O**, *M.?* *pyramidata* (Bronn, 1837) (NHMUK PI G15293). Scale bars: 10 mm.

TYPE MATERIAL. — Lectotype, MCZ16028, Harvard, Bronn Collection (Fig. 4).

TYPE LOCALITY. — May-sur-Orne, Calvados, Normandy, France.

TYPE HORIZON. — Ordovician, Caradocian (Sandbian or Katian), Grès de May, Grand May Formation.

TOPOTYPES. — Muséum national d'Histoire naturelle, Paris, collection de paléontologie: MNHN.FA00023, d'Orbigny Collection no. 25, specimens (a), (b) and (c); NHMUK PI C3407, NHMUK PI C3408a-f, NHMUK PI C3409a-b, NHMUK PI PG4465-4466 and NHMUK PI CL1000 (Figs 5; 6).

MATERIAL EXAMINED. — **France.** Grès de May (Ordovician, Caradocian), May-sur-Orne, Normandy: NHMUK PI C3407, Pratt Collection 1857; NHMUK PI C3408a-f, Ward Collection 1869; NHMUK PI C3409a-b, no collection details. NHMUK PI PG4465-6, Geological Society of London Collection 1911; NHMUK PI CL1000, Deyrolle Collection.

England. Budleigh Salterton Pebble Beds Formation (Lower Triassic, as reworked fossils), Budleigh Salterton, Devon: NHMUK PI G15288, NHMUK PI G15293, NHMUK PI G15294, Vicary Collection 1903. In addition, the following specimens from the same locality are indeterminate or juvenile conulariids, the latter possibly of *M. pyramidata*: NHMUK PI G15287, G15289-G15292, G15295.

STRATIGRAPHICAL DISTRIBUTION. — Stratigraphical: Middle-Upper Ordovician. Recorded from arkoses of the Dobrotivá and Bohdalec formations (Middle to Upper Ordovician) and the Letná and Libeň formations (Upper Ordovician) of Bohemia, and the Grès de May (Upper Ordovician) of Normandy.

GEOGRAPHICAL DISTRIBUTION. — May and Jurques, Calvados, Normandy, France; Ille-et-Vilaine, Normandy; Saint-Germain, Normandy; Mt Ded (= Mt Drabov), Bohemia, Czech Republic; Budleigh Salterton, Devon, England.

DESCRIPTION

Conulariidae with tetrameral symmetry and straight pyramidal exoskeleton, usually found incomplete and preserved as a steinkern. Incomplete specimens up to 230 mm long by 50 mm wide, complete specimens probably as much as 300 mm long. Length/width ratio varies from about 4 to 6. Cross-sectional shape square, rectangular or rhomboidal. Apical angle ranging from 8 to 13° in the best preserved specimens, although in specimen NHMUK PI

C3409b it is 19° due to deformation and crushing. Corner sulcus narrow and shallow, approximately 0.5 mm wide. Edges blunt. Faces slightly convex. Midline grooved, about 1 mm wide. Secondary lines seemingly present in specimen NHMUK PI G15288, but accessory lines have not been observed in other specimens. Transverse corrugations observed in some BSPBF specimens (NHMUK PI G15293 and G15294), with a density ranging from three to four per 5 mm, regular, weak. Transverse ribs formed by tubercles (seen in specimens NHMUK PI G15288 and G15293), with a density of 15-19 per 5 mm, apparently coalescing at midline and corner sulcus; tubercle density of 50 per 5 mm. Aperture preserved in a specimen from the Grès de May (NHMUK PI C3408d), showing apparently very long, triangular, lappet-like ends juxtaposed to form a pyramid opposed to the rest of the exoskeleton, comprising 41% of total exoskeleton length. Apex blunt, preserved in a few specimens (NHMUK PI C3408d, C3409b, PG4465).

REMARKS

The authorship of this species is problematical. It was first figured by Deslongchamps (1825, pl. 20, figs 6-7; Fig. 1 herein) as “Conulaire ondulée (var.)”, that is, a corrugated variety of a conulariid. The trivial name “pyramidata” was introduced by Hoeninghaus (1830) as “*C. pyramidata* Grès quartz. micacé. May bei Caen”. The lack of an author’s name suggests that Hoeninghaus’ intention was to describe it as a new species (many other species listed in his work are suffixed by an author’s name). However, *C. pyramidata* Hoeninghaus, 1830 is not an available name as it fails to satisfy the criteria of an indication (ICZN: art. 12) for names published before 1931. De la Beche (1832) and Bronn (1837) both attributed *C. pyramidata* to Hoeninghaus but it was Bronn (1835-1838: 1284) who first made the name formally available by describing it thus: “pyramidata HOENINGHAUS, GOLDF. bei DECH. 535, und scheint sich rücksichtlich ihres Vorkommens auf den Übergangs-Sandstein von May in Calvados zu beschränken.” By mentioning an earlier bibliographical reference (Hoeninghaus) that refers to Deslongchamps, as well as a distinguishing occurrence of the species (sandstone from May in Calvados), Bronn was the first to make “*pyramidata*”

available in a nomenclatural sense. Therefore, the authorship of *Conularia pyramidata* should be attributed to Bronn (1837).

The synonymy for this species lists *Metaconularia pyramidata* of Pillet & Beaulieu (1998) preceded by a "p." (*pro partim*) according to the terminology of Matthews (1973), because Pillet & Beaulieu (1998) included *Conularia consobrina* and *C. rugulosa* as synonyms of *M. pyramidata*.

We have questionably assigned this species to the genus *Metaconularia* Foerste, 1928. Unfortunately, all of our material consists of steinkerns from which diagnostic features such as secondary lines are absent or difficult to see. However, the deep grooves in the steinkerns may represent the positions of strong internal midline carinae which distinguish *Metaconularia* from *Exoconularia* Sinclair, 1952 according to the author of the latter genus.

It is usually difficult to observe all of the characteristics of this species in the steinkerns from the Grès de May Formation and the BSPBF. Traverse ribs and tubercles may be scarcely visible, the grain of the sandstone being coarser than these structures. Four specimens from the BSPBF could be juvenile specimens of *M.?* *pyramidata* but there are not enough characteristics to affirm this. These specimens are up to about 100 mm long by 30 mm wide, with a length/width ratio varying from 3.65–5.80 (Fig. 7).

CONCLUSIONS

Metaconularia? *pyramidata* is a large species of conulariid that has the distinction of being one of the first examples of this group to have been figured in the scientific literature. Deslongchamps, who figured the species in 1825, did not name it and the authorship of the species was attributed to Hoeninghaus (1830) by subsequent authors. However, Hoeninghaus introduced the name *Conularia pyramidata* without sufficient indication to satisfy the International Code of Zoological Nomenclature. It was left to Bronn (1837) to validate the name "*pyramidata*" by providing this when referring to Hoeninghaus & Goldfuss' work and also stating the occurrence of the species, in the sandstones from May, Calvados (France). Therefore, authorship of the species should be attributed

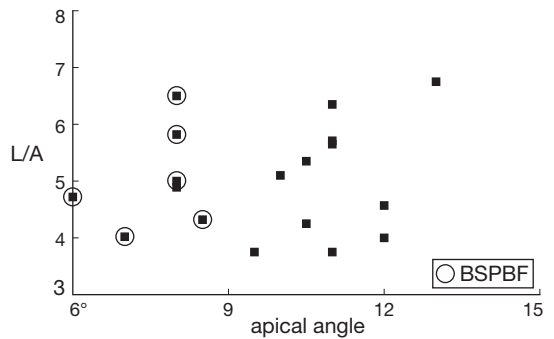


FIG. 7. — Relationship between length/width ratio and apical angle in *Metaconularia?* *pyramidata* (Bronn, 1837) specimens from the Grès de May of Normandy and reworked conulariids from the Budleigh Salterton Pebble Beds of Devon (circled squares).

to Bronn (1837). Fortunately, there is a specimen from the type locality at the MZC that we hereby designate as the lectotype of *C. pyramidata* Bronn, 1837. Other topotypes from May-sur-Orne are in the d'Orbigny Collection at the MNHN. Incomplete preservation of specimens of this species, which are characteristically found as steinkerns, makes generic assignment problematical. We questionably place the species in *Metaconularia*, in contrast to Moore & Harrington (1956) and Fischer (1980).

Indigenous specimens of *Metaconularia?* *pyramidata* all occur in Upper Ordovician rocks. From a palaeobiogeographical standpoint, the species occurred in two areas during the Late Ordovician, Normandy and Bohemia, both within the Gondwana palaeocontinent. Reworked specimens found in the Triassic BSPBF occur on a different Ordovician palaeocontinent as Devon is on the other side of the Rheic Suture and was part of Avalonia during the Ordovician (Fig. 2). They were therefore reworked from one Ordovician palaeocontinent (Gondwana) to another (Avalonia) after closure of the Rheic Ocean. This reinforces the palaeobiogeographical patterns that have been documented for some brachiopod species by Cocks & Lockley (1981) and Cocks (1993). Transportation during Triassic times in an apparently powerful, generally northward-flowing, braided river system containing heavy loads of coarse sediment was responsible for redeposition of Ordovician *M.?* *pyramidata* in the Budleigh Salterton Pebble Bed Formation of Devon.

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