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A New Hyolithid *Australolithes troffsensis* gen. et sp. nov. from an Early Devonian (Lochkovian) Limestone in Central New South Wales

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ABSTRACT

Hyoliths have a sparse fossil record worldwide in the Devonian, with only one Devonian hyolith from Australia – the orthothecid *Costulatotheca schleigeri* – treated systematically to date. The material described here, from the Connemarra Formation of central New South Wales, comprises disarticulated conches and opercula showing a range of sizes. Since all have the same proportions and structural features, they are considered a growth series from a single species *Australolithes troffsensis* gen. et sp. nov., characterized by a smooth external surface on the conch and operculum, as well as a pair of smooth straight hollow clavicles with a circular cross-section on the operculum. The specimens described here are unusual in being completely replaced by goethite (iron oxide-hydroxide), allowing their preservation in residues from acetic acid etching of a limestone sample.

INTRODUCTION

Hyoliths were somewhat enigmatic animals of the Palaeozoic Era, considered most likely to have been lophotrochozoans, and possibly lophophorates (Moysiuk et al. 2017; Liu et al. 2019). The group is characterised by a distinctive elongate conical shell and lid-like operculum. They were most abundant and diverse in the early Cambrian, with occurrences decreasing through the Palaeozoic until they likely disappeared in the late Permian (Malinky and Racheboeuf 2010). The Hyolitha are divided into two orders, the Hyolithida and Orthothecida. The Hyolithida are distinguished from the Orthothecida by having helens (additional paired protruding appendages), and clavicles developed on the inner surface of the operculum. The family Hyolithidae are characterized by having a conch with a rounded (convex) dorsum and a flat or slightly inflated venter (Malinky 1988). The youngest species were possibly the orthothecid hyoliths *Australotheca lanceolata* (Morris, 1845), originally assigned to the Pteropoda, and *Illawarratheca wilkesi* Malinky, 2009, from upper Permian strata of the Sydney Basin and Hunter Valley, New South Wales (Malinky 2009).

Tate (1892) was the first to recognize and describe hyoliths from Australia, in the Cambrian of South Australia. Most records of hyoliths from Australia are of Cambrian age (e.g. Bengtson et al. 1990; Kruse 1990, 1991, 1998, 2002; Skovsted et al. 2014, 2016, 2020; Smith et al. 2015, 2020), but poorly preserved hyoliths have also been described from late Silurian and Lochkovian (Early Devonian) sediments of central

Victoria (Chapman 1903, 1904; Talent 1963, 1964; Williams 1964), and more recently from the Devonian and Carboniferous of New South Wales. The only mid-Palaeozoic Australian taxa formally described to date are *Hyolithes spryi* Chapman, 1904 from the Melbourne Formation of Ludlow age (late Silurian) in Victoria, *Hyolithes (Pharetrella) pyramidalis* Talent, 1963 from the ?early Pragian (Early Devonian) of Victoria, *Lentitheca*? *semicostata* Talent, 1964 from the Dargile Formation of Ludlow age in Victoria, *Costulatotheca schleigeri* Earp, 2019 from the Early Devonian (Pragian–Emsian?) Norton Gully Sandstone, Victoria, and *Hyolithes minitissimus* Yoo, 1988, from early Carboniferous (late Tournaisian) limestone bands of the Dangarfield Formation near Gundy, New South Wales. Earp (2019) considered that Talent's (1963, 1964) taxa were probably orthothecids. *Costulatotheca schleigeri* is an orthothecid hyolith, erected for internal and external molds of conches and an operculum. The type material of *H. minitissimus* was preserved with a rich molluscan fauna, and is based on conches only, as no opercula were recovered. The specimens are also very small (3–6 mm long) and preserved via chlorite replacement of the shells. The generic assignment of this species is questionable, as Malinky (2009, p. 149) considered *Hyolithes* to be an exclusively European genus, characterized by its short ligula, flared apertural rim, low dorsum, and prominent longitudinal sulcus on each edge of the rounded dorsum (Malinky 1988). '*Hyolithes*' *minitissimus* appears to lack the longitudinal sulci (Yoo 1988, figs. 155–157, 163, 165).

Here we describe a new genus and species of hyolithid from the earliest Devonian (Lochkovian) of central New South Wales. The specimens were preserved in the residues from acetic acid etching of a limestone sample to retrieve vertebrate microremains.

GEOLOGICAL SETTING

The Connemarra Formation is a mostly subsurface stratum in the Trundle Group of central western New South Wales (Sherwin 1996). Fossiliferous limestone beds of the formation crop out in locality GSNSW C669, to the north of the Trundle-Fifield Road (Fig. 1; see Burrow 2006 for further site information). The provenance of the hyolith-bearing sample is not necessarily from the outcrop, as loose limestone rocks from the surrounding pastureland have been collected and concentrated in its vicinity. However, it seems reasonable to assume, based on the accompanying vertebrate assemblage, that the hyolith-bearing sample is from the same level as the outcrop. The vertebrate assemblages found in all samples collected from the site (Burrow 1997, 2002, 2006) comprise mostly fractured and remineralised micro-remains in lag deposits. The invertebrate assemblage is also rich, and includes brachiopods, bryozoans, conodonts, corals, crinoids, ostracods, scolecodonts and tentaculites. Only the brachiopods and conodonts from the Connemarra Formation have been described (Sherwin 1996), and just one of the samples collected contains hyoliths. Dating of the outcrop is uncertain, as the conodonts recovered in the samples are long- ranging and the other invertebrates have not been studied, but a late Lochkovian age seems most likely by comparison with similar vertebrate faunas preserved in better dated strata to the east (Basden et al. 2000).

MATERIALS AND METHODS

The hyolith-bearing sample was collected by the senior author in 2008. The specimens were picked from the residues left after dissolving the limestone blocks in buffered acetic acid, following the standard technique of Jeppson et al. (1999). Remnants of close to a hundred conches and opercula were recovered, with nearly all being broken. They appear to be preserved by goethite (iron oxide-hydroxide) replacement of the calcium carbonate (aragonite) shells, which presumably would have been dissolved by the acid if the specimens had not been remineralised. Very few conches are preserved intact, and all have adhesions on them. Ultrasonic cleaning was tested on a few specimens, but was unsuccessful as the elements disintegrated. Selected specimens were imaged with the Tabletop ESEM at the Queensland Museum, and one was sacrificed for powder X-Ray diffraction (XRD). The latter was performed at the X-Ray Diffraction Laboratory of the University of New South Wales using an Empyrean diffractometer fitted with Co source with following optics: Incident Beam = BBHD optics with 1/4° fixed slit and 1° Antiscatter slit, Diffracted Beam = 11.2 mm antiscatter Slit and PIXCel detector. Data collection for the X-ray diffraction was performed over 5° to 120° 2-theta with 0.04 step size and 500s/step. Data was processed using HighScore software.

Institutional abbreviations: GSNSW, Geological Survey of New South Wales; MMMC, microfossil collection of the GSNSW. Anatomical abbreviations: co, conch lateral sinus; cp, cardinal process; cl, clavicle; dorsum; l, ligula; r, rooflet; v, venter.

SYSTEMATIC PALAEONTOLOGY

CLASS HYOLITHA Marek, 1963

ORDER HYOLITHIDA Sysoev, 1957

Family HYOLITHIDAE Sysoev, 1958

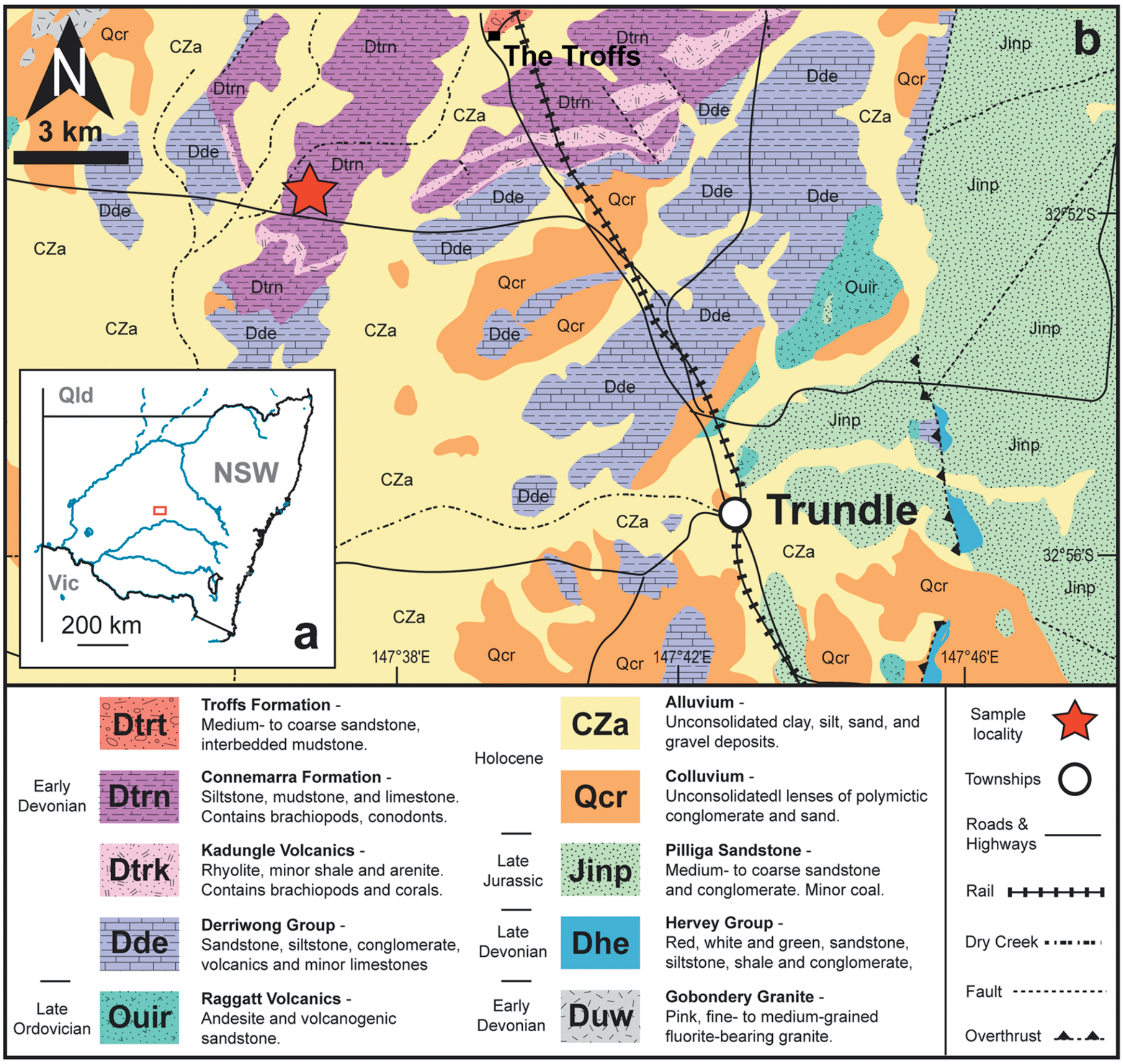

Figure 1. a, Map of New South Wales showing location of Trundle district, denoted by a red rectangle; b, Simplified geological map of the Trundle district (modified from Colquhoun et al. 2022) with hyolith sample locality indicated by red star.

Genus *Australolithes* gen. nov.

Diagnosis

Small hyolithids, conch up to 12 mm in length, external surface unornamented, apical angle 20º, ligula D-shaped, with flat venter and arched dorsum; operculum length c. 2/3 width, clavicles with circular cross-section, clavicles converge at 110º angle, cardinal processes meet at 70º.

Type species

Australolithes troffsensis

Etymology

Latin australis, meaning southern, referring to the Southern Hemisphere and Australia, the country, and -lithes, from Hyolitha.

Australolithes troffsensis gen. et sp. nov.

Etymology

Troffs-, based on the name of the 'township' (The Troffs) nearest to the sampling site, and -ensis, for origin.

Repository

MMMC, microfossil collection of the Geological Survey of New South Wales (GSNSW), Londonderry (western Sydney).

Type material

Holotype conch MMMC 05943. Paratypes: conches MMMC 05944–05951, opercula MMMC 05952–05958.

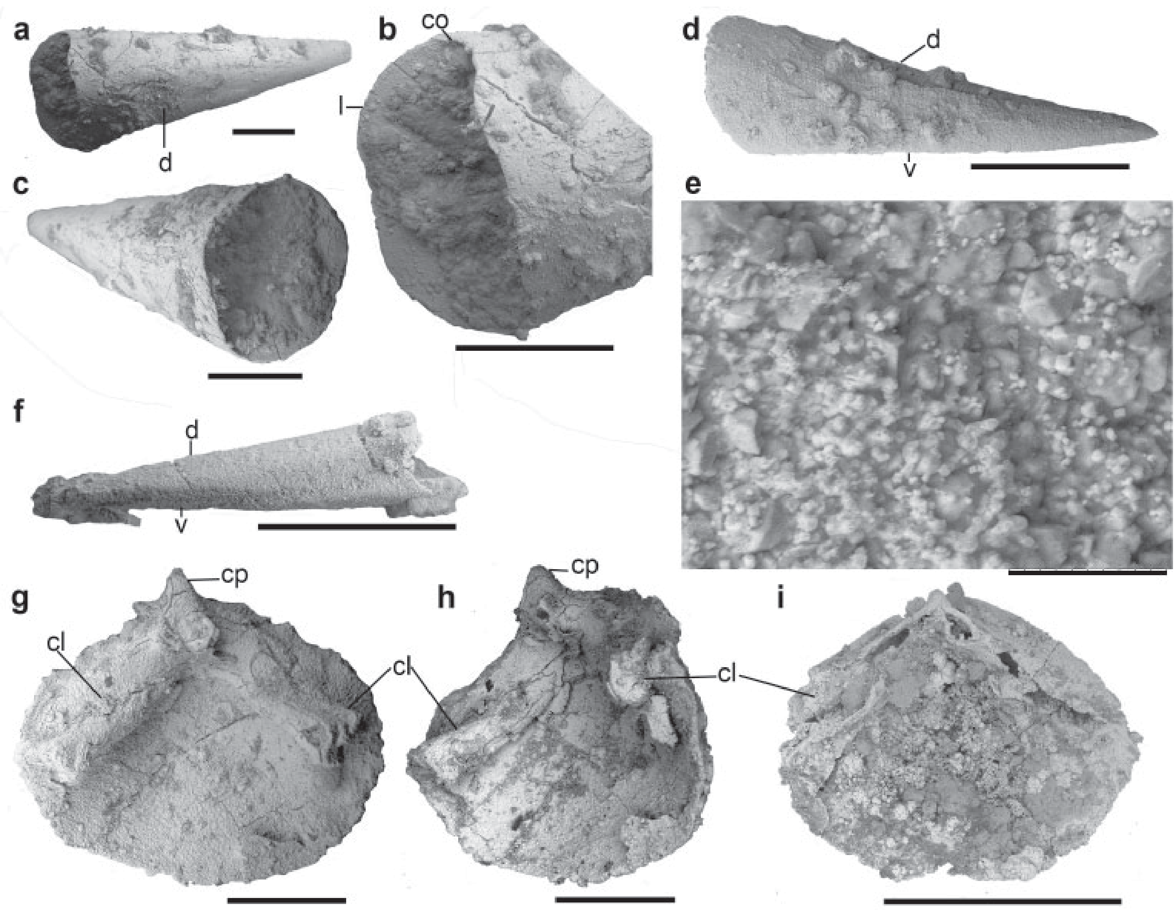

Figure 2. ***Australolithes troffsensis*** **gen. et sp. nov. type material from the Lochkovian Connemarra Formation, central New South Wales; SEM images. a–c, holotype MMMC05943, conch; d, paratype MMMC05944, conch, goethite crystals on surface magnified in e; f, paratype MMMC05945; g, h, paratype MMMC05946, operculum, internal views; i, paratype MMMC05947, operculum, internal view. Scale bar is 1.0 mm in a–d, f–i, 0.2 mm in e.**

Type locality and stratigraphy

GSNSW locality C669, northwest of Trundle, central New South Wales.

Diagnosis

As for genus, presently monospecific.

Description

Conches 3–12 mm in length, up to 4 mm wide, and 2.5 mm high, with flat venter and arched dorsum. Apical angle 20º (Figs 2a–f and 3a–e). Relatively smooth outer surface without longitudinal ridges or grooves; fine longitudinal striae visible at high magnification on some conches (Fig. 2b, 2d and 2f). Transverse growth lines vaguely visible on one conch (Fig. 2d), potentially hidden due to loss of outer layer. Conch ligula and ventral margin of the aperture D-shaped, strongly curved at each end and straight to slightly bowed anteromedially (Figs 2a, 2b, 3a, 3b, 3d and 3e).

Opercula length c. 2/3 width (Figs 2g–2i and 3f–3k). Smooth, straight, hollow clavicles with circular cross-section. Cardinal processes broken in most specimens, few have remnants of two processes (Fig. 3g). The angle between the clavicles c. 110º; angle between cardinal processes c. 70º. No clearly identifiable helens recovered; small cylindrical fragments of an appropriate size were noted, but lacked any longitudinal curvature. Rooflets well developed on the opercula; presumably helens projected between the rooflets and the conch lateral sinus (see Martí Mus and Bergström 2005, text-fig. 13C; Skovsted et al. 2020, fig. 1C).

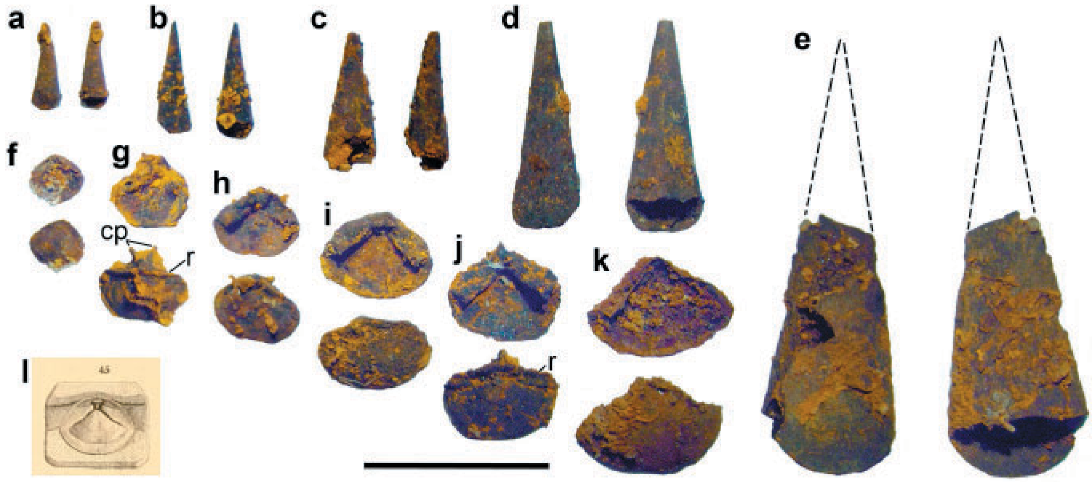

Figure 3. a–k, *Australolithes troffsensis* gen. et sp. nov. paratypes from the Lochkovian Connemarra Formation, central New South Wales; light microscope images of venter and dorsum of conches and internal and external views of opercula. a, MMMC05948, conch; b, MMMC05949, conch; c, MMMC05950, conch; d, holotype MMMC05943, conch; e, MMMC05951, conch; f, MMMC05952, operculum; g, MMMC05953, operculum; h, MMMC05954, operculum; i, MMMC05955, operculum; j, MMMC05956, operculum; k, MMMC05957, operculum. l, isolated operculum from the lowermost Lochkovian at Sancta Benigna, Czech Republic (Barrande 1867, pl. 15 fig. 45; scale not known). Scale bar is 5 mm.

Remarks

Conches show no evidence of pores in the walls or horizontally oriented tubules like those described by Kouchinsky (2000) for orthothecids. Neither could any muscle attachment areas on the opercula like those described by Martí Mus and Bergström (2005) be distinguished, but the poor preservation and extensive adhesions no doubt obscure subtle features on the specimens.

The microstructure of the conches, comprising longitudinal and transverse fibres, is exposed on specimens which possibly lost their external surface layer (Fig. 2d). Also visible at high magnification are crystals of goethite (Fig. 2e), replacing aragonite, likely as a result of iron mobilization from volcanic or volcano-clastic source rocks (e.g. see Holocene example of coral replaced by goethite by Lee and Taib 2006). XRD analysis of a conch fragment (Fig. 4) showed goethite as the major phase (more than 30%), quartz as minor phase (5-10%), and rutile and albite in trace (less than 2%).

DISCUSSION

Lamellar structures in hyolith conches from the Ordovician and Permian were described by Runnegar et al. (1975). Similarly phosphatized internal moulds of Cambrian hyolith conches from western Queensland preserve identical inner surface features (Runnegar 1985, fig. 6). Based on these observations, the conch structure likely comprised several layers forming ‘crossed-lamellar aragonite’. This agrees with the observations of Moore and Porter (2018) who demonstrated that Cambrian hyoliths from the Georgina Basin of western Queensland have a fibrous or lamello-fibrillar microstructure. Indeed conches and opercula from the same taxon possess similar microstructures. They noted that in some cases the conches are formed of elongate elements arranged longitudinally in the outer part of the wall. This is contra Runnegar’s (1985) interpretation, and also differs from the ‘linear first-order lamellae’ seen in gastropods, as the fibres are parallel to the conch surface. Moore and Porter (2018) observed that, unlike some orthothecids, the fibres in the hyolithidid conch walls they studied did not form distinct bundles; similarly, the fibres in *Australolithes troffsensis* do not appear to be arranged in bundles. Skovsted et al. (2020, figs. 2 and 6D–6K) described and figured phosphatized hyolith helens and opercula, showing that the helens and clavicles also have a fibrous structure.

The only other named taxon from the Devonian of Australia, *Costulatotheca schleigeri*, is clearly different from *Australolithes troffsensis*, being an orthothecid hyolith ornamented with narrow

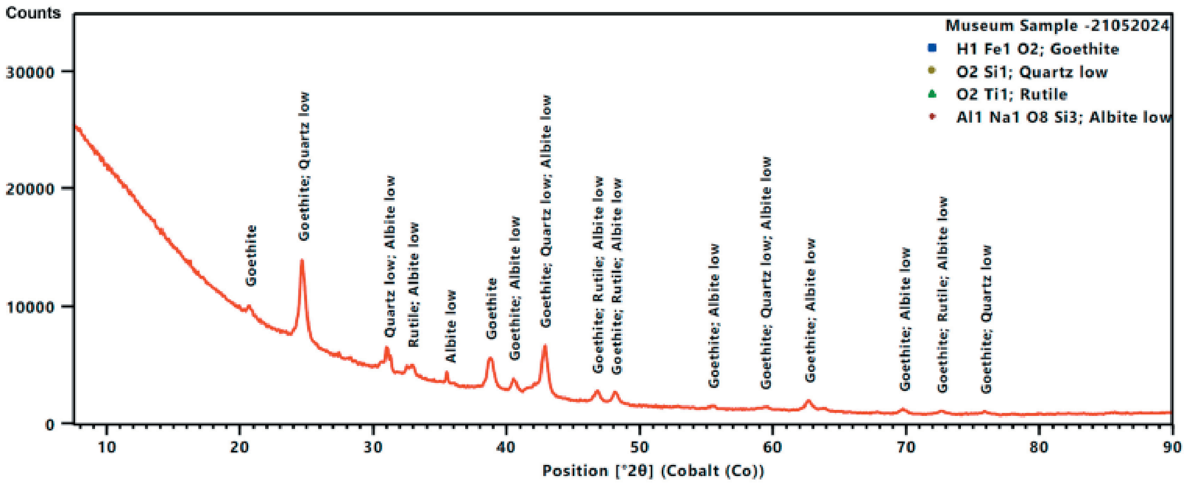

Figure 4. Processed plot for XRD analysis of *Australolithes troffsensis* conch fragment. Goethite is the major phase (more than 30%), quartz is minor phase (5-10%), and Rutile and Albite are in trace (less than 2%).

longitudinal ridges (Earp 2019, fig. 3). The Connemarra Formation hyoliths show similarities with some other Early Devonian taxa. *Bolithes* specimens from the ?Pragian or Emsian of the Icla Formation in the Central Subandan Zone, Bolivia (Malinky and Racheboeuf 2011) are of a comparable size, with the conch and operculum having a similar outline and shape to that of *Australolithes troffsensis*. However, in *Bolithes* the conches are ornamented, they possess a sharper apical angle, and the internal structure of the operculum is unknown. Conches of '*Hyolithes*' *dorbignyi* Kozlowski, 1923 from the Givetian Belén Formation in Bolivia have a similar cross-sectional shape (Malinky and Racheboeuf 2011, fig. 4.9 and 4.10), but that species was based on incompletely preserved internal molds with no specific diagnostic characters distinguishable.

Some of the taxa from the Early Devonian of the Czech Republic erected by Barrande (1867) resemble *Australolithes troffsensis*. Of these, *Ottomarites discors* (Barrande, 1867) differs in having a conch with a high triangular cross-section and a moderately convex venter; also the operculum has two pairs of narrow clavicles (Barrande 1867, pl. 16, figs 1–6; Valent and Malinky 2008, fig. 1). The conches of *Hyolithes alter* (Barrande 1867, pl. 15, fig. 27–31; level G, g1) from the Pragian–lower Emsian most closely resemble those of *A. troffsensis* in having a subtriangular cross-section, but they are transversely ornamented externally, and have the two longitudinal sulci on the dorsum considered by Malinky et al. (1987) to be a diagnostic character of *Hyolithes* sensu lato and *Hallotheca* Malinky et al., 1987. At least one of the isolated opercula from the lowermost Lochkovian which was illustrated by Barrande (1867, pl. 15, fig. 45; table p. 70, level D, d1; Fig. 3l herein) is possibly similar to those of *Australolithes troffsensis* in its shape and position of the clavicles, based on the illustration; that operculum was not assigned to a taxon.

The hyolithid with conches most similar to those of *Australolithes troffsensis* is possibly the only other named Australian hyolithidid, '*Hyolithes*' *minitissimus* of early Carboniferous age. Both species are small, with unornamented conches having a subtriangular or rounded D-shaped cross-section. Unfortunately, as no opercula have been identified for the latter species, we can only speculate that it would be better referred to tentatively as *Australolithes*? *minitissimus*.

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