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RESEARCH ARTICLE

Ninmarooceras gen. nov., a unique cephalopod from the Cambrian-Ordovician transition of Australia

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The Ellesmeroceratida contains some of the oldest known fossil cephalopods. The order is almost entirely restricted to the latest Cambrian to Early Ordovician and is crucial for understanding the origin and early radiation of cephalopods. Here, we describe the new ellesmeroceratid genus *Ninmarooceras* from the Cambrian-Ordovician transition of the Ninmaroo Formation at Black Mountain, western Queensland, Australia. This genus is unique among cephalopods in its peculiarly shaped siphuncular diaphragms that are steeply inclined and branch towards the venter. Besides the straight to very slightly endogastrically curved type species *Ninmarooceras ramosum* gen. et sp. nov., we describe a second species, *N. exoundulatum* gen. et sp. nov. The latter species is slightly older and combines an exogastrically curved conch with shallow undulations. The combined occurrence of these features within a single genus calls into question their diagnostic potential in distinguishing between taxonomic groups above genus level of the Ellesmeroceratida and related early cephalopods. The variability of diaphragm morphology also supports the restriction of the Yanhecerati-dae as a family within the Ellesmeroceratida instead of its own order. We further discuss evolutionary and functional implications of the unique internal siphuncle structure of *Ninmarooceras*.

Cephalopoda | Ellesmeroceratida | Stage 10 | Tremadocian | Mount Unbunmaroo | Ninmaroo Formation | siphuncle | diaphragms

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Introduction

Cephalopods originated in the Cambrian and underwent a rapid radiation during the Early Ordovician (e.g., Kröger *et al.*, 2011; Pohle *et al.*, 2022). Despite the importance of the interval around the Cambrian-Ordovician transition for cephalopod evolution, many of these taxa remain poorly studied (Flower, 1954, 1964; Chen and Teichert, 1983; Kröger and Landing, 2007; Landing and Kröger, 2009; Dzik, 2020; Cichowolski *et al.*, 2023; Pohle *et al.*, 2024). The Ellesmeroceratida contains most of the currently known Cambrian species (Chen and Teichert, 1983; Pohle *et al.*, 2024). While the second major order of Cambrian cephalopods, the Plectronoceratida, was recently revised (Pohle *et al.*, 2024), the same treatment for the Ellesmeroceratida is still pending. This task is complicated by the fact that many species and genera are defined using subjective criteria, such as 'high expansion rate' or 'strong curvature' (Flower, 1964). Quantitative threshold values are typically missing or have only been defined relatively recently for few taxa (Kröger and Landing, 2007). In contrast to the comparatively low-diversity Plectronoceratida, the Ellesmeroceratida contains more than 400 recognised species in dozens of genera (MolluscaBase eds., 2025), complicating comparisons and attempts at revision.

A characteristic feature of many ellesmeroceratidans are the diaphragms, thin calcareous structures crossing the siphuncle transversely, effectively forming irregular septa within the siphuncle (Flower, 1964). Little is known about their morphological variability, although some species appear to possess more closely spaced, deeply conical, or strongly inclined diaphragms (Flower, 1964; Chen *et al.*, 1979a). It has been hypothesised that 'stacked' diaphragms represent the ancestral form of endocones, which are characteristic of endoceratoids (Evans, 1992; Evans and King, 2012). Knowledge of diaphragms is typically restricted to 2D-sections, where the influence of the plane of section on the reconstructed shape may be unclear. At least in plectronoceratidans, the diaphragms have complex 3D-morphologies that may be misinterpreted when viewing them from a single thin section only (Pohle *et al.*, 2024). In other cases, the rounded apical end of the siphuncle of specimens preserved as internal moulds has been interpreted as reflecting the shape of the diaphragms (Flower, 1964; Evans, 1992, 2005). The variability of diaphragms is expressed in their shape, i.e., concave or deeply conical, and different spacings. The function of diaphragms is interpreted as sealing off the apical end of the siphuncle to prevent passive flooding of apical chambers (Evans, 1992). Apart from ellesmeroceratidans and plectronoceratidans, diaphragms also occur in the Cyrtocerinida (Evans, 2005), early Oncoceratida (Evans and King, 1990), Cyclostomiceratidae Foerste, 1925 (Mutvei and Stumbur, 1971), Endoceratida and Bisonoceratida (Evans and King, 2012) and some early orthoceratoids belonging to the Riocerati-da or Dissidoceratida (Kröger and Landing, 2009; Kröger and Evans, 2011; Kröger and Pohle, 2021). They are thus present in all major cephalopod groups that were present during the Ordovician, i.e., Orthoceratoidea, Endoceratoidea and Multiceratoidea. Although it is possible that not all diaphragms are homologous (Evans and King, 2012), it appears that the presence of diaphragms is plesiomorphic in cephalopods and they were independently lost in multiple lineages (compare Pohle *et al.*, 2022). Generally, diaphragms seem to be almost entirely restricted to the Cambrian and Early Ordovician, with the Darriwilian cyclostomiceratid *Pictetoceras* Foerste, 1926 representing one of the few exceptions (Mutvei and Stumbur, 1971).

Here, we describe a new genus *Ninmarooceras* from the Cambrian-Ordovician boundary interval of western Queens-

land, with peculiarly shaped diaphragms unknown in any other cephalopod. Two new species of the genus are described. The material originates from the Ninmaroo Formation at Mount Unbunmaroo (Black Mountain), an important reference section for Australian Cambrian stratigraphic correlations (e.g., Druce *et al.*, 1982; Shergold *et al.*, 1991; Shergold and Nicoll, 1992; Laurie *et al.*, 2024; Zhen *et al.*, 2025) and is part of a large collection of fossil cephalopods made by the late Dr. Mary Wade and colleagues during the 70s and 80s, housed at the Queensland Museum (Wade, 1988; Wade and Stait, 1998; Pohle *et al.*, 2024). Her career and significance in Australian palaeontology have been summarised by (Turner, 2007). The material itself remained undescribed during Mary Wade's lifetime and mostly overlooked by later researchers until the recent description of abundant material of the plectronoceratid *Sinoeremoceras marywadeae* Pohle, Jell and Klug, 2024. Ellesmeroceratidans are even more numerous in the collection and are still in the process of being described. The genus described here is published separately due to its uniqueness deserving special attention.

Materials and methods

All material was collected between 1970 and 1990 during various field trips by Mary Wade and colleagues to Mount Unbunmaroo (see Pohle *et al.*, 2024, for additional background). The locality, which is also known as Black Mountain, is situated in the south-eastern Georgina Basin, western Queensland, Australia (Figure 1A). Unfortunately, the only evidence for the stratigraphic position of the specimens are labels on the fossils with the prefix 'BMT' (presumably an abbreviation for Black Mountain) and a number. Several of these numbers were marked by Mary Wade on a printed copy of text-fig. 4 in Druce *et al.* (1982). This includes BMT 1 and BMT 1/2 in the Ninmaroo Member, BMT 2 in the upper part of the Jiggamore Member, BMT 3 at the base of the Mort Member and 19 BMT [sic.] and BMT 20 in the lower Corrie Member. The specimens described here carry the labels BMT 15 and BMT 17. Their precise position was not noted by Mary Wade. Since BMT 3 and BMT 19 mark the lower and upper boundary of the Mort Member, it appears reasonable to assume that the specimens originate here. A note by Mary Wade reads 'very patchy nauts' (= nautiloids), marking an interval in the middle Mort Member between approximately 820–860 m in the section of Druce *et al.* (1982). Thus, it appears reasonable to assume that BMT 4–18 represent successive low-abundance horizons within the Mort Member. Accordingly, the material described here likely belongs to the upper half of the Mort Member, representing the *Cordylodus lindstromi* Zone of the Warendan Regional Stage (Druce *et al.*, 1982; Shergold and Nicoll, 1992; Zhen *et al.*, 2025).

There has been extensive discussion around the placement of the Cambrian-Ordovician boundary at Mount Unbunmaroo in particular and in Australia more generally (e.g., Druce and Jones, 1971; Jones *et al.*, 1971; Druce, 1978; Druce *et al.*, 1982; Nicoll and Shergold, 1991; Shergold *et al.*, 1991; Webby *et al.*, 1991; Shergold and Nicoll, 1992; Zhen *et al.*, 2017, 2025; Laurie *et al.*, 2024). The most recent publications place the boundary high or at the top of the *C. lindstromi* Zone (Zhen *et al.*, 2025; Brock *et al.*, 2026). This means that placement of the boundary in Pohle *et al.* (2024) was slightly too low, as pointed out by Brock *et al.* (2026). All specimens described here therefore are likely latest Cambrian (Stage 10, Furongian) in age (Figure 1B).

Terminology follows Teichert (1964) and Pohle *et al.* (2022). Abbreviations of conch parameters and their calculation are accordingly the following: CWI = conch width index (conch width / conch height), RCL = relative cameral length (cameral length / conch height), RSD = relative siphuncular diameter (siphuncle diameter / conch height), HER = height expansion rate (2 * arctan((maximum height / 2 - minimum height / 2) / fragment length)), WER = width expansion rate (2 * arctan((maximum width / 2 - minimum width / 2) / fragment length)).

We apply the '-ceratida' suffix for orders, as appears to have become consensus among most Palaeozoic cephalopod workers following a proposal by King and Evans (2019). When referring to members of an order in plural, we use the ending '-ceratidans', to clearly distinguish from family level taxa, which

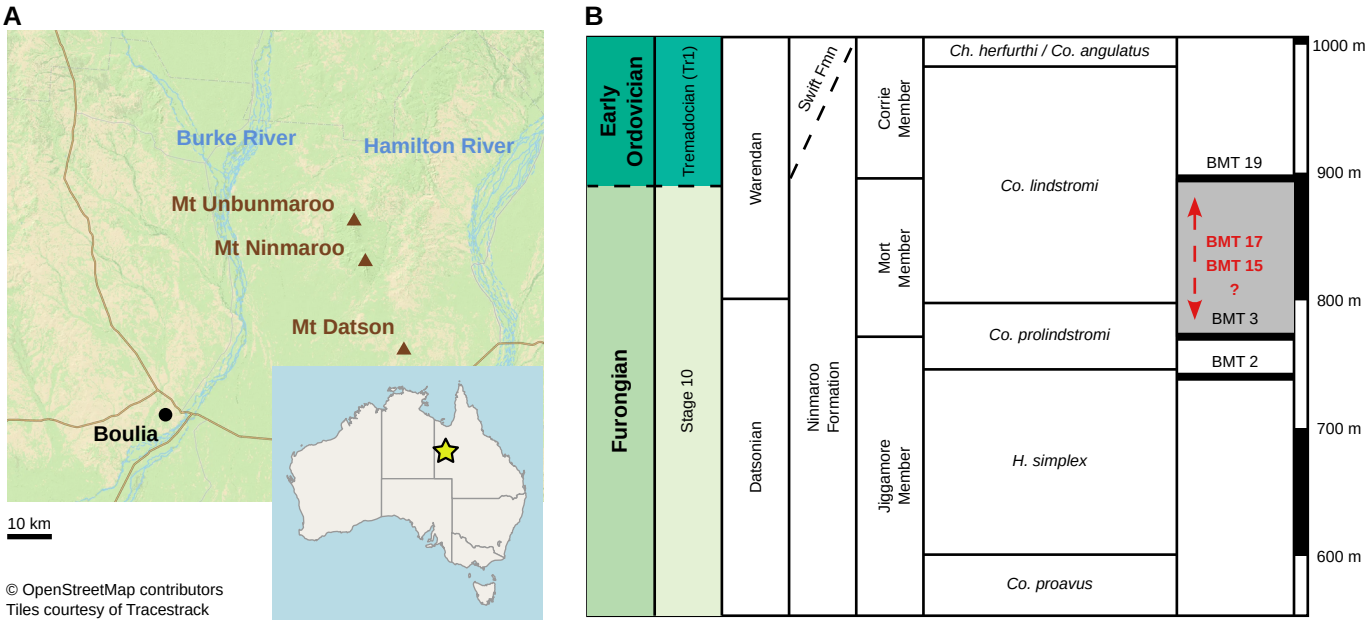


Figure 1. Stratigraphy and map. (A) Stratigraphic overview and correlation of the locality, modified from Pohle *et al.* (2024). BMT horizons represent 'nautiloid bands' marked by Mary Wade. Note that the Cambrian-Ordovician boundary may be situated as high as the top of the *C. lindstromi* Zone (Zhen *et al.*, 2025; Brock *et al.*, 2026) but is here shown lower due to uncertainty and display reasons. **(B)** Map showing the location of Mount Unbunmaroo (Black Mountain) within the south-eastern Georgina Basin and Australia.

are referred to as '-ceratids'. Thus, 'ellesmeroceratidans' refers to the order Ellesmeroceratida and 'ellesmeroceratids' to the family Ellesmeroceratidae Kobayashi, 1934, avoiding ambiguity when using these terms.

Results

Systematic palaeontology

Class **Cephalopoda** Cuvier, 1797
Order **Ellesmeroceratida** Flower in Flower and Kummel, 1950
Family **Ellesmeroceratidae** Kobayashi, 1934

Genus ***Ninmarooceras*** gen. nov.
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Type species. *Ninmarooceras ramosum* gen. et sp. nov.; from the Mort Member of the Ninmaroo Formation (Stage 10, Furongian, Cambrian), Queensland, Australia.

Included species. *Ninmarooceras ramosum* gen et sp. nov., *N. exoundulatum* gen. et sp. nov.

Derivation of name. Referring to the Ninmaroo Formation, where all known specimens were collected.

Diagnosis. Orthoconic to slightly cyrtoconic, endogastric or exogastric conch with compressed cross section. Dorsoventral angle of expansion moderate, constant throughout ontogeny (HER ~ 8–10°). Sutures with shallow lateral lobes and equally high ventral and dorsal saddles. Septa relatively shallowly curved, with narrow septal spacing (RCL ~ 0.1). Siphuncle ventral, marginal and moderate in size (RSD ~ 0.2). Septal necks loxochoanitic with gradual neck transition, their length micro- to mesochoanitic. Connecting rings layered, thick, widening adapically within siphuncular segment and concave inwards. Diaphragms present, more closely spaced than chambers and strongly sloping dorsaperturally, but approximately in the centre of the siphuncle branching into multiple sheets that are almost transverse towards the dorsal side of the siphuncle.

Remarks. The peculiar shape of the diaphragms distinguishes this genus from all other known cephalopods. This comes with the caveat that the shape of the diaphragms is entirely unknown for many other ellesmeroceratidans, making comparisons difficult. *Ninmarooceras* is most similar to the early Tremadocian *Ectenolites* Ulrich and Foerste, 1936 and *Ellesmeroceras* Foerste, 1921 in general conch shape. However, both of these genera are distinctively endogastrically curved in early ontogenetic stages, which is not visible in the material of *Ninmarooceras* at hand. In addition, those species from which diaphragms are well-documented (e.g., *Ectenolites primus* Flower, 1964, *Ellesmeroceras progressum* Flower, 1964 and *Annoceras costatum* Flower, 1964) differ in lacking the branched shape of the diaphragms, but instead possess simple transverse, apparently convex diaphragms. In general, the siphuncle of *Ninmarooceras* is more similar to Ordovician ellesmeroceratidans than to Cambrian taxa with its thick connecting ring and concave siphuncular segments. A good example is the type material of *Ellesmeroceras bridgei* Flower, 1941. In contrast, Cambrian ellesmeroceratidans display relatively thin connecting rings (same or less than thickness of septa) and straight segments. One of the few exceptions is *Sinolebetoceras* Chen and Qi in Chen, Zou, Chen and Qi, 1979b, which differs in having much longer septal necks.

While the exclusively Cambrian Yanheceratidae Chen & Qi in Chen, Zou, Chen and Qi, 1979a share modified, elongated diaphragms, they are uniformly conical in *Yanheceras* Chen in Chen, Zou, Chen and Qi, 1979a and *Archendoceras* Chen and Qi in Chen, Zou, Chen and Qi, 1979a. In *Aetheloxoceras* Chen and Qi in Chen, Zou, Chen and Qi, 1979a, they appear more complex and tightly spaced, but they are steeply sloping towards the venter in apertural direction, opposite of the condition in *Ninmarooceras*. The diaphragms in *Aetheloxoceras* also lack clear indication of branching. In *Oonendoceras* Chen and Qi, 1982, the diaphragms are tightly spaced, conical and potentially perforated. We conclude that if the Yanheceratida is to be accepted as an order, then the same rank would be warranted for a taxon containing *Ninmarooceras*. However, such an approach would not seem to serve any practical purpose, as it would lead to an inflation of low-diversity high-rank taxa and render any 'ellesmeroceratid-like' fossil without known (apical) internal siphuncle structures unidentifiable at order level and below. Therefore, we here consider the order Yanheceratida Chen in Chen, Zou, Chen and Qi, 1979a as a junior synonym of the Ellesmeroceratida. Potentially, the same reasoning could be applied at family level, but we reserve this judgement for a future revision, as it is possible that many Cambrian and Ordovician ellesmeroceratidans may be differentiated by their siphuncle as indicated above, and this would require reclassifying many genera.

Ninmarooceras ramosum gen. et sp. nov.
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Figures 2, 3 and 4A, B

Holotype. QMF 61655, a sectioned phragmocone fragment.

Type locality and horizon. Mount Unbunmaroo (Black Mountain), near Boulia, NW Queensland, Australia; upper Ninmaroo Formation, upper Mort Member (BMT 17), *Cordylodus lindstromi* Zone, Latest Stage 10, Furongian, Cambrian.

Paratypes. QMF 61656, a sectioned phragmocone fragment and QMF 13188a–c, thin sections of a single phragmocone fragment, with a and b representing parallel longitudinal sections presumably close to the median plane, while c represents a cross section at the apertural end of the specimen.

Derivation of name. Ramosum (lat.) = branching; referring to the branched diaphragms in longitudinal section.

Diagnosis. *Ninmarooceras* with orthoconic conch and smooth shell. Diaphragms branching into bundles of 3–5 ventrally, tightly spaced on dorsal side. Distance between diaphragm bundles shorter than distance between first and last diaphragm within bundle. Septal necks loxo- and mesochoanitic.

Description. QMF 61655 (Figure 2) is chosen as holotype here, because it shows the three-dimensional outline of the conch combined with internal characters. The fragment is 8.7 mm long and expands from a height of 8.3 mm and a width of 7.4 mm at its apical end to a height of 9.5 mm and a width of 8.8 mm at its apertural end (widths estimated). The conch thus expands at 8.3° in height and 8.8° in width. CWI is approximately 0.9. Nine phragmocone chambers are preserved, plus two fragmentary chambers at the apertural end where only the siphuncle and the septal necks are present. Cameral length is approximately 0.7 mm apically and 1.1 mm aperturally (RCL ~ 0.1). The siphuncle has a diameter of approximately 1.5 mm and remains constant in the fragment (RSD ~ 0.17). The septal necks



Figure 2. Holotype QMF 61655 of *Ninmarooceras ramosum* gen. et sp. nov. Upper Ninmaroo Formation, upper Mort Member (BMT 17), latest Cambrian, Mount Unbunmaroo, Queensland, Australia. **(A)** Lateral view, siphuncle on left side. **(B–C)** Sectioned halves, median views. **(D)** Sectioned right half, apertural view, with missing part outlined. **(E)** Sectioned right half, apical view, with missing part outlined. **(F)** Detail of siphuncle. **(G)** Detail of septal necks, connecting ring and initial steep part of diaphragms. **(H)** Detail of branching convex part of diaphragms.

are loxochoanitic and somewhat hard to differentiate from the connecting ring. They appear to be slightly less than half of the length of the corresponding chamber. The connecting rings are layered, thick and concave inwards, widening towards the apical septal neck. Numerous diaphragms are present in the siphuncle, steeply sloping dorsally and branching into convex bundles ventrally. Each bundle contains 3–5 diaphragms. Individual diaphragms are difficult to distinguish due to their high density and the presence of calcite cements. Nevertheless, a single diaphragm can be traced for the length of at least six chambers in the steep part, while the convex, branching part spans less than the length of one chamber. The distance between two bundles is less than the distance between the apicalmost and aperturalmost diaphragm within the same bundle.

Three thin sections of the paratype QMF 13188a–c (Figure 3) are available for study. Two of these represent nearly identical longitudinal sections (QMF 13188a, b); thus, they are separated by only a very short distance (probably the width of the stone saw). The third section is a cross section of an apertural portion of the same specimen. The shape of the diaphragms

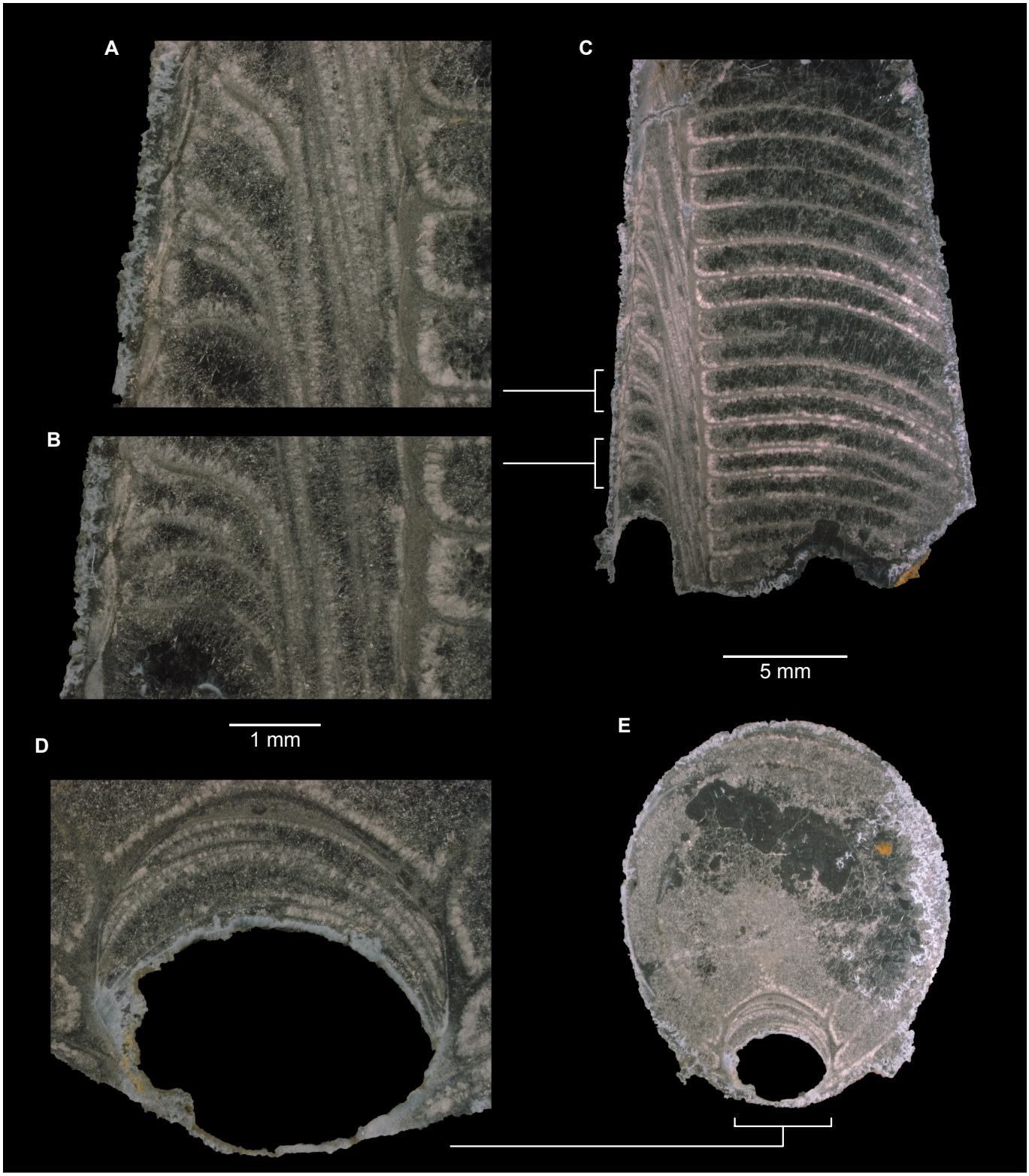


Figure 3. Thin sections of paratype QMF 13188 of *Ninmarooceras ramosum* gen. et sp. nov. Upper Ninmaroo Formation, upper Mort Member (BMT 17), latest Cambrian, Mount Unbunmaroo, Queensland, Australia. **(A–C)** QMF 13188b, longitudinal median section, including details of siphuncle and diaphragms. **(D–E)** QMF 13188c, cross section, with details of siphuncle.

and siphuncle structure are essentially identical to the holotype, but the specimen is larger, with a height of 14 mm at the apertural end and 11.5 mm at the apical end. The length of the fragment is 16.4 mm, resulting in a height expansion rate of 8.5°. Cameral length varies between 1–1.4 mm (RCL = 0.07–0.12). The diameter of the siphuncle increases from 2 mm (RSD = 0.17) to 3.1 mm (RSD = 0.22), although this may be influenced by measuring errors or a potentially slightly off-centred section. The cross section has a height of 15.3 mm and a width of 13.1 mm (CWI = 0.86). The diameter of the siphuncle is 2.8 (RSD = 0.19). Within the siphuncle, there are at least six diaphragms visible, regularly arched in the dorsal part, forming crescent shapes in the spaces between. Only one half of the paratype QMF 61656 was present in the collection. It is similar to the holotype in dimensions, 11.8 mm high and 9.7 mm (estimated) wide near the apical end (CWI = 0.82). The siphun-

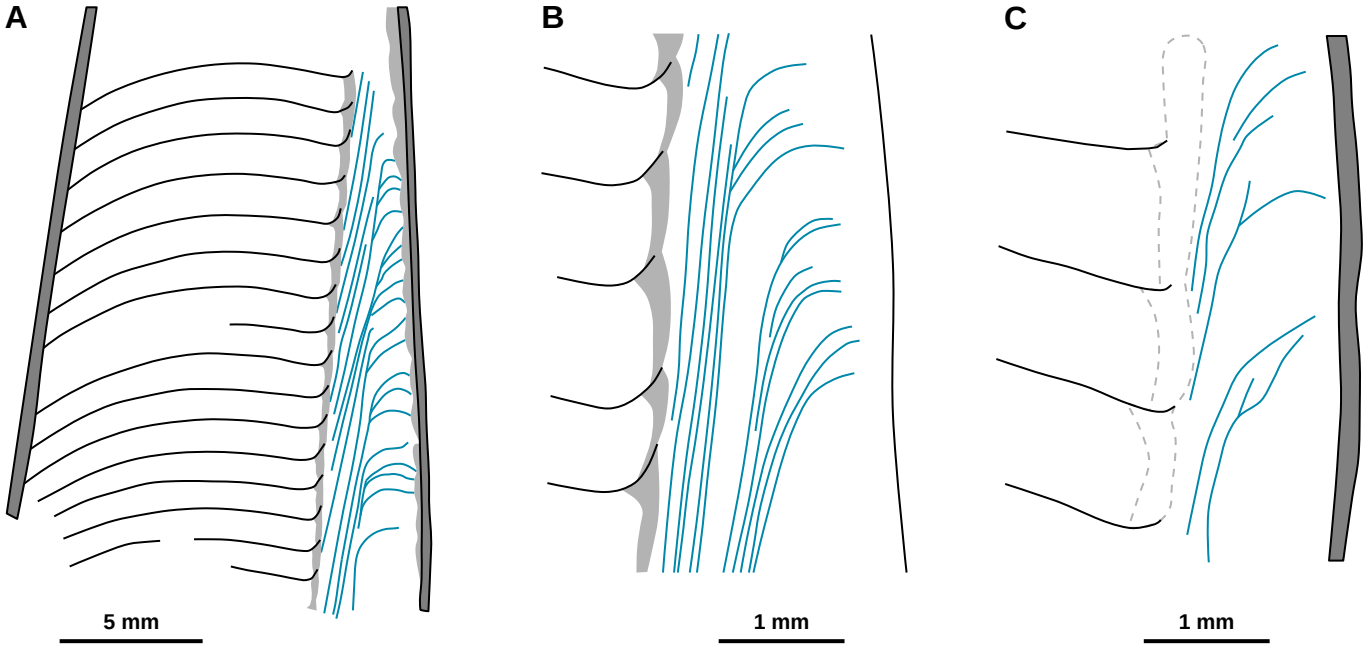


Figure 4. Interpretative drawings of median sections of *Ninmarooceras* gen. nov. (A) *Ninmarooceras ramosum* gen. et sp. nov., paratype QMF 13188b. **(B)** *Ninmarooceras ramosum* gen. et sp. nov., holotype QMF 61655. **(C)** *Ninmarooceras exoundulatum* gen. et sp. nov., holotype QMF 61570.

cle is 2.6 mm high (RSD = 0.22) and the chambers around 1 mm long. The slightly lower CWI and higher RSD compared to the other specimens makes it conceivable that the specimen represents a slightly off-centred section, thus leading to underestimated width. This may also explain the slight differences in the shape of the diaphragms, which appear to be steeply sloped with only a subtle transition to a convex shape close to the venter. However, the ventral side of the siphuncle is also slightly obscured due to invading sediment and recrystallisation.

Remarks. The thin sections of the paratype QMF 13188a–c unfortunately contained no precise locality information, meaning that the stratigraphic horizon is uncertain. However, the strong similarities with the holotype (apart from size) indicate that the specimens are conspecific. There is also no evidence that N. ramosum occurs outside the type horizon.

In all specimens, the growth of the diaphragms has apparently ceased, as the ventral side of the siphuncle is free of diaphragms adaperturally. Consequently, the three specimens represent different growth stages, sexual dimorphism or other intraspecific variation. The conch height of the aperturalmost convex diaphragm is 9 mm (holotype QMF 61655), 12 mm (paratype QMF 61656) and 14 mm (paratype QMF 13188), respectively. Thus, even if small in absolute terms, the largest specimen is more than 50% larger than the smallest specimen. More material, including body chambers, is needed to assess intraspecific variation.

Occurrence. Known only from the type locality and horizon.

Ninmarooceras exoundulatum gen. et sp. nov.
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Figures 6 and 4C

Holotype. QMF 61570, a sectioned phragmocone fragment.

Type locality and horizon. Mount Unbunmaroo (Black Mountain), near Boulia, NW Queensland, Australia; upper Ninmaroo Formation, upper Mort Member (BMT 15), *Cordylodus lindstromi* Zone, latest Stage 10, Furongian, Cambrian.

Paratype. QMF 61571, a phragmocone fragment.

Derivation of name. Combination of exo-, referring to the exogastrically curved conch, and undulatum, referring to the undulated shell wall.

Diagnosis. *Ninmarooceras* with slightly exogastrically curved, irregularly undulated conch. Diaphragms branching into bundles of 2–3 ventrally, slightly more tightly spaced dorsally than ventrally. Distance between diaphragm bundles longer than distance between first and last diaphragm within bundle. Septal necks loxo- and microchoanitic.

Description. QMF 61570 shows the structure of the siphuncle and was therefore selected as holotype. The specimen is a phragmocone fragment of 31.8 mm length, expanding from a height of 7.5 mm and width of 6.8 mm to a height of 13.1 mm and a width of 12 mm (CWI = 0.92), resulting in an expansion rate of 10.1° in height and 9.3° in width. Chambers range in length between 0.7 mm to 1.1 mm (RCL = 0.06–0.1). The siphuncle expands from 1.5 mm to 2.8 mm (RSD = 0.2). The details of the septal necks and connecting ring are not well discernible due to recrystallisation. Nevertheless, the septal necks appear short and loxochoanitic with a thick connecting ring and concave siphuncular segments. The diaphragms slope steeply adapically towards the venter and branch into bundles of 2–3 irregular but shallower diaphragms. The bundles are separated from each other, with the distance between neighbouring bundles larger than the distance between the diaphragms of same bundle.

The paratype QMF 61571 is a slightly undulated and exogastric phragmocone fragment. It is 49.6 mm long, expanding from a height of 5.1 mm and a width of 4.6 mm to a height of 12.4 mm and a width of 10.9 mm (CWI = 0.88). Height expands at 8.4° and width at 7.3°. Chambers are on average 1.2 mm long, with RCL between 0.1–0.13. The siphuncle expands from a diameter of 1.1 mm (RSD = 0.21) to 3 mm (RSD = 0.24 mm). Although internal characters are unknown, the specimen corresponds in its proportions to the holotype. Even if the exact values slightly differ, the range of variability through ontogeny

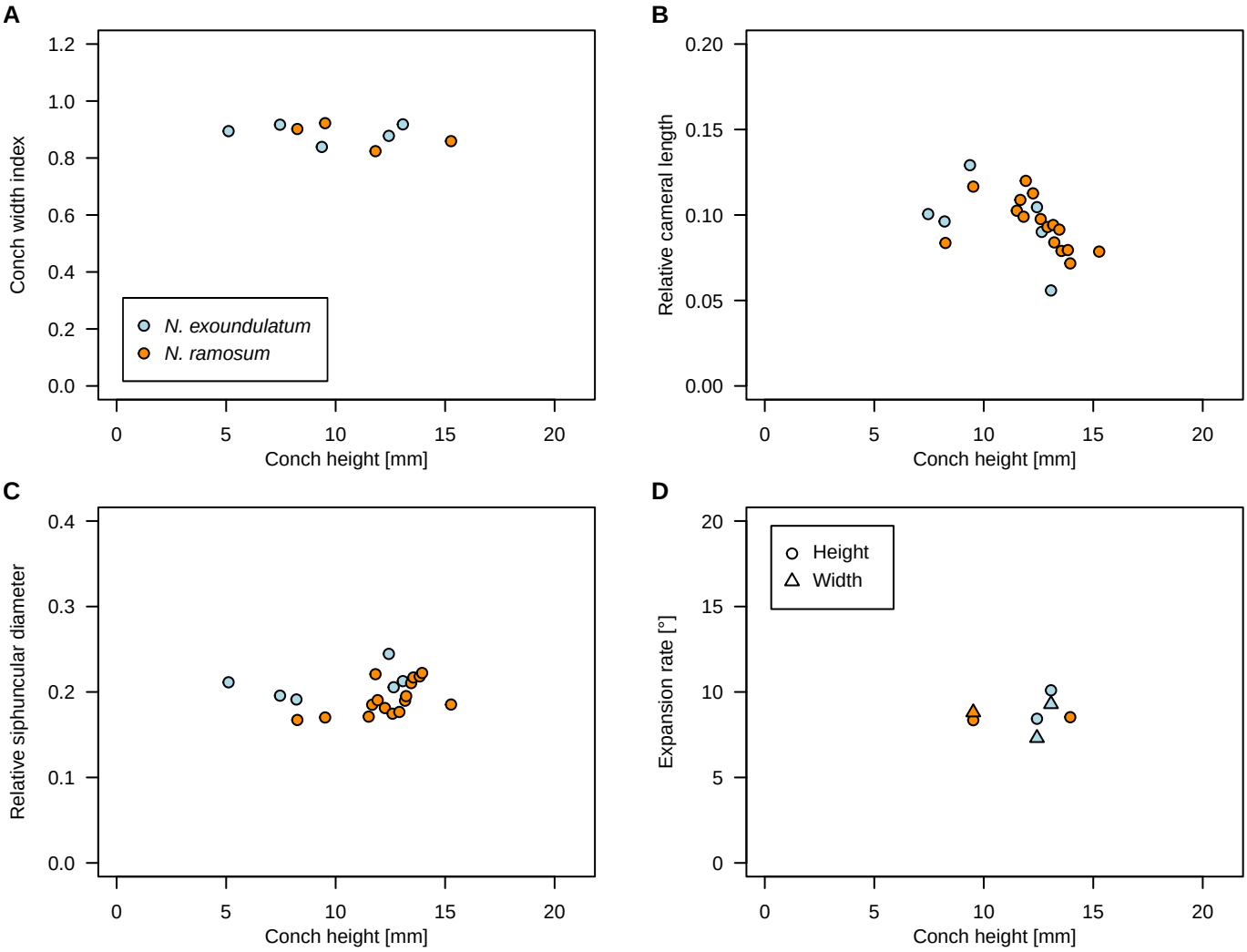


Figure 5. Conch parameters of *Ninmarooceras ramosum* gen. et sp. nov. and *N. exoundulatum* gen. et sp. nov. throughout ontogeny, represented by conch height. **(A)** Conch width index (CWI). **(B)** Relative cameral length (RCL). **(C)** Relative siphuncular diameter (RSD). **(D)** Height expansion rate (HER) and width expansion rate (LER).

in *N. exoundulatum* falls within the range seen in *N. ramosum* (5), and thus acceptable limits for intraspecific variation. The fact that these are the only two exogastric specimens in a large collection, both from the same horizon, support assigning both to the same species.

Remarks. *N. ramosum* differs from *N. exoundulatum* by its orthoconic conch and the absence of undulations. In addition, the diaphragms are more tightly bundled and regularly curved. Otherwise, the two species are closely similar in terms of conch proportions.

Among the hundreds of specimens in Mary Wade's collection from the Ninmaroo Formation, there were only two specimens with an exogastric curvature (i.e., convex prosiphuncular side of the conch), which also shared a slightly undulated conch. Initially expecting a member of the Basslerocerati dae Ulrich, Foerste, Miller & Unklesbay, 1944, Rudolfoceratidae Ulrich, Foerste, Miller & Unklesbay, 1944 or one of the Cambrian, supposedly exogastric genera (see Chen and Teichert, 1983), the holotype was sectioned. To our surprise, the internal structures resembled most closely those seen in the slightly younger *N. ramosum*. The unique morphology of the diaphragms appears to be a much better indicator for generic affinities compared to curvature and undulations. Families that are mainly based on exogastric curvature character, such as the Basslerocerati dae, Huaiheceratidae Zou & Chen in Chen, Zou, Chen & Qi, 1979b or Xiaoshanoceratidae Chen & Teichert, 1983 need to be critically re-evaluated and if necessary reduced or extended in scope or otherwise synonymised with other families. A similar case was already made for the Balkoceratidae Flower, 1964, where species of *Balkoceras* Flower, 1964 are indistinguishable from co-occurring *Palaeoceras* Flower, 1954 apart from very minute differences in curvature, leading to the conclusion that there was only a single species, i.e., *Palaeoceras mutabile* Flower, 1954 (Pohle *et al.*, 2024). Likewise, although the Rudolfoceratidae were re-established by Kröger and Landing (2009) for exogastric undulated or annulated ellesmeroceratidans, these characters seem equally questionable to define families. There is a continuous spectrum between smooth and strongly annulated conchs, and this character has likely evolved many times independently (e.g., Flower, 1964). For similar reasons, the Protocycloceratidae Kobayashi, 1935, containing annulated orthocones, had been restricted to taxa containing endosiphuncular rods and possibly cameral deposits, i.e., the genus *Protocycloceras* Hyatt, 1900 (Kröger and Landing, 2009). More recently, the family Protocycloceratidae has been abandoned (Kröger and Pohle, 2021). Further contradictions exist in that the Ellesmeroceratidae contains genera with a distinctly annulated conch such as *Walcottoceras* Ulrich and Foerste, 1936 or *Chabactoceras* Malinovskaya, 1964.

Occurrence. Known only from the type locality and horizon.

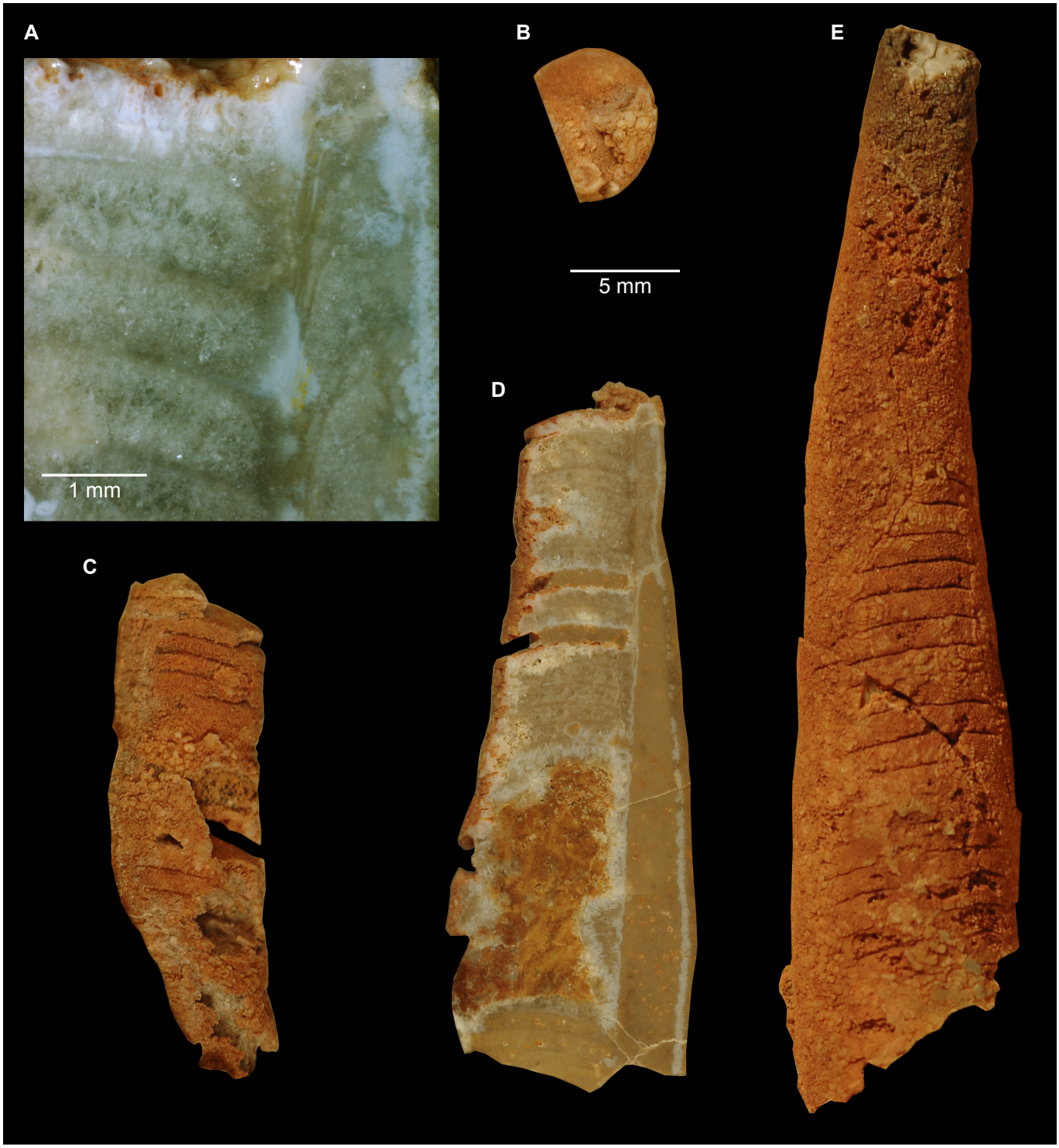


Figure 6. Type specimens of *Ninmarooceras exoundulatum* gen. et sp. nov. Upper Ninmaroo Formation, upper Mort Member (BMT 15), latest Cambrian, Mount Unbunmaroo, Queensland, Australia. **(A–D)** Holotype QMF 61570. **(A)** Detail of siphuncle. **(B)** Apical view. **(C)** Lateral view, siphuncle on left side. **(D)** Polished section, slightly oblique and off-center. **(E)** Paratype QMF 61571, lateral view, siphuncle on left side.

Discussion

The branching diaphragms in *Ninmarooceras* gen. nov. are remarkable. All hitherto described cephalopod diaphragms consist of repeated, transverse calcareous sheets crossing the siphuncle, with the morphological variability mainly expressed as slight variations in inclination, tapering or spacing (compare, e.g., Ulrich *et al.*, 1944; Flower, 1964; Chen and Teichert, 1983; Kröger *et al.*, 2007). More complex diaphragms are, so far, only known from the Plectronoceratida, with their shape having been misinterpreted when first discovered (Chen and Teichert, 1983; Mutvei *et al.*, 2007; Pohle *et al.*, 2024). The key difference to the diaphragms in *Ninmarooceras* is that all other diaphragms are essentially individual unipartite structures. The question is whether branching diaphragms are restricted to *Ninmarooceras* or whether they were simply overlooked in previously studied material. In some cases, conical diaphragms were inferred based on the shape of the apical mould of the siphuncle (e.g., Flower, 1964; Evans, 1992). Judging by our material, distinguishing between simple conical and branching

diaphragms would be impossible in this state of preservation, as only the shape of the most apertural diaphragm is visible. The findings presented here therefore call for increased scrutiny regarding the structure of diaphragms of ellesmeroceratidans, as they may hold potential to better resolve the present unsatisfactory state of classification.

It has long been hypothesised that the characteristic endocones of the endoceratoids evolved from tightly stacked diaphragms (Flower, 1964; Evans and King, 2012). *Ninmarooceras* provides perhaps the best hitherto known example of an ellesmeroceratidan with such tightly spaced diaphragms. This is further combined with a strong inclination of the diaphragms reminiscent of endocones. It might thus be tempting to suggest that *Ninmarooceras* represents a direct ancestor of the order Endoceratoidea. However, there are several differences from endoceratoid endocones: 1) The diaphragms of *Ninmarooceras* consist of a single continuous layer and there is no evidence for any biomineralization between them; 2) No branching has ever been observed in endocones; 3) Endocones are apically perforated, but the diaphragms in *Ninmarooceras* appear to be unperforated; 4) Although some endoceratoids have endocones that are arranged dorsally, thus forming a ventral open space or 'endosiphotube', the endocones in the earliest endoceratoids are radially arranged to leave a central opening. In *Ninmarooceras*, the diaphragms grow exclusively from the dorsal side of the siphuncle. These differences make a close relationship between *Ninmarooceras* and endoceratoids unlikely, unless transitional forms are discovered in the future. At the current state, it appears more parsimonious to derive endoceratoids through simple conical diaphragms.

Apart from morphological and evolutionary considerations, the peculiar siphuncular structures of *Ninmarooceras* raise new questions regarding the function of diaphragms. Previous functional interpretations envisioned diaphragms as able to close off the siphuncle to prevent passive flooding of apical chambers (Evans, 1992). This makes sense for simple transverse diaphragms but presents a considerable challenge for the diaphragm morphology of *Ninmarooceras*. Branching diaphragms require more material and thus carry a higher metabolic cost, without immediately obvious benefits (assuming the same function). The branching pattern increases the surface are of the diaphragms, so it might be argued that they play a role in liquid transport instead. Curiously, however, this surface increase occurs mostly on the ventral side, where the siphuncle is directly attached to the shell wall, meaning that there can be only limited exchange with the chamber at this position. This arrangement thus appears counter-intuitive and not optimised for this function. Furthermore, active siphuncle tissue must have been present as far back as the apical tip of the aperturalmost diaphragm to enable precipitation, which extends the diaphragm for the length of about six chambers. However, if the diaphragms sealed the siphuncle, then why was active siphuncle tissue needed this far back in the siphuncle? Perhaps the diaphragms were porous and allowed for the storage of liquid in the apical siphuncle, potentially adjusting buoyancy with respect to mobility-stability trade-offs (see, e.g., Peterman *et al.*, 2019; Peterman and Ritterbush, 2022). Alternatively, the branching pattern of the diaphragms may be the result of irregular detachment of the siphuncle from the previous diaphragm and thus reflects developmental rather than functional constraints. At this point, we can only speculate, but the structures in *Ninmarooceras* suggest a higher morphological and possibly functional variability of siphuncular diaphragms.

Conclusions

We describe *Ninmarooceras* gen. nov. (Cephalopoda, Ellesmeroceratida) from the latest Cambrian of western Queensland, containing the new species *N. ramosum* gen. et sp. nov. and *N. exoundulatum* gen. et sp. nov. The genus is characterised by the unique morphology of its siphuncular diaphragms, displaying a complex branching pattern. The shape of these diaphragms highlights the need for a revised classification of the Ellesmeroceratida. A full revision is out of the scope of the current study, but we suggest synonymy of the Yanheceratida with the Ellesmeroceratida. Furthermore, our findings have implications for the origin of the order Endoceratoidea and the functional interpretation of siphuncular diaphragms.

Data availability

All data needed to replicate the study findings are available in the article and the supplementary information. Measurements and conch parameters are provided in Table S1. All specimens are housed at the Queensland Museum (QMF), Brisbane Australia. Nomenclatural acts are registered in ZooBank, with LSIDs (Life Science Identifiers) listed for each new taxon. The LSID for this publication is urn:lsid:zoobank.org:pub:A480203E-1F78-4D29-9009-1DC8C1DD5B74.

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Author contributions

AP: Conceptualisation, data curation, formal analysis, investigation, project administration, visualisation, writing – original draft. PJ: Conceptualisation, investigation, resources, validation, writing – review and editing. CK: Conceptualisation, funding acquisition, investigation, supervision, validation, writing – review and editing.

Competing interests

The authors declare no competing interests.

Ethics and AI use

No AI was used in the preparation of this manuscript.

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