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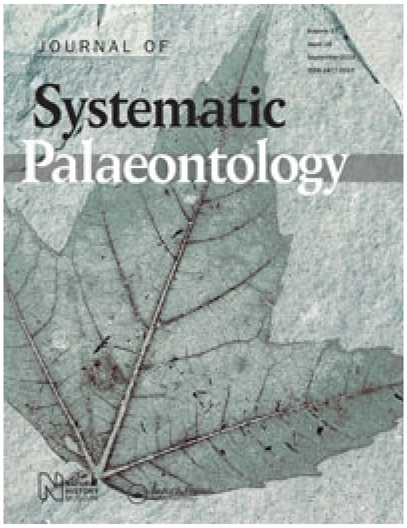

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Phylogeny of Middle–Late Ordovician lituitid cephalopods based on cladistic analysis

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Abstract: Phylogenetic studies are rare in early Palaeozoic cephalopods. Here, we present the first cladistic analysis of the order Lituitida based on published, as well as some new material. Three clades are recovered within the ingroup of lituitids, which are the *Sinoceras*, *Ancistroceras* and *Lituites* groups, and the former two groups correspond to the families Sinoceratidae, and the latter one to Lituitidae. The topology shows that Sinoceratidae represents the basal branch, while the Lituitidae represents a monophyletic, derived clade. Furthermore, we describe new material of four species (three of which are newly defined) in four genera of the order Lituitida from the well-exposed, Middle to Upper Ordovician of Hubei (South China). The described species include *Lituites evolutus* Fang, Chen & Zhang, *Sinoceras complexum* Fang (sp. nov.), *Tyrioceras longicameratum* Fang (sp. nov.), and *Rhynchorthoceras yizanense* Fang (sp. nov.). *T. longicameratum* from South China is the first reported occurrence of *Tyrioceras* in China, which has significant palaeogeographic implications.

Keywords: cladistic analysis; maximum parsimony; Lituitidae; Sinoceratidae; Lituitida; Middle–Late Ordovician

Introduction

Several attempts of cladistic analysis have been conducted with focus on the phylogeny of different groups of ‘nautiloid’ cephalopods, including the classification at lower taxonomic levels (Kröger & Isakar 2006; Kröger 2008a), the generic affinities (Kröger & Mapes 2007a), and the evolutionary path at higher taxonomic levels (Kröger & Mapes 2007b; Kröger *et al*. 2011). However, a systematic and comprehensive analysis is still pending, and many taxa have never been investigated. Lituitid cephalopods are distinguished from other Ordovician cephalopods by their specific conch shape and ornaments (Aubrechtová & Meidla 2020). Most of them have a coiled or cyrtoconic part at the early growth stage, and then develop the uncoiled or fully straight conch at the late stage.

The taxonomic position and ancestry of lituitids have long been debated intensely. Members of the order Lituitida Starobogatov, 1983 were previously placed within the Tarphyceratida or Barrandeoceratida based on the morphology of the siphuncle, and the spiral or cyrtoconic juvenile phragmocone form (Flower & Kummel 1950; Sweet 1958; Teichert *et al*. 1964; Flower 1975). By contrast, Schindewolf (1942) concluded that the predecessors of the Lituitida must be sought within the order Orthoceratida. Similarly, Dzik (1984) proposed a new suborder Lituitina (see King & Evans (2019) for discussion on the original authorship of the Lituitina and Lituitida, p. 77), which he assigned to the Orthoceratida. Dzik (1984) additionally assigned sinoceratids to the Lituitina (Lituitida), based on the phragmocone form and the presence of thin connecting rings, which was later supported by King (1993, 1999). In the view of Dzik (1984), members of the

Lituitida were characterized by a ‘subcentral, cylindrical siphuncle with long septal necks, exogastric coiling of the apical part of the conch, extended in phylogeny over later ontogenetic stages, and funnel sinus narrow and deep, except in the most primitive forms’.

Mutvei (2002) suggested that the connecting ring ultrastructure of orthoceratids agrees with that of lituitids, because in both groups the connecting rings consist of an outer spherulitic-prismatic layer and an inner calcified-perforate layer, the latter transversed by numerous large and elongated pores. Another common feature of orthoceratids and lituitids is the dorsal position of the retractor muscle scars (see also Schröder 1882; Noetling 1882; Sweet 1958).

Concerning the evolutionary relationship among lituitids, Flower (1955) suggested that *Lituites* evolved from lineage leading from *Angelinoceras* to *Rhynchorthoceras* (or *Holmiceras*) and *Ancistroceras*. Sweet (1958) considered that the group including *Lituites*, *Trilacinoceras* and *Cyclolituites* evolved from the group consisting of *Ancistroceras*, *Angelinoceras* and *Rhynchorthoceras*, and regarded *Cyclolituites* as a specialized form of *Lituites*, modified in size and shape as an adaptation to a restricted ecological niche. Chen (in Qi 1980) suggested *Ancistroceras* is the basal form, from which the other lituitids evolved. Based on conch structure and biostratigraphic information, three groups were recognized by Lai (1986): one basal group, i.e. *Ancistroceras*, *Angelinoceras*, *Holmiceras*, which evolved into the other groups, including *Lituites*, *Trilacinoceras*, *Cyclolituites* and *Sinoceras*, *Tyrioceras* and *Rhynchorthoceras* during the late Darriwilian, then gradually vanished starting in the mid-Katian. It is important to note that most of these hypotheses were based on the assumption that lituitids were derived from tarphyceratids, and the coiled juvenile phragmocone would therefore represent the ancestral state. In contrast, Dzik (1984) proposed a different evolutionary sequence, with *Rhynchorthoceras* as the ancestral taxon, which evolved into the *Sinoceras* lineage on the one hand, and into the *Ancistroceras* and *Lituites* lineages on the other hand. In addition, Dzik (1984) included the Silurian Ophidioceratidae among the lituitids, which, however, properly belong to the Tarphyceratida according to more recent evidence (Turek & Manda 2016).

Hence, as shown above, the origin and phylogeny of the lituitids has been controversial, but the recent research strongly suggests orthoceratidan instead of tarphyceratidan affinities (Evans 2005; Kröger 2006; King & Evans 2019). In the currently proposed classification of ‘nautiloid’ cephalopods for the revised Treatise Part K (King & Evans 2019), the Lituitina is proposed to be assigned to the order Astroviida Zhuravleva & Doguzhaeva, 2004 of the subclass Orthoceratia Teichert, 1967. However, in the present study, we follow the assignment of lituitid cephalopods to the order Lituitida after several scholars (Starobogatov 1983; Kröger *et al*. 2007; Aubrechtová & Meidla 2020).

Lituitids are regarded as the dominant elements of Middle to early Late Ordovician cephalopod faunas in several parts of the world, e.g. South China, Baltica and Tarim (Sweet 1958; Wang 1981; Lai 1986). In the present contribution, some new information on the morphology of lituitid cephalopods was acquired from plentiful intact, newly collected specimens, mostly from the Middle and Upper Ordovician limestones of the Middle Yangtze Platform, and from previously published materials. A preliminary cladistic analysis of the lituitids is conducted in order to assess their phylogenetic relationships.

Geological setting

The newly studied materials were collected at the Chenjiahe section in Yichang, Hubei Province (Fig. 1A), and the Mengxiao and Yizan sections in the Yongshun, Hunan Province (Fig. 1B). All the sections are located on the southeast margin of the Yangtze Platform, South China Block, and their lithostratigraphic and biostratigraphic sequences have precise intraplatform correlations (Fig. 1C; Fang *et al*. 2020). The Darriwilian (Middle Ordovician) strata of the Yangtze Platform are characterized by the transition from interbedded clastics and carbonates to a carbonate succession. The Kuniutan Formation, characterized by nodular and reticulated limestones, yields shelly faunas, dominated by cephalopods, as well as brachiopods, trilobites, and conodonts (Zhan & Jin 2007).

[Insert Fig. 1 here]

The Sandbian Datianba and Miaopo formations and the early Katian Pagoda Formation consist mainly of limestones on the Yangtze Platform. The Datianba

Formation is characterized by medium-bedded argillaceous banded limestone, with small-scale network structures, yielding abundant cephalopods (Fang *et al*. 2017a). The contemporaneous Miaopo Formation consists of limestones interbedded with black shales. During the deposition of the Datianba and Miaopo formations, the seafloor probably consisted of a relatively gently dipping ramp lacking steep slopes and interfingering with more distal facies (Song *et al*. 2017). Contemporaneous graptolitic facies were developed on the Jiangnan Slope, where the Hulo and Jiuxi formations were deposited. These two formations are characterized by black shales, mudstones and cherts, and stratigraphically range from the upper *Acrograptus ellesae* Zone to the *Nemagraptus gracilis* Zone (Zhang *et al*. 2008, 2019).

Carbonate strata of the overlying Pagoda Formation were deposited across the entire Yangtze Platform in the late Sandbian to the early Katian. These carbonates are characterized by a polygonal reticulate structure that formed as shrinkage cracks on the sea bottom (Chen & Qiu 1986), or are alternatively interpreted as due to the prolonged growth of nodular carbonate (Zhan *et al*. 2016). The Pagoda Formation yields mainly cephalopods (Fang *et al*. 2017b), trilobites (Zhou *et al*. 2016) and conodonts (Wang *et al*. 2017; Fang *et al*. 2019), as well as some brachiopods (Zhan & Jin 2007). In the studied area, the carbonate strata of the Kuniutan, Datianba and Pagoda formations are divided into, in ascending order, the *Pygodus serra*, *Pygodus anserinus–Yangtzeplacognathus jiangyeensis*, *Baltoniodus variabilis*, *Baltoniodus alobatus*, and *Hamarodus brevirameus* conodont zones, ranging from the upper Middle to the lower Upper Ordovician (Wang *et al*. 2018; Fang *et al*. 2019). Six cephalopod biozones can be recognized within this limestone succession, including *Proterovaginoceras incognitum* (synonymized with *Dideroceras wahlenbergi*; Kröger 2012), *Ancistroceras*, *Lituites–Cyclolituites*, *Sinoceras chinense*, *Richardsonoceras simplex* and *Dongkalaceras–Discoceras* zones (Fang *et al*. unpublished data).

Material and methods

Species sampling

The studied material includes published specimens of some genera, which have in part been remeasured from previous publications (e.g. Sweet 1958; Frye 1982; Yun 1999, 2003; Kröger 2004, 2013; Fang *et al*. 2017a, b; Aubrechtová & Meidla 2020), as well as material representing three new species collected from Hunan and Hubei provinces of South China. In total, seventeen species of the Lituitida belonging to nine genera were selected, consisting of two species of *Ancistroceras*, one of *Angelinoceras*, one of *Cyclolituites*, two of *Holmiceras*, three of *Lituites*, two of *Rhynchorthoceras*, three of *Sinoceras*, one of *Trilacinoceras*, and two of *Tyrioceras*. Detailed information of the species sampled, and their distributions and horizons are presented in Table 1. All nine well known and confidently assigned lituitid genera are represented by one to three taxa in the analysis. Several disputed taxa are excluded due to the lack of key characters preserved. Those excluded are *Tapinolituites* (Gao *et al*. 1982), *Sinoceroides* (Xu & Lai 1987), *Pseudoancistroceras* (Xu & Lai 1987), *Nevadaceras* (Flower 1968). *Michelinoceras chaoi* Chang, 1957 and *Orthoceras regulare* Schlotheim, 1820, representing two genera of the family Orthoceratidae, are treated as outgroups, determining the evolutionary path. All species in this analysis occur in the Middle and Late Ordovician in different parts of the world, e.g. South China, North China (including Korea), Sibumasu (Thailand), Baltica, Precordillera and Himalaya (Table 1).

Institutional abbreviations

NIGP: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Methods

Morphological terminology used in this study follows several previous publications (e.g. Chao *et al*. 1965; Frey 1995; Kröger *et al*. 2007; Kröger 2008b; Fang *et al*. 2017b; Aubrechtová & Turek 2018). In the present analysis, twenty-four multistate characters comprising 55 unordered character states were used to code the genera selected for this study. Cladistic analysis was undertaken using TNT version 1.5 (Goloboff & Catalano 2016), with traditional search employing 1000 random addition sequences. Unambiguous characters were mapped on the tree using WinClada version 1.00.08 (Nixon 2002). The bootstrap analysis was conducted in 100 replicates to demonstrate support for derived groups. Jackknife analyses proceeded via deletion of 33% of characters.

Characters and coding

1. Hyponomic sinus: 0) absent; 1) present.

2. Hyponomic sinus length: 0) short (< 20% of conch width); 1) deep (≥ 20% of conch width).

Inapplicable if character 1 is scored as state 0

3. Hyponomic sinus width: 0) broad (≥ 75% of conch width); 1) narrow(< 75% of conch width).

Inapplicable if character 1 is scored as state 0

4. Hyponomic sinus shape: 0) round; 1) sharp.

Inapplicable if character 1 is scored as state 0

5. Dorsal sinus: 0) absent; 1) present.

6. Lateral sinuses: 0) absent; 1) present.

7. Annulations: 0) absent; 1) present.

8. Body chamber length: 0) short (≤ 200% of body chamber height); 1) long (> 200% of body chamber height).

9. Cameral deposits: 0) restricted apically; 1) well developed.

10. Epichoanitic deposits: 0) absent; 1) present.

11. Ontogeny cameral length: 0) decreasing; 1) constant; 2) increasing.

12. Ontogeny expansion rate: 0) decreasing; 1) constant; 2) increasing.

13. Conch size: 0) small (≤ 100 mm conch height); 1) large (> 100 mm conch height).

14. Adult phragmocone form: 0) orthocone; 1) cyrtocone; 2) coiled.

15. Juvenile phragmocone form: 0) orthocone; 1) cyrtocone; 2) coiled.

16. Looseness index: 0) small; 1) large.

Inapplicable if character 15 is scored as state 0 or 1

17. Early uncoiled part form: 0) straight; 1) sigmoidal.

Inapplicable if character 15 is scored as state 0 or 1

18. Umbilical perforation: 0) absent; 1) present.

Inapplicable if character 15 is scored as state 0 or 1

19. Expansion rate: 0) slow (< 6°); 1) moderate (≥ 6°, < 15°); 2) rapid (≥ 15°).

20. Conch width: 0) compressed; 1) circular

21. Cameral length: 0) short (< 20% of conch width); 1) moderate (≥ 20% of conch width).

22. Siphuncle position: 0) central; 1) subdorsal; 2) dorsal.

23. Siphuncular segment shape: 0) tubular; 1) slightly expanded.

24. Septal neck length: 0) short (< 50% of cameral length); 1) long (≥ 50% of cameral length).

The codings for all taxa studied are listed above. Table 2 gives the data matrix used in the analyses containing 19 taxa (including outgroup *M. chaoi* and *O. regulare*) and 24 characters. All characters are treated as unordered and equally weighted, and inapplicable data are coded with '-', and unavailable or unpreserved data are coded with '?'. The continuous characters were defined to create discrete groups. Whilst the boundary values were arbitrary, they were chosen to reflect observed variation, and which are commonly employed in systematic studies.

Systematic palaeontology

Order **Lituitida** Starobogatov, 1983

Family **Lituitidae** Phillips, 1848

Genus ***Lituites*** Bertrand, 1763

Type species. *Lituites lituus* de Montfort, 1808, Middle Ordovician, Baltoscandia (type locality unknown; see Aubrechtová & Turek 2018).

Diagnosis (adapted from Teichert *et al*. 1964). Gradually expanded annulate conchs with whorls of spiral portion in contact or loosely coiled, but not impressed; body chamber may equal or exceed the length of sigmoid orthoconic phragmocone; fully mature aperture characterized by pair of pronounced ventrolateral lappets, and similar, but shorter dorsolateral lappets; dorsal sinus generally divided by low salient; siphuncle subdorsal.

Remarks. Based on the expansion rate and coiling geometry, Fang *et al*. (2017a) proposed three ontogenic stages in *Lituites*: the juvenile stage with variable characters, corresponding to the coiled part; the rapid growth stage, typified by rapidly expanding straight conch; and the mature stage for which a decreasing growth rate at the body chamber is characteristic. Ontogenetic changes of characters need to be considered in taxonomic identifications and consequently, poorly preserved specimens should not be assigned to different species.

Lituites evolutus Fang, Chen & Zhang in Fang *et al*. 2017a

(Figs 2A–D, 3A)

2017a *Lituites evolutus* Fang, Chen & Zhang in Fang *et al*.: 340, fig. 7-1–3, 7, 8.

Diagnosis. *Lituites* species with a sigmoid conch and moderate expansion rate. Whorls of the coiled part are significantly loose.

Materials. Two specimens, NIGP169582 and NIGP173636.

Locality and horizon. Datianba Formation, Sandbian Stage, Mengxiao section, Yongshun, China, Upper Ordovician.

[Insert Fig. 2 here]

Description. Specimen NIGP173635 (Fig. 2C) is 33 mm long, nearly complete phragmocone and part of the body chamber; the diameter changes from 2–13.1 mm, more than 15 camerae are contained in the phragmocone (*c*. 2.5–3 chambers per corresponding conch diameter). The coiled part is composed of 1.5 contiguous whorls followed by half a whorl that is completely separated from the preceding whorls; the siphuncle is subdorsal in position, and the siphuncular perforation is narrow (diameter *c*. 0.08 of corresponding conch diameter), septal necks are orthochoanitic. The connecting rings are thin and straight. Cameral deposits are developed, but recrystallized in the curved growth stages. The conch surface ornament has not been preserved.

Specimen NIGP173636 (Fig. 2D) is a 37 mm long fragment of a phragmocone, with a diameter between 1.3–14.4 mm; the body chamber is not preserved. The coiled part of the conch consists of two and half whorls, where the first two are contiguous, and the last half whorl is then separated from the previous. There are over 42 camerae preserved in the entire phragmocone, with *c*. two chambers per corresponding conch diameter; the siphuncular perforation is narrow, subdorsal in position (diameter *c*. 0.1 of corresponding conch diameter), septal necks are orthochoanitic (length *c*. 0.25 of corresponding camera length). The connecting rings are thin and straight. Cameral deposits are developed, but recrystallized in the curved growth stages. The conch surface ornament is not preserved.

Remarks. In Fang *et al*. (2017a), the looseness index of the coiled part was defined to determine the *Lituites* species. The helix polar formula, $r(\theta) = b \times \theta + a$, could be used to represent the form of the coiled phragmocone. The looseness of the coiled part is positively correlated with the index b, namely looseness index. The specimens described above meet the diagnostic features of *L. evolutus* established by Fang *et al.* (2017a), differing from other species of the genus *Lituites* in the looseness index (Fig. 3B, C). Herein, *L. evolutus* has a low looseness index in the early coiled part which increases sharply in the last half whorl.

[Insert Fig. 3 here]

Family **Sinoceratidae** Shimizu & Obata, 1935a

Genus ***Sinoceras*** Shimizu & Obata, 1935b

Type species. *Orthoceras chinense* Foord, 1888, from the Pagoda (Limestone) Formation, lower Katian Stage, Nanjing? (200 miles from Shanghai), South China, by original designation.

Emended diagnosis. (Modified from Fang *et al.* 2017b). Conch orthoconic, subcylindrical; the surface of conch ornamented by well-marked flexuous transverse growth lines; septal necks slightly expanded, nearly half of camera length; connecting rings slightly expanded; siphuncle central or subcentral; without longitudinal impressions of the body chamber.

Sinoceras complexum Fang (sp. nov.)

(Fig. 4A–E)

Diagnosis. Sinoceras species with orthoconic conch; septal necks over half of the camera length; connect rings slightly expanded; siphuncle central.

Derivation of name. Referring to the Latin ‘complex’, because of its more complicated internal structure compared to the type species *S. chinense*.

Holotype. Specimen NIGP173637.

Paratype. Specimen NIGP173638.

Type locality and horizon. *Richardsonoceras simplex* Zone (cephalopod), lowest Linhsiang Formation, lower–middle Katian Stage, Chenjiahe section, Yichang, South China.

[Insert Fig. 4 here]

Description. Specimen NIGP173637 (Fig. 4A) is a phragmocone fragment, with a total conch length of 65 mm and a conch diameter of 7.2–16.8 mm (expansion rate *c.* 9°). The surface ornaments are not preserved, and the suture is straight (Fig. 4B). The phragmocone is almost straight, with 13 camerae preserved. The conch cross-section is circular. The apex and body chamber are absent. The siphuncle is central, and the diameter of the septal perforation occupies *c*. 0.1 of the conch diameter. The septal necks are orthochoanitic with a length *c*. 0.6 of cameral length. The chambers are filled with episeptal, hyposeptal and mural deposits.

Specimen NIGP173638 (Fig. 4D, E) is a fragment of a phragmocone, with a conch length of 96.1 mm and a diameter of 6.6–11 mm (expansion rate *c*. 9°). The siphuncle is located 8.4 mm from the conch margin at the corresponding conch diameter of 19.2 mm; the diameter of the septal perforation is *c*. 0.1 of the conch diameter. The septal necks are orthochoanitic, with a length *c*. 0.6 of camera length, and connecting rings are slightly thickened and expanded (Fig. 4C).

Remarks. *Sinoceras complexum* Fang (sp. nov.) differs from other *Sinoceras* species, such as the type species *S. chinense* and *S. huanghuaense* Wang, 1978, in having long septal necks, which are longer than half of the camera length, and in having slightly expanded siphuncular segments.

Genus ***Tyrioceras*** Strand, 1934

Type species. *Tyrioceras kjaerulfi* Strand, 1934, from Grimsøy Formation, lower Katian Stage, Upper Ordovician, Furuholmen, Asker District, Norway.

Diagnosis (adapted from Kröger 2013). Large straight, compressed to depressed conch cross-section; ornamented with broad bands or narrower raised transverse lines, which form broad and well-marked, but not very deep ventral sinus with ventrolateral and dorsolateral salients, siphuncle eccentric; septal necks orthochoanitic, relatively long, siphuncular segments tubular.

Tyrioceras longicameratum Fang (sp. nov.)

(Fig. 5A–E)

Diagnosis. *Tyrioceras* species showing extremely wide septal spacing (1.2 times conch diameter). Conch is cyrtoconic in the juvenile stage, straight in later growth stages. Conch cross-section is slightly compressed. Septal necks are relatively long, just slightly shorter than half of cameral length. The siphuncle is tubular with diameter *c*. 0.13 of corresponding conch diameter.

Derivation of name. Referring to the Latin ‘long camera’, due to the characteristically high septal spacing differing the new species from other species of the genus *Tyrioceras*.

Holotype. Specimen NIGP173643.

Paratype. Specimen NIGP173644.

Type locality and horizon. *Richardsonoceras simplex* Zone (cephalopod), lowest

Linhsiang Formation, lower–middle Katian Stage, Chenjiahe section, Yichang, South China.

[Insert Fig. 5 here]

Description. Specimen NIGP173643 (Fig. 5D) is a fragment of a phragmocone, with a total length of 98 mm, and a diameter of 5.4–20 mm, indicating the expansion rate 8°. The conch is slightly cyrtoconic in the initial 15 mm, straight in the later stages, with ten camerae preserved. Conch cross-section is slightly compressed (Fig. 5C). The septal spacing is extremely wide, equal to 1.2 of conch diameter. The siphuncle is tubular and central in position, occupying 0.13 of corresponding conch diameter, with orthochoanitic septal necks, shorter than 0.5 of cameral length. The ornaments on the conch surface are not preserved (Fig. 5E).

The other specimen NIGP173644 (Fig. 5A, B) is a fragment of a straight conch with five camerae. The specimen has a length of 65 mm, and a diameter of 11–20 mm, with expansion rate 10°. The septal spacing is 1.2 times conch diameter. The siphuncle is central, its diameter is 0.15 of conch diameter. Septal necks are orthochoanitic, yet slightly inclined apically, with the length shorter than half the cameral length.

Remarks. According to Kröger *et al.* (2013), *Tyrioceras* species have orthochoanitic and relatively long septal necks, and plentiful cameral deposits. Based on the present specimens, very long camerae are characteristic for *Tyrioceras*, distinguishing the genus from *Rhynchorthoceras*. The above-described specimens also represent the first record of *Tyrioceras* in China, as well as the record from Northern Ireland (Evans 1993), indicating the palaeogeographical affinity among South China, Baltica and Luarentia during the Late Ordovician. *Tyrioceras longicameratum* sp. nov. is unique in the genus with its wide septal spacing and relatively long septal necks. *T. kjaerulfi* and *T. warburgae* differ in having narrower septal spacing.

Genus ***Rhynchorthoceras*** Remelé, 1882

Type species. *Lituites breynii* Boll, 1857, from Orthoceratite Limestone erratics, Darriwilian Stage, Middle Ordovician, northern Germany.

Diagnosis (modified from Kröger *et al*. 2007). Lituitidans with orthoconic conchs with a slight curvature at the apex. The siphuncle is tubular or slightly expanded within chambers, large (diameter one-sixth of conch diameter), subcentral or central. Septal necks are orthochoanitic, cameral deposits cover septal necks in some specimens. Cameral deposits with single vertical lamella on the concave side of the conch.

Rhynchorthoceras yizanense Fang (sp. nov.)

(Fig. 6A–I)

Diagnosis. *Rhynchorthoceras* species showing moderate septal spacing (0.3 of corresponding conch diameter), and expansion rate *c*. 10°. Conch is cyrtoconic in the juvenile stage, nearly straight in the later growth stages, lirae strongly sinuous. Septal neck length is *c*. half the corresponding cameral length. The siphuncle is tubular with diameter *c*. 0.1 of corresponding conch diameter.

Derivation of name. Referring to the type locality, Yizan village, Sangzhi county, South China.

Materials. Four specimens, NIGP173639, NIGP173640, NIGP173641 and NIGP173642.

Holotype. Specimen NIGP173639 from the Datianba Formation, Sandbian Stage, Yizan section, Sangzhi, South China.

Paratype. Specimens NIGP173640, NIGP173641 and NIGP173642 from the Datianba Formation, Sandbian Stage, Sangzhi, South China.

Type locality and horizon. *Lituites-Cyclolituites* Zone (cephalopod), Datianba Formation, Sandbian Stage, Sangzhi, South China.

[Insert Fig. 6 here]

Description. Holotype specimen NIGP173639 (Fig. 6E–G) is an almost complete phragmocone and part of the body chamber, with a total conch length of 69 mm, and diameter of 3.5–14 mm (expansion rate 9.5°). The conch is slightly cyrtoconic in the initial 10 mm, straight in the later stages, with over 30 camerae with moderate septal spacing (0.3 of corresponding conch diameter). The conch cross-section is circular. The conch is ornamented with strongly sinuous lirae, with seven lirae per 1 mm apically and two lirae per 1 mm adorally. The ornaments indicate a very shallow and broad ventral lobe (hyponomic sinus). The tubular siphuncle is central, the septal perforation is narrow, *c*. 0.1 of corresponding conch diameter, the septal necks are orthochoanitic, and shorter than half of the camera length.

The second specimen, NIGP173640 (Fig. 6H, I) is a nearly complete phragmocone and body chamber, lacking an apical part, with a length of 75 mm and a diameter of 4.6–16 mm (expansion rate 10°). The conch cross-section is circular. The conch is ornamented with lirae, yet apically inclined lirae (six lirae per 1 mm apically and three lirae per 1 mm adorally). The tubular siphuncle is central (0.1 of corresponding conch diameter), with orthochoanitic septal necks, reaching half of cameral length.

The other specimens NIGP173641 (Fig. 6C, D) and NIGP173642 (Fig. 6A, B) of this species are both fragments of phragmocones, possessing some ten septa, with expansion rate 10°. Septal spacing is moderate, 0.3 of conch diameter. The siphuncle is tubular, and its diameter occupies 0.13 of the corresponding conch cross-section. Septal necks are orthochoanitic with a length of 0.4–0.5 of cameral length.

Remarks. *Rhynchorthoceras yizanense* conchs are unique in the genus, because of the combination of long septal necks, moderate cameral spacing and low expansion rate. *R. guiyangense* Yang, 1978 and *R. conicum* (Hisinger, 1837) differ in having shorter septal necks (a quarter of conch diameter). *R. minor*, *R.* aff. *beyrichi* Remelé (Dzik 1984) and *R. jurongense* differ in narrow septal spacing (0.2 times conch diameter). *R. zaddachi* Remelé, 1882 has similar expansion rate (*c.* 11°), and similar type of ornament (sinuous lirae), whereas differs in having a wider siphuncle (*c.* 0.14 of the conch diameter).

Results

Maximum parsimony analyses of the 19 taxa with 24 characters by TNT yielded four most parsimonious trees (MPTs) with branch length = 54, consistency index (CI) = 0.57 and retention index (RI) = 0.76. Four most parsimonious trees are given in Figure 7, one of which with unambiguous characters is shown in Figure 8. The strict consensus tree with added bootstrap and jackknife values is given in Figure 9.

[Insert Fig. 7 here]

The four MPTs (Fig. 7A–D) are closely similar and differ only in the position of *Sinoceras chinense* relative to *S. complexum*, and in the relationship between *Cyclolituites lynnensis*, and the other species of the *Lituites* group (see below). In addition, while two of the four MPTs agree on the monophyly of the *Lituites* group, the phylogenetic position of the species within this group agrees across all MPTs.

The high bootstrap and jackknife values (90% and 92%; Fig. 9) indicate strong support for the monophyly of the ingroup, namely the order Lituitida (Fig. 8, node A). Its monophyly is well supported by several non-homoplasious apomorphies, including the presence of a hyponomic sinus (character 1: 1), the apically restricted cameral deposits (character 9: 0), the presence of epichoanitic deposits (character 10: 1), the moderate expansion rate (character 19: 1) and the long septal necks (character 24: 1).

[Insert Fig. 8 here]

The MPTs show that within the Lituitida, species of the same genus are always resolved to be closely related, although not all genera represent monophyletic groups. *Sinoceras* species are distributed along the basal branch in all trees. *S. eccentrica* is resolved as the most basal species of the ingroup (Fig. 7). Paraphyly is supported for the clade consisting of *Rhynchorthoceras* and *Tyrioceras*, which branch successively. The paraphyletic Sinoceratidae therefore represents the basal group of the Lituitida, which accordingly represents a derived, monophyletic clade with the Lituitidae.

Within the Lituitidae, two distinct monophyletic clades can be recognized in two of the four MPTs, namely the *Ancistroceras* and *Lituites* groups (Fig. 7). The monophyletic *Ancistroceras* group contains the genera *Ancistroceras* and *Holmiceras*, out of which the former is resolved as monophyletic, and the latter as paraphyletic, with *Holmiceras kjerulfi* as the ancestral taxon in the group. Within the *Lituites* group, the genera *Angelinoceras*, *Cyclolituites* and *Trilacinoceras* are all represented by a single species in our dataset, and their monophyly cannot be evaluated. *Trilacinoceras* and *Angelinoceras* are resolved as the sister taxon to the monophyly of the *Lituites* species in all MPTs (Fig. 7).

Discussion

The present phylogenetic reconstruction indicates that several lituitid genera represent monophyletic groups, i.e. *Ancistroceras* and *Lituites*, which is well supported. The paraphyly of the genus *Sinoceras* is probably a result of its basal position among lituitids. All species of the genus occupy a position close to each other on the tree, and are closely similar in terms of morphology. We consider that it is nevertheless practical to retain the genus in its current state. *Lituites* represents a monophyletic genus, forming a monophyletic clade with *Angelinoceras*, *Trilacinoceras* and *Cyclolituites*. The genus *Cyclolituites* is so distinctly different from *Lituites* in its conch form lacking the orthoconic portion that we propose retaining it. Because *Cyclolituites* retained the coiled conch form throughout its life, this represents a case of neoteny (Stephen 2001). *Angelinoceras* is closely similar to *Lituites* (see also Teichert *et al*. 1964), and mainly differs from the latter in its higher looseness index, more rapid expansion rate, and much larger diameters of the coiled parts. However, the material investigated here indicates that there is some variation in the looseness index of *Lituites* and expansion rate alone may not be sufficient for a separation at the genus level. In addition, most of the differences between *Angelinoceras latum* and species of *Lituites* are homoplasious characters (Fig. 8). We therefore propose that the two genera may be synonymized and *Angelinoceras latum* (the only species of that genus) accordingly should be transferred to *Lituites*, pending confirmation through future studies. *Tyrioceras* and *Rhynchorthoceras* may also be synonymized, since none of the most parsimonious trees recovered either of them as monophyletic, but the four species were always recovered basal to the Lituitidae. Nevertheless, more derived when compared to *Sinoceras*. This result needs confirmation by further studies of better preserved material, since the surface ornaments are missing in *Tyrioceras longicameratum*. This, if known, could potentially change the phylogenetic position of the genus.

[Insert Fig. 9 here]

Despite some of the problems with the monophyly of certain genera, the two families belonging to the Lituitida, namely the Sinoceratidae and Lituitidae, are distinctly recognized in the phylogenetic trees. The Sinoceratidae, which constitutes a paraphyly, represents the ancestral group of lituitids, while the monophyletic Lituitidae represents the derived clade. The boundary between the Sinoceratidae and Lituitidae is traced rather arbitrarily between *Rhynchorthoceras minor* and its sister group. However, this represents a useful distinction, because all members of the Lituitidae share the coiled juvenile phragmocone as a synapomorphy. This is probably highly relevant, because of the palaeoecological affinity between South China and Baltic blocks, which could be exactly explained by the equatorial cold-water tongue in the Late Ordovician (Jin *et al*. 2018).

The earliest stratigraphic records of lituitid cephalopods are *Ancistroceras densum* and *A*. *subcurvatum* from the Dawan Formation of South China, *Rhynchorthoceras minor* from the San Juan Formation of western Argentina, and *R*. aff. *beyrichi* from the erratic boulders of the Baltic region (Qi 1980; Dzik 1984; Kröger *et al*. 2007), all of which are constrained to the *Paroistodus originalis* Zone of the lower Dapingian, Middle Ordovician (Wang *et al*. 2019). However, juvenile phragmocones of *A*. *densum* and *A*. *subcurvatum* are unknown, which results in their uncertain assignment at the genus level (Kröger *et al*. 2007). In the present phylogenetic trees (Figs 7, 8, 9), a close relationship between *A*. *undulatum* and *A*. *subcurvatum* is supported, suggesting that the assignment of *A*. *subcurvatum* is reasonable. The hypothetical ancestral group displayed in the phylogenetic reconstruction, namely species of *Sinoceras*, is still mainly recorded from the Upper Ordovician of Chinese blocks/terranes. However, some previous studies suggest that the first appearance datum (FAD) of *Sinoceras* could be extended to the Middle

Ordovician, maybe Dapingian (e.g. *Sinoceras fenxiangense* Xu & Lai, 1987 from the Dawan Formation of South China), and the early representatives of the genus are thus probably coeval to *A. densum*, *A. subcurvatum* and *R. minor*. Therefore, it appears that the Lituitida was already present in different parts of the world in the late Dapingian, suggesting that it may have originated slightly earlier, and undergone a rapid diversification with wide geographic dispersal. The basal position of most species of *Sinoceras* is probably the most significant deviation from the stratigraphic sequence shown by our study. A possible solution to the problem might be that while *Sinoceras* originated earlier (e.g. *S. fenxiangense*), other species are descendant from that species, rather than representing individual long-ranging ghost lineages. More studies with additional species and material are needed to resolve these incongruencies.

Apart from the clade comprising the ingroup, the bootstrap and jackknife values are relatively low (Fig. 9). This is likely a result of frequent homoplasies. The fact that only four MPTs were retained, and that previously recognized genera and families were also recovered suggests that the results are nonetheless relevant. Future studies with additional species, more detailed characters (e.g. continuous or morphometric geometric data) may provide additional insights.

Overall, the evolutionary history of lituitids leading from the Sinoceratidae to the Lituitidae supports previously published schemes proposing, e.g. the derivation of the Lituitidae from *Rhynchorthoceras* and related taxa (Dzik 1984), the close relationship between *Ancistroceras* and *Holmiceras* (Sweet 1958) and between *Angelinoceras*, *Trilacinoceras* and *Lituites* (Sweet 1958). Together with the fact that both the Sinoceratidae and the Lituitidae are recovered as distinct groups in the phylogenetic trees indicates that phylogenetic methods are appropriate for lituitids despite frequent homoplasies.

This contribution presents the first phylogenetic analysis within the order Lituitida, and briefly discusses the phylogenetic relationships and history among the lituitid genera. However, the poorly preserved and limited number of samples have resulted in low support values of several nodes, and their phylogenetic relationship. In the future, more specimens should be examined, and more characters described to confirm this hypothesis.

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Biodiversification Event) and 735 (Rocks and the Rise of Ordovician Life).

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Figures and tables

Figure 1. A, Fossil localities and lithofacies distributions of the Darriwilian Stage (Middle Ordovician) of South China (modified from Fang *et al*. 2020); B, detailed locality and transportation map in Yichang; C, detailed localities and transportation map in Yongshun and Sangzhi. 1. Chenjiahe section, Yichang; 2. Yizan section, Sangzhi; 3. Mengxiao section, Yongshun.

Figure 2. *Lituites evolutus* Fang, Chen & Zhang, Datianba Formation (Sandbian Stage, Upper Ordovician), South China. A, NIGP164742 (Fang *et al*. 2017b), lateral view; B, NIGP164748 (Fang *et al*. 2017b), dorso-ventral polished section; C, NIGP169582 (Fang *et al*., 2019), dorso-ventral polished section; D, NIGP173636, dorso-ventral polished section. Scale bar = 1 cm.

Figure 3. Horizontal ~~Conch~~ conch cross-section of the coiled part of *Lituites* species. A, NIGP173645, *Lituites evolutus* Fang, Chen & Zhang, showing the separation between last two whorls; B, NIGP173646, *Lituites lii* ~~(~~Yü~~)~~, showing the completely separation among each whorl; C, NIGP173647, *Lituites ningkiangense* Lai, showing the contact whorls. Scale bar = 1 cm.

Figure 4. *Sinoceras complexum* Fang (sp. nov.), Linhsiang Formation (Katian Stage, Upper Ordovician), South China. A, B, NIGP173637; A, median polished section; B,

lateral view, scale bar = 1 cm; C–E, NIGP173638; C, detail of connecting rings, scale bar = 1 mm; D, median polished section; E, lateral view, scale bar = 1 cm.

Figure 5. *Tyrioceras longicameratum* Fang (sp. nov.), Linhsiang Formation (Katian Stage, Upper Ordovician), South China. A, B, NIGP173644; A, median polished section; B, latral view; C–E, NIGP173643; C, conch cross-section; D, dorso-ventral polished section; E, lateral view. Scale bar = 1 cm.

Figure 6. *Rhynchorthoceras yizanense* Fang (sp. nov.), Datianba Formation (Sandbian Stage, Upper Ordovician), South China. A, B, NIGP173642; A, lateral view showing the sinuous lirae; B, dorso-ventral polished section; C, D, NIGP173641; C, lateral view showing the sinuous lirae; D, median polished section; E–G, NIGP173639; E, dorso-ventral polished section; F, lateral view showing the sinuous lirae; G, conch cross-section; H, I, NIGP173640; H, lateral view and growth lines; I, dorso-ventral polished section. Scale bar = 1 cm.

Figure 7. Four most parsimonious trees with *M. chaoi* and *O. regulare* as outgroups. Abbreviations of the genera: *M.* = *Michelinoceras*, *O.* = *Orthoceras*, *A.* = *Ancistroceras*, *Ang.* = *Angelinoceras*, *C.* = *Cyclolituites*, *H.* = *Holmiceras*, *L.* = *Lituities*, *R.* = *Rhynchorthoceras*, *S.* = *Sinoceras*, *T.* = *Trilacinoceras*, *Ty.* = *Tyrioceras*.

Figure 8. One of the four most parsimonious trees with *M. chaoi* and *O. regulare* as outgroups. Only unambiguous characters are shown. Non-homoplasious characters are marked by filled circles and homoplasious characters by open circles. The character numbers and states are placed above and below the circles, respectively. For the genus abbreviations, see Fig. 7.

Figure 9. The strict consensus tree with *M. chaoi* and *O. regulare* as outgroups, with bootstrap and jackknife values above and below the branches, respectively. Three groups are recognized in the ingroup. For the genus abbreviations, see Fig. 2. The depicted representative of *Sinoceras* group is modified from Fang *et al*. (2017), the representative of *Ancistroceras* group is modified from Teichert *et al*. (1964), and the representative of *Lituites* group is modified from Teichert *et al*. (1964) and Aubrechtová & Meidla (2020).

Table 1. Lituitida species sampled and their distributions and horizons.

Table 2. Character code-taxa matrix used for cladistic analysis. For the genus abbreviations, see Fig. 2.

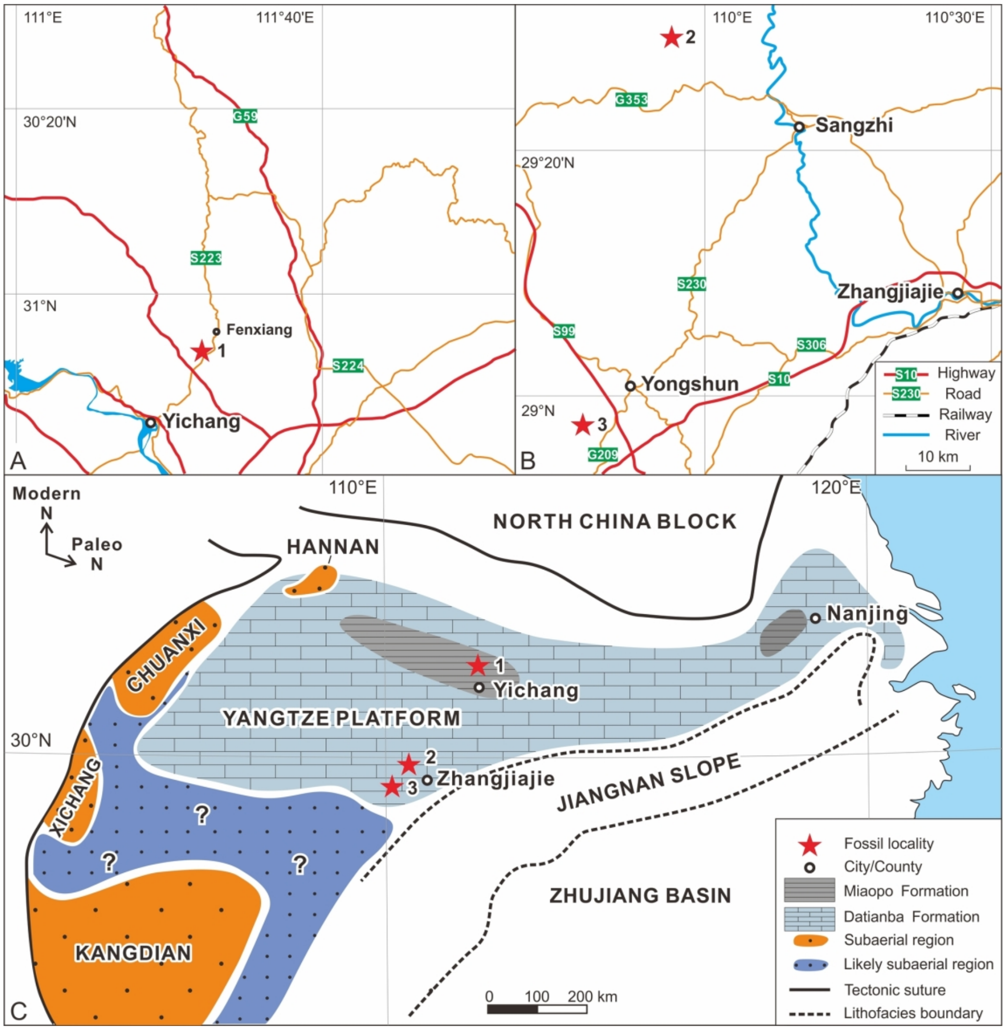

Figure 1

173x176mm (300 x 300 DPI)

Figure 2

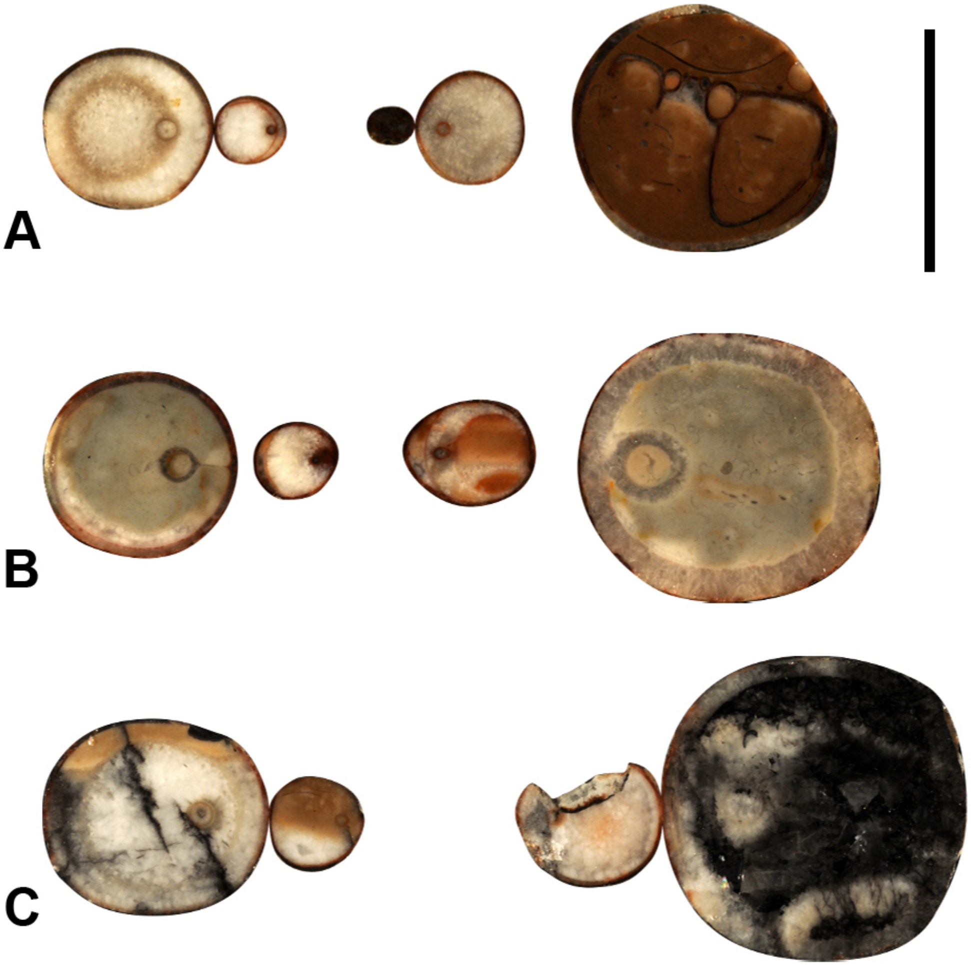

Figure 3

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Figure 4

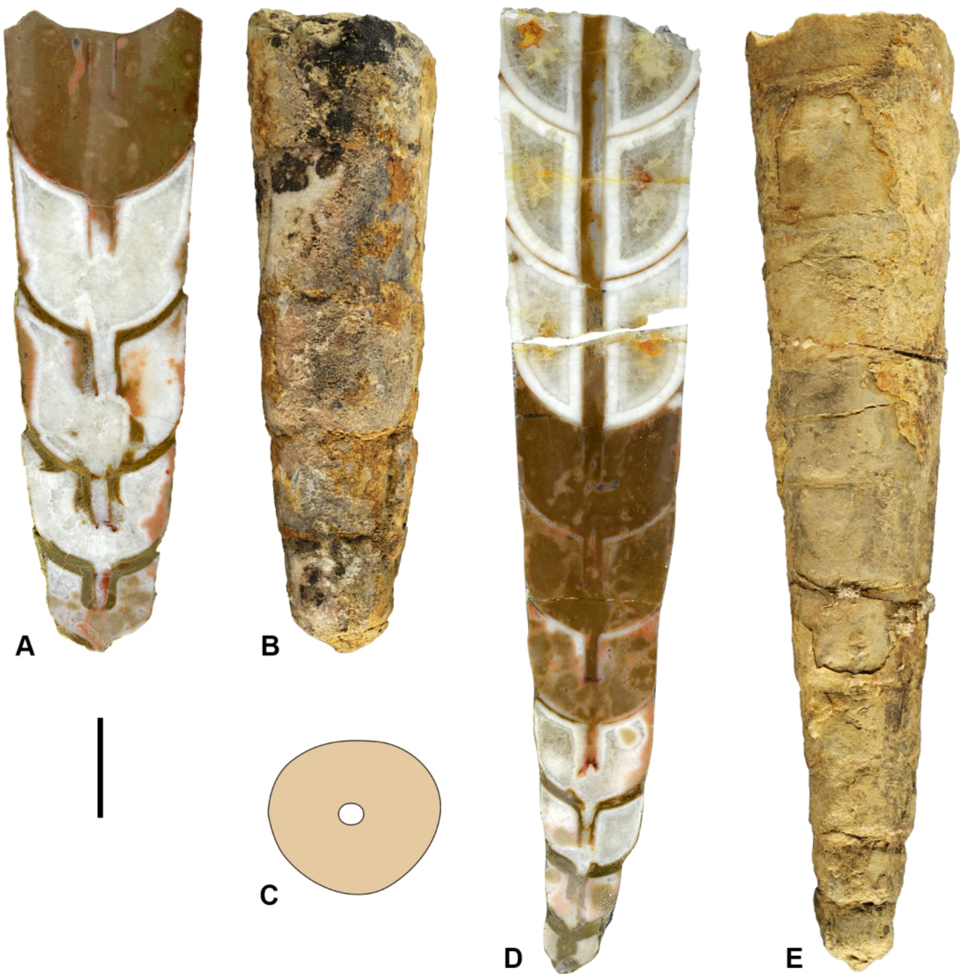

Figure 5

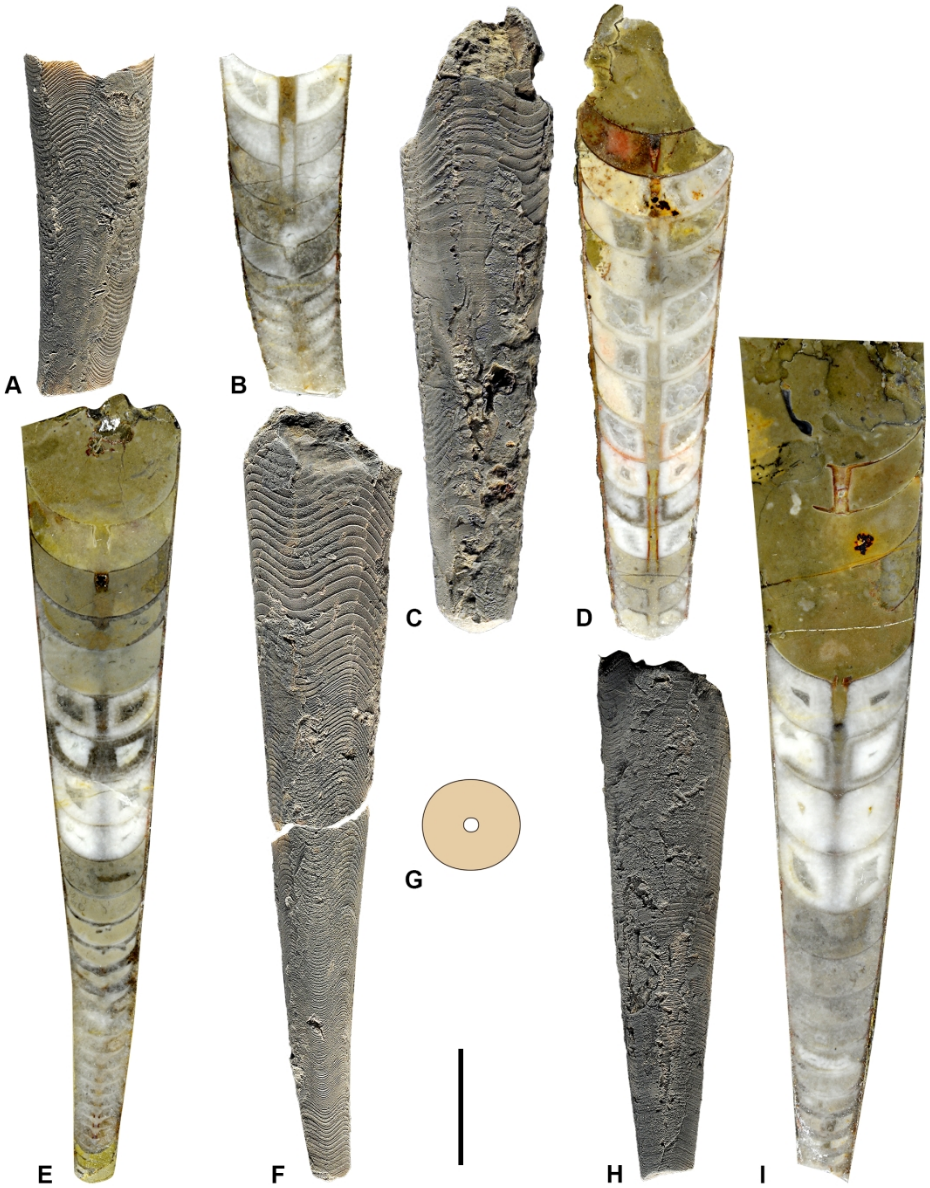

Figure 6

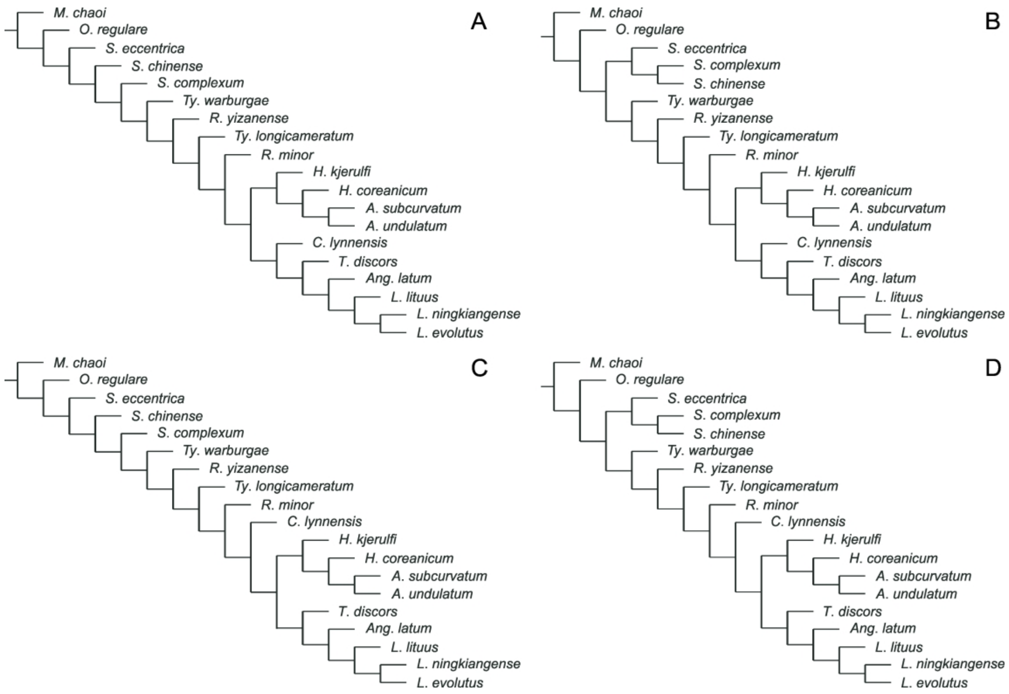
A
M. chaoi
O. regulare
S. eccentrica
S. chinense
S. complexum
Ty. warburgae
R. yizanense
Ty. longicameratum
R. minor
H. kjerulfi
H. coreanicum
A. subcurvatum
A. undulatum
C. lynnensis
T. discors
Ang. latum
L. lituus
L. ningkiangense
L. evolutus
B
M. chaoi
O. regulare
S. eccentrica
S. complexum
S. chinense
Ty. warburgae
R. yizanense
Ty. longicameratum
R. minor
H. kjerulfi
H. coreanicum
A. subcurvatum
A. undulatum
C. lynnensis
T. discors
Ang. latum
L. lituus
L. ningkiangense
L. evolutus
C
M. chaoi
O. regulare
S. eccentrica
S. chinense
S. complexum
Ty. warburgae
R. yizanense
Ty. longicameratum
R. minor
C. lynnensis
H. kjerulfi
H. coreanicum
A. subcurvatum
A. undulatum
T. discors
Ang. latum
L. lituus
L. ningkiangense
L. evolutus
D
M. chaoi
O. regulare
S. eccentrica
S. complexum
S. chinense
Ty. warburgae
R. yizanense
Ty. longicameratum
R. minor
C. lynnensis
H. kjerulfi
H. coreanicum
A. subcurvatum
A. undulatum
T. discors
Ang. latum
L. lituus
L. ningkiangense
L. evolutus

Figure 7

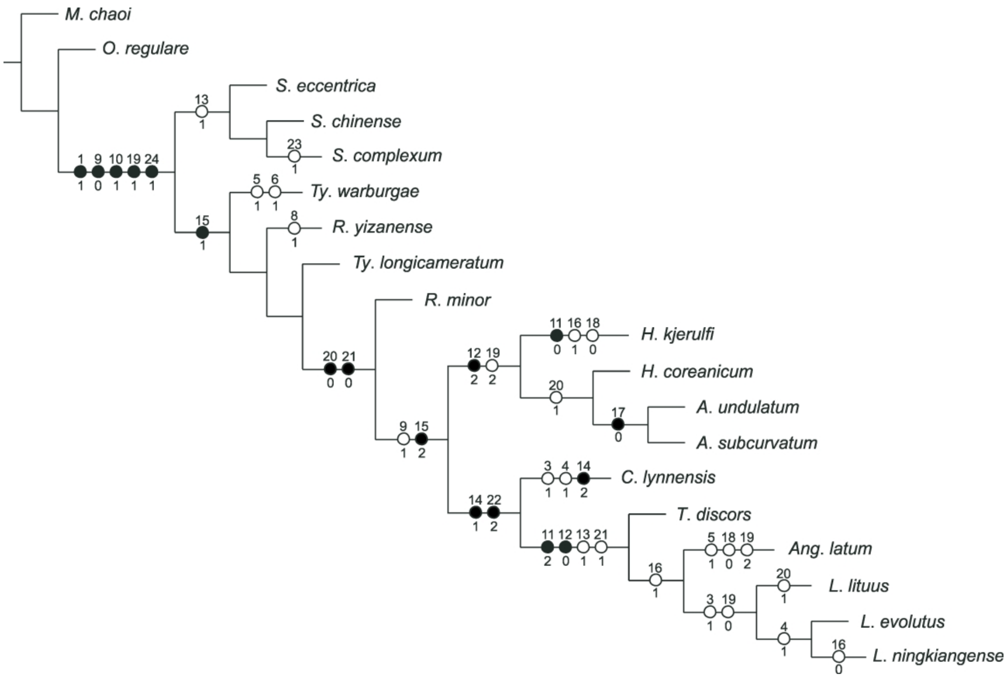
M. chaoi
O. regulare
1 9 10 19 24
1 0 1 1 1
13
1
S. eccentrica
S. chinense
23
1
S. complexum
15
1
5 6
1 1
Ty. warburgae
8
1
R. yizanense
Ty. longicameratum
20 21
0 0
R. minor
9 15
1 2
12 19
2 2
11 16 18
0 1 0
H. kjerulfi
20
1
H. coreanicum
17
0
A. undulatum
A. subcurvatum
14 22
1 2
3 4 14
1 1 2
C. lynnensis
11 12 13 21
2 0 1 1
T. discors
16
1
5 18 19
1 0 2
Ang. latum
3 19
1 0
20
1
L. lituus
4
1
L. evolutus
16
0
L. ningkiangense

Figure 8

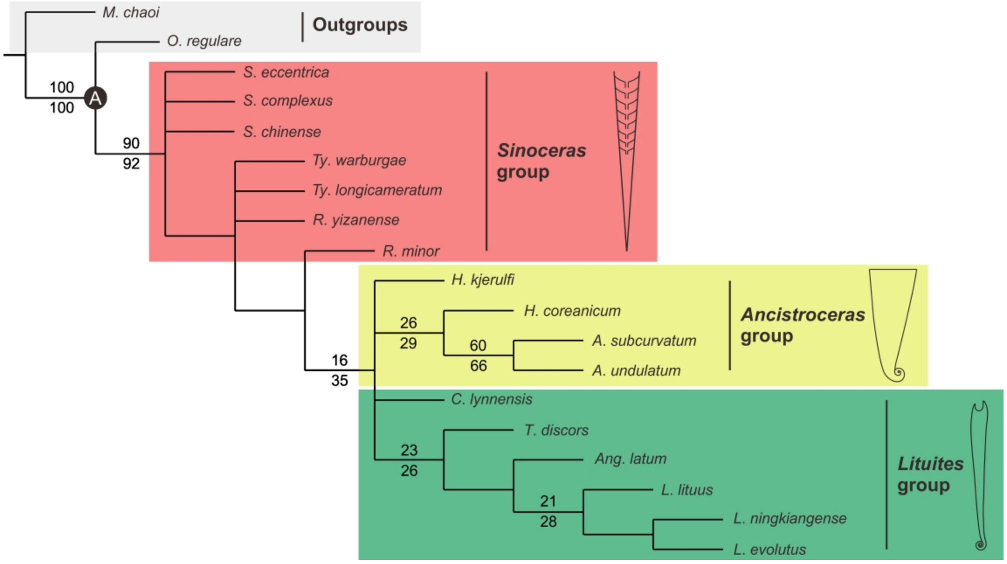
M. chaoi
O. regulare
Outgroups
100
100
A
S. eccentrica
S. complexus
S. chinense
90
92
Ty. warburgae
Ty. longicameratum
R. yizanense
R. minor
Sinoceras group
H. kjerulfi
H. coreanicum
26
29
60
66
A. subcurvatum
A. undulatum
16
35
Ancistroceras group
C. lynnensis
T. discors
23
26
Ang. latum
L. lituus
21
28
L. ningkiangense
L. evolutus
Lituites group

Figure 9

Table 1. Lituitida species sampled and their distributions and horizons.

Species	Distributions	Horizons	References
Ancistroceras undulatum	Baltica; South China	Darriwilian Stage, Middle Ordovician	Noetling 1883; Aubrechtová & Meidla 2020
Ancistroceras subcurvatum	South China; Himalaya	Dapingian Stage, Middle Ordovician	Qi 1980; Chen 1984
Angelinoceras latum	Baltica	Darriwilian Stage, Middle Ordovician	Angelin & Lindström 1880
Cyclolituites lynnensis	Baltica; South China	Sandbian Stage, Upper Ordovician	Sweet 1958; Fang *et al*. 2017b
Holmiceras coreanicum	North China	Darriwilian Stage, Middle Ordovician	Yun 1999, 2003
Holmiceras kjerulfi	Baltica	Darriwilian Stage, Middle Ordovician	Brøgger 1882; Sweet 1958
Lituites evolutus	South China	Sandbian Stage, Upper Ordovician	Fang *et al*. 2017b
Lituites lituus	Baltica	Darriwilian Stage, Middle Ordovician	Sweet 1958; Aubrechtová & Meidla 2020
Lituites ningkiangense	South China	Sandbian Stage, Upper Ordovician	Fang *et al*. 2017b
Rhynchorthoceras minor	Precordillera, Argentina	Darriwilian Stage, Middle Ordovician	Kröger *et al*. 2007
Rhynchorthoceras yizanense	South China	Sandbian Stage, Upper Ordovician	New species in this study
Sinoceras chinense	South China; Sibumasu	Darriwilian Stage, Middle Ordovician–Katian Stage, Upper Ordovician	Fang *et al*. 2017*a*
Sinoceras complexus	South China	Katian Stage, Upper Ordovician	New species in this study
Sinoceras eccentrica	South China	Katian Stage, Upper Ordovician	Fang *et al*. 2017*a*
Trilacinoceras discors	Baltica	Darriwilian Stage, Middle Ordovician	Sweet 1958; Aubrechtová & Turek 2018
Tyrioceras longicameratum	South China	Katian Stage, Upper Ordovician	New species in this study
Tyrioceras warburgae	Baltica	Katian Stage, Upper Ordovician	Frye 1982; Kröger 2013

Table 2. Character code-taxa matrix used for cladistic analysis. For the genus abbreviations, see Table 1.

Selected taxa	Character numbers and codes																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
M. chaoi	0	-	-	-	0	0	0	?	1	0	1	1	0	0	0	-	-	-	0	1	1	1	0	0
O. regulare	0	-	-	-	0	0	0	1	1	0	1	1	0	0	0	-	-	-	0	1	1	1	0	0
A. undulatum	1	0	0	0	?	1	1	?	1	1	1	2	1	0	2	0	0	1	2	1	0	0	1	0
A. subcurvatum	?	?	?	?	?	?	?	?	1	1	1	2	?	0	?	?	0	?	2	1	0	0	1	0
Ang. latus	1	1	0	0	1	1	1	?	?	?	?	0	1	1	2	1	1	0	2	0	?	?	?	?
C. lynnensis	1	1	1	1	0	1	0	1	1	1	1	1	0	2	2	0	?	1	1	0	0	2	0	1
H. coreanicum	1	0	0	0	0	0	1	1	1	1	1	2	0	0	2	?	1	?	2	1	0	0	1	0
H. kjerulfi	?	?	?	?	?	?	?	?	?	?	0	2	0	0	2	1	1	0	2	0	0	1	?	?
L. evolutus	1	1	1	1	0	1	1	?	1	1	2	0	?	1	2	1	1	1	0	0	1	2	0	1
L. lituus	1	1	1	0	0	1	1	0	1	?	2	0	1	1	2	1	1	1	0	1	1	2	0	1
L. ningkiangense	1	1	1	1	0	1	1	?	1	1	2	0	1	1	2	0	1	1	0	0	1	2	0	1
R. minor	1	0	0	0	0	0	0	?	0	1	1	1	?	0	1	-	-	-	1	0	0	0	0	1
R. yizanense	1	0	0	0	?	0	0	0	0	1	1	1	0	0	1	-	-	-	1	1	1	0	0	1
S. chinense	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	-	-	-	1	1	1	0	0	1
S. complexum	?	?	?	?	?	?	?	?	0	1	1	1	1	0	0	-	-	-	1	1	1	0	1	1
S. eccentrica	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	-	-	-	1	1	1	1	0	1
T. discors	1	0	0	0	0	1	1	?	?	?	2	0	1	1	2	0	1	1	1	0	1	2	?	?
Ty. longicameratum	?	?	?	?	?	?	?	?	0	1	1	1	0	0	1	-	-	-	1	1	1	0	0	1
Ty. warburgae	1	0	0	0	1	1	0	?	0	1	1	1	0	0	1	-	-	-	1	1	1	0	0	1