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Claude Monnet, Hugo Bucher, Arnaud Brayard, James F. Jenks. Globacrochordiceras gen. nov. (Acrochordiceratidae, late Early Triassic) and its significance for stress-induced evolutionary jumps in ammonoid lineages (cephalopods). *Mitteilungen aus dem Museum für Naturkunde in Berlin*, 2013, 16 (2), pp.197-215. 10.1002/mmng.201300010 . hal-00851965

**HAL Id: hal-00851965**

**<https://hal.science/hal-00851965>**

Submitted on 5 Jan 2021

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# *Globacrochordiceras* gen. nov. (Acrochordiceratidae, late Early Triassic) and its significance for stress-induced evolutionary jumps in ammonoid lineages (cephalopods)

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## Abstract

Received 28 September 2012

Accepted 4 March 2013

Published 5 August 2013

*Globacrochordiceras transpacificum* gen. et sp. nov. is an ammonoid (Ammonoidea, Cephalopoda) with a shell characterized by plicate ribbing (rounded and undulating ribs strengthening on the venter without interruption), increasing involution through ontogeny, overhanging and deep umbilical wall, absence of tuberculation, subtriangular whorl section, globose adult shape with a closed umbilicus followed by an abrupt egressive coiling, and a subammonitic adult suture line. This new taxon occurs in Nevada (USA) and in Guangxi (South China). It has its typical occurrence within the *Neopopanoceras haugi* Zone of late Spathian age (Early Triassic). The plicate ribbing, suture line and general shell shape are diagnostic of the family Acrochordiceratidae. The large adult size, high degree of involution and subammonitic suture line of *Globacrochordiceras* markedly contrast with the next younger genus of the family (*Paracrochordiceras* of early Anisian age, Middle Triassic), which is evolute and displays a ceratitic suture shape. Shell coiling and suture line of *Globacrochordiceras* are closer to that of the youngest member of the family: *Acrochordiceras carolinae* (late middle Anisian). The latter is the end-member of a long-term morphological evolutionary trend of the family during the early and middle Anisian. This trend composed of classical increases in adult size (Cope's rule), shell involution and suture indentation, lasted ca. four Myr. The sudden morphological evolutionary jump between *Globacrochordiceras* and *Paracrochordiceras* at the Spathian/Anisian (Early/Middle Triassic) boundary may correspond to a generalized morphological reset of long-term trends, a process that differs from classic paedomorphic transformations. A dramatic global sea level change and carbon isotope positive excursion at the Early/Middle Triassic boundary both indicate stressful environmental changes that may have triggered this evolutionary jump.

## Key Words

Ammonoids  
Anisian  
Evolution  
Nevada  
South China  
Spathian

## Introduction

The family Acrochordiceratidae (Ammonoidea, Cephalopoda, Mollusca) was established by Arthaber (1911, p. 179) and represents one of the main components of ammonoid faunas during the Anisian (ca. 248–241 Ma; Middle Triassic). Representatives of this family occur in rocks of upper Spathian to middle Anisian (Early–

Middle Triassic) from North America, Arctic, Western Pacific, Tethys and Germanic Basin. The broad palaeogeographical and temporal distribution of this family, as well as its moderate evolutionary rates, suggests that this clade was well-adapted to its environment (Fig. 1).

Based on exceptionally large collections from North America, Monnet et al. (2012) highlighted that the family evolved by displaying significant long-term mor-

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phological evolutionary trends during the Anisian (see discussion). Here we report on the oldest acrochordiceratids recently discovered from the Spathian of Nevada (USA) and of Guangxi (South China). This oldest member of the family represents a new genus and a new species. Although easily distinguishable and clearly belonging to the Acrochordiceratidae (see systematic palaeontology), the new genus displays a morphology which stands in sharp contrast with the temporally succeeding taxa of the family. This new genus brings additional data to the evolutionary history of the group and provides insights on the morphological reactions of ammonoids under intense external stress. We therefore first report on the taxonomy and biostratigraphy of this new acrochordiceratid genus, then provide a short revision of the family, and finally discuss the evolutionary implications of this new ammonoid genus.

## Material and geological setting

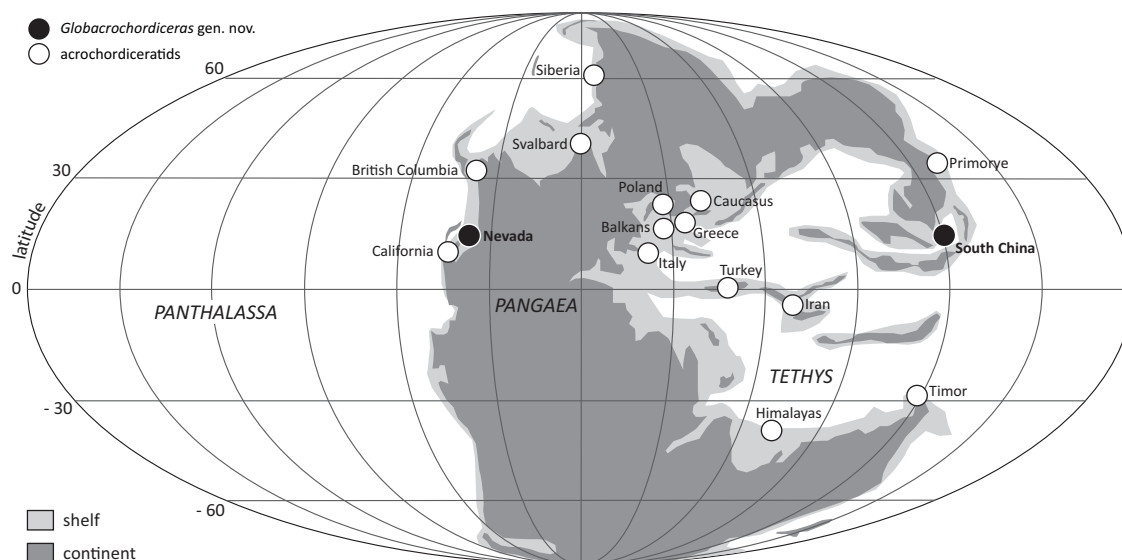
The new taxon is based on specimens collected in two distinct regions (Fig. 1): Guangxi (South China) and Nevada (USA). These specimens are part of systematic bed-by-bed collections of Spathian ammonoids (sampled by HB). In Nevada, the new taxon described herein occurs in the upper part of the carbonate unit of the Lower Member of the Prida Formation exposed in Coyote Canyon (northern Humboldt Range). Bucher (1989) described in detail the stratigraphy and facies changes of the Spathian/Anisian boundary in the Humboldt Range.

In South China, most of the material comes from NW Guangxi Province. This area provides numerous exposures covering the interval from the uppermost Permian to the Middle Triassic. The new acrochordiceratid genus occurs in the uppermost part of the Luolou Formation in the Jinya area, which has been described

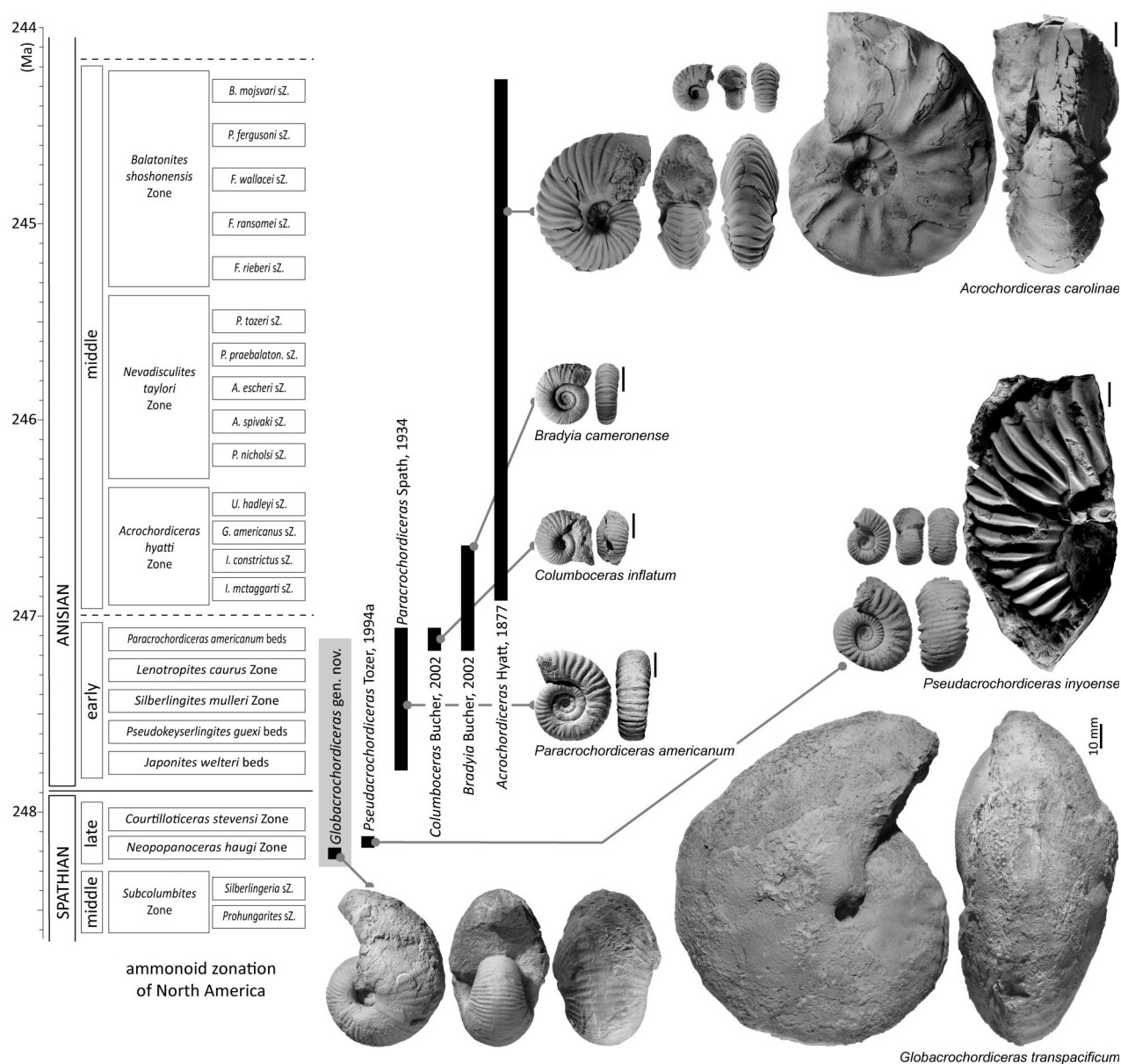
exhaustively by Galfetti et al. (2008). The Luolou Fm. crops out extensively in the Nanpanjiang Basin of the South China Block (see Lehrmann et al. 1998, 2005 and Galfetti et al. 2008), which was located at an equatorial position during the Early Triassic (Gilder et al. 1995). At its type locality, the Luolou Formation is composed of mixed carbonate-siliciclastic rocks deposited in an outer platform setting (for details about lithologies, microfossils and carbon isotope changes, see Galfetti et al. 2007a, 2007b, 2008). The lithological unit of the Luolou Formation yielding the new acrochordiceratid (Unit V in Galfetti et al. 2008) is ca. 40 m thick and composed of thin-bedded, grey, nodular and highly bioturbated limestones. This unit brackets a conspicuous greywacke horizon (called “Green Bean Rock”) of regional extension within its upper part (Galfetti et al. 2008) with a radiometric age of 248.12 Ma (Ovtcharova et al. 2006).

## Biostratigraphy

The standard biochronological scheme of Spathian and Anisian in North America was produced by Silberling & Tozer (1968), Silberling & Wallace (1969), Bucher (1989), Tozer (1994b), and Monnet & Bucher (2005a). Monnet & Bucher (2005b) analysed the biochronology and biodiversity of Anisian ammonoid faunas from Nevada and British Columbia. The complete taxonomical and biostratigraphical revision of Spathian ammonoids in the USA is in progress (Guex et al. 2005a, 2005b, 2010; Bucher et al., ongoing work). The new taxon sampled in the northern Humboldt Range is associated with *Ceccaiculitoides elegans*, *Subhungarites yatesi*, *Inyoceras* sp. nov., *Metadagnoceras pulchrum*, *Sulioticeras* sp. nov., *Arnautoceltites* sp. nov., and *Svalbardiceras* aff. *S. spitzbergensis*. This association of taxa occurs just below an assemblage composed of



**Figure 1.** Distribution of Spathian and Anisian ammonoid Acrochordiceratidae (white circles) and the two basins currently recording *Globacorchordiceras* (black circles). Palaeogeographical reconstruction modified after Blakey (2011).



**Figure 2.** North American ammonoid zonation, stratigraphical age of the newly described genus *Globacrochordiceras*, and illustration of all genera belonging to the Acrochordiceratidae as revised here. Ammonoid zonation of the Anisian after Monnet & Bucher (2005a, 2005b) and Monnet et al. (2008). Ammonoid zonation of the Spathian modified after Guex et al. (2010) and Bucher et al. (ongoing work). Age calibration of the ammonoid zonation after Galfetti et al. (2007b). Ammonoid figures (all at the same scale) after Bucher (2002; *Bradyia cameronense*, pl. 1, figs 9–10; *Columboceras inflatum*, pl. 1, figs 5–6; *Paracrochordiceras americanum*, pl. 1, figs 1–2), Guex et al. (2010; the largest figured specimen of *Pseudacrochordiceras inyoense*, pl. 24, fig. 2), Monnet et al. (2010; *Acrochordiceras carolinae*, pl. 7, figs 9–11, pl. 10, figs 4–6, and text-fig. 12a–b) and this study (*Globacrochordiceras transpacificum* gen. et sp. nov.; *Pseudacrochordiceras inyoense* after unpublished collection of Jim Jenks).

*Hemilecanites fastigatus*, *Neopopanoceras haugi*, *Keyserlingites pacificus*, *Prohungarites lenticularis*, *Pseudacrochordiceras inyoense*, and *Eodanubites* cf. *E. costulatus*. These two ammonoid faunas are diagnostic of the *Neopopanoceras haugi* Zone of the late Spathian (Fig. 2).

Preliminary data suggest that the Chinese Spathian biostratigraphical record is rather good and correlates well with the reference succession from North America (Galfetti et al. 2007b). The new genus sampled in NW Guangxi is typically associated with *Procarnites*, *Japonites*, *Eodanubites zyunensis*, *Deweeveria*, *Pseudosage-*

*ceras*, *Paleophyllites*, and *Ceccaisculitoides*. This association of taxa is also diagnostic of the *Neopopanoceras haugi* Zone in the late Spathian (see references above; Fig. 2). Noteworthy, in Jinya, samples containing the new taxon bracket an ash layer dated of  $248.12 \text{ Ma} \pm 0.28$  (Ovtcharova et al. 2006; Galfetti et al. 2007b).

The new acrochordiceratid genus is spatially restricted to the low palaeolatitudes, and temporally to the *Neopopanoceras haugi* Zone (late Spathian, Early Triassic). This zone is documented in the Union Wash Formation in California (Smith 1914; Guex et al. 2010)

and the Prida Formation in Nevada (Silberling & Wallace 1969; Bucher 1989; this work), as well as in the Luolou Formation in China (Galfetti et al. 2007a; this work). Several authors (Silberling & Tozer 1968; Bucher 1989; Tozer 1994a) considered that the *haugi* Zone correlates with the high-palaeolatitudinal *Keyserlingites subrobustus* Zone. Although this point of view has been questioned (Waterhouse 1999), the ammonoid faunas recently documented by Guex et al. (2010) corroborate this hypothesis again. The assignment of both zones to either latest Spathian (Early Triassic) or earliest Anisian (Middle Anisian) has also been repeatedly debated (Silberling & Wallace 1969; Weitschat & Dagys 1989; Tozer 1994a; Waterhouse 2002). Given the newly described faunas from the United States (Guex et al. 2010; Bucher, ongoing work), the *haugi* Zone displays clear Spathian affinities with only very few taxa ranging up into the Anisian. Hence, the *haugi* Zone will be considered of Spathian age throughout the rest of this study.

## Systematic palaeontology

Taxonomical descriptions follow the terminology of Arkell et al. (1957) and Korn (2010). Definition of size classes follows the classification of Korn (2010). The supra-familial classification of Acrochordiceratidae follows Tozer (1981, 1994b) but the infra-familial classification is here revised. The new material described herein is housed at the Palaeontological Institute and Museum of Zürich (PIMUZ; University of Zürich, Switzerland).

Phylum **Mollusca** Linnaeus, 1758  
 Class **Cephalopoda** Cuvier, 1797  
 Subclass **Ammonoidea** Zittel, 1884  
 Order **Ceratitida** Hyatt, 1884  
 Superfamily **Ceratitaceae** Mojsisovics, 1879  
 Family **Acrochordiceratidae** Arthaber, 1911, p. 179

### Type genus *Acrochordiceras* Hyatt, 1877

**Diagnosis.** Ammonoids characterized by plicate ribbing (rounded ribs enlarging when crossing the venter without interruption), usually high oval to inflated whorl section, and a relatively indented ceratitic to subammonitic suture line without well-individualized auxiliary lobes.

**Composition of the family.** Only the following genera are here considered as valid members of the family (Fig. 2): *Acrochordiceras* Hyatt, 1877; *Bradyia* Bucher, 2002; *Columboceras* Bucher, 2002; *Paracrochordiceras* Spath, 1934; *Pseudacrochordiceras* Tozer, 1994a; and *Globacrochordiceras* gen. nov. Additional acrochordiceratid genera have been described but are here considered as synonyms to the previously listed genera (see below and Spath 1934, p. 392).

**Occurrence.** The family shows a broad palaeogeographical distribution (Fig. 1) and occurs in North Ameri-

ca (Nevada, California and British Columbia), the Western Pacific (Primorye), the Tethys (Italy, Austria, Hungary, Balkans, Greece, Caucasus, Turkey, Iran, Himalayas and Timor, South China), the Germanic Basin (Poland) and the Arctic (Svalbard, Siberia). It is recorded with certainty from the late Spathian *Neopopanoceras haugi* Zone (Early Triassic) to the middle Anisian *Balatonites shoshonensis* Zone (Middle Triassic) (Fig. 2).

**Description.** Coiling very evolute (serpenticone) to very involute; generally decreasing on outer whorls. Whorl section depressed to moderately compressed, high oval or subtriangular to subquadrangular. Ornamentation composed of thin to strong ribs, which strengthen and are more prominent as they cross the arched venter without interruption; this plicate ribbing is the major diagnostic feature of the family. In addition to the typical ribbing, some species may bear umbilical or lateral tubercles from which may stem usually two or three ribs. Ornamentation on the mature body chamber is commonly, if not invariably, different; ribbing may either completely fade or may strengthen and become more distant but without crossing the venter. Body chamber of about three quarters of a whorl. Suture line ceratitic with smooth saddles to subammonitic with slightly but distinctly crenulated saddles; lobes slightly to deeply indented; formula characteristically 6-lobed (E, L, U2, U3, U1, I).

**Remarks.** The origin of the family remains poorly understood. Spath (1934, p. 392) briefly discussed the phylogenetic relationship of Acrochordiceratidae and considered three possible origins (Sibiritidae, Danubitidae, and Ceratitidae). Waterhouse (1999, p. 71) argued for a completely different origin and considered Eoptychitidae as a likely source for Acrochordiceratidae. Bucher (2002, p. 282) suggested that Acrochordiceratidae may have branched off from Balatonitidae during the Spathian, because of the common presence of constrictions and plicate ribbing between members of these two families. Now, given the additional documentation available for Acrochordiceratidae, we hypothesize that the family may root into mid-Spathian Columbidae. However, the origin of Acrochordiceratidae remains unclear and awaits evidence from a detailed phylogenetic analysis of Triassic ammonoids.

### Genus *Pseudacrochordiceras* Tozer

#### Figure 2

\* 1994a *Pseudacrochordiceras* Tozer, p. 163 (type *Acrochordiceras inyoense* Smith, 1914, p. 40).

**Type species.** *Acrochordiceras inyoense* Smith, 1914, p. 40, pl. 34, figs 11–13 from the Union Wash Formation (California).

**Diagnosis.** Large-sized acrochordiceratid characterized by depressed whorl section (cadicone), rounded flanks, low-arched venter, moderately evolute coiling, strong, slightly concave and rectiradiate ribs, sharp plicate ribbing, and absence of real tubercles, but sometimes presence of faint nodes where ribs branch off (see e.g., Guex et al.

2010, pl. 23, figs 3–5). Suture line ceratitic with rounded, smooth saddles, moderately crenulated lobes, a narrow external lobe (E) and a small suspensive lobe. Mature shell imperfectly known, with rounded to high-oval whorl section, slightly egressive coiling and with an estimated maximum diameter of ca. 120 mm.

*Composition of the genus.* Type species only.

*Occurrence.* The genus is restricted to the late Spathian (Early Triassic). It was originally described from the *Neopopanoceras haugi* Zone in California (USA) and is now also documented in Nevada.

## Genus *Paracrochordiceras* Spath

Figure 2

- \* 1934 *Paracrochordiceras* Spath, p. 400 (type *Acrochordiceras anodosum* Welter, 1915, p. 111).
- ? 1978 *Preflorianitoides* Wang, p. 158 (type *P. reniformis* Wang, 1978, p. 158).
- . 1978 *Eoacrochordiceras* Wang, p. 165 (type *E. ziyunense* Wang, 1978, p. 165).
- . 1983 *Proacrochordiceras* Korschinskaya, p. 109 (type *P. kiparisovae* Korschinskaya, 1983, p. 110).
- ? 1995 *Caucasochordiceras* Shevyrev, p. 76 (type *Acrochordiceras* (*Paracrochordiceras*) *simplex* Shevyrev, 1968, p. 128).

*Type species.* *Acrochordiceras anodosum* Welter, 1915, p. 111, pl. 89, figs 3a–c from Nifekoko (Timor).

*Diagnosis.* Small-sized acrochordiceratid distinguished by high-oval to rounded whorl section, serpentine to very evolute coiling, dense, straight to polyfurcate, rectiradiate, sharp to weak ribs, sharp to subdued plicate ribbing, absence of real tuberculation but presence of parabolic nodes on inner whorls, and ceratitic suture line with narrow external lobe (E) and no suspensive lobe. Maturity is marked by more subquadrangular whorl section and decreasing number of branching ribs, and is reached at shell diameter of ca. 60 mm.

*Composition of the genus.* Several species of *Paracrochordiceras* are currently known. This genus is the one having the highest number of species in Acrochordiceratidae. However, several of these species are poorly documented and it is probable that a taxonomical revision accounting for their intraspecific variation will suggest that some of them are conspecific. For instance, some species are distinguished only by a stronger or weaker ribbing (see e.g., discussion of Tozer 1994a on *Paracrochordiceras welteri*), which typically fits in the common intraspecific variation of coiled ammonoids, which has been coined as the Buckman's first law of covariation (Westermann 1966); see e.g., Kennedy & Cobban (1976); Silberling & Nichols (1982); Dagys & Weitschat (1993); Yacobucci (2004); Hammer & Bucher (2005); Monnet & Bucher (2005a); Monnet et al. (2010); and see De Baets et al. (2013) for a comparison with uncoiled ammonoids.

The following species of *Paracrochordiceras* have been described (published indeterminate species of *Paracrochordiceras* are omitted here): *Sibirites pandya* Diener, 1895 (p. 104, pl. 29, fig. 3); *Acrochordiceras anodosum* Welter, 1915 (p. 111, pl. 89, figs 3a–c); *Acrochordiceras* (*Paracrochordiceras*) *americanum* McLearn, 1946 (p. 16, pl. 5, fig. 1); *Acrochordiceras*

(*Paracrochordiceras*) *simplex* Shevyrev, 1968 (p. 128, pl. 7, fig. 5, text-fig. 32); *Eoacrochordiceras ziyunense* Wang, 1978 (p. 165, pl. 2, figs 22–26, text-figs 7a–b); *Eoacrochordiceras evolutum* Wang, 1978 (p. 166, pl. 2, figs 20–21, text-fig. 7c); *Paracrochordiceras asseretoi* Fantini Sestini, 1981 (p. 48, pl. 4, fig. 1); *Paracrochordiceras denseplicatum* Fantini Sestini, 1981 (p. 49, pl. 4, figs 2–3); ? *Acrochordiceras* (*Paracrochordiceras*) *pacificum* Zharnikova, 1981 (p. 34, pl. 4, fig. 5, text-figs 3–4); *Proacrochordiceras kiparisovae* Korschinskaya, 1983 (p. 110, figs 1a–h, 2a–b); *Proacrochordiceras negriense* Korschinskaya, 1983 (p. 111, figs 2c, 3); *Paracrochordiceras silberlingi* Bucher, 1989 (p. 971, pl. 1, figs 6–7, text-fig. 12); *Paracrochordiceras mclearni* Bucher, 1989 (p. 973, pl. 7, figs 6–7, text-fig. 14); *Paracrochordiceras plicatus* Bucher, 1989 (p. 974); *Paracrochordiceras welteri* Tozer, 1994a (p. 164, pl. 1, figs 1a–d); and *Paracrochordiceras benderi* Tozer, 1994b (p. 110, pl. 45, figs 2–3, text-fig. 32d).

*Occurrence.* Species of *Paracrochordiceras* have been documented worldwide and are restricted to the entire early Anisian (Middle Triassic; Fig. 2) in North America (British Columbia, Nevada), Tethys (Greece, Himalayas, Timor) and Western Pacific (Primorye).

*Remarks.* When assigning a standard intraspecific variation to species of *Paracrochordiceras* (see above), several other genera fit within the morphological spectrum of *Paracrochordiceras* and are considered here as synonyms.

The genus *Eoacrochordiceras* Wang, 1978 was defined as being closely related to *Paracrochordiceras*, except for subdued plicate ribbing on the venter and more denticulate lobes. However, this kind of morphology is typical of juvenile *Paracrochordiceras* (e.g., *P. americanum*; see McLearn 1969, pl. 1, fig. 1; Bucher 1989, pl. 7, figs 3–5; Bucher 2002, pl. 1, figs 1–4) and does not justify assignment to a distinct genus (Waterhouse 1999; this work).

The genus *Proacrochordiceras* Korschinskaya, 1983 was diagnosed by the presence of umbilical tubercles on inner whorls. However, in our opinion, these supposed tubercles are just faint nodes due to strengthening of ribs when bifurcating. There is no other character to justify a distinction of *Proacrochordiceras* from *Paracrochordiceras* Spath, 1934, to which it was not compared when Korschinskaya erected the genus. Although Korschinskaya dated *Proacrochordiceras* of the *subrobustus* Zone (late Spathian), it appears that the genus is known only from loose concretions with no other age-diagnostic ammonoid species (see Weitschat & Dagys 1989). Therefore, we here tentatively consider *Proacrochordiceras* as a junior synonym of *Paracrochordiceras* and strongly suspect that the specimens described by Korschinskaya are of early Anisian and not of late Spathian age. Additional data from the type locality of *Proacrochordiceras* will be necessary to further test this hypothesis.

*Preflorianitoides* Wang, 1978 can be regarded as related to *Paracrochordiceras* with its subdued plicate

ribbing and evolute coiling (Waterhouse 1999), but the low-whorled section and narrow first lateral saddle are also suggestive of a danubitid affinity. Shevyrev (1995) erected the genus *Caucasochordiceras* since it differs from *Paracrochordiceras* by a more denticulate suture line and slower increasing whorl height. However, this kind of morphology is also suggestive of danubitids. Besides, Shevyrev (1968) initially placed the *simplex* species within *Paracrochordiceras* to which it closely resembles with the evolute coiling, subdued plicate ribbing and absence of tubercles. Hence, the systematic position of *Preflorianitoides* and *Caucasochordiceras* remain uncertain and awaits additional material before a firm systematic assignment can be proposed. Noteworthy, taking (or not) into account these genera has no influence on the morphological patterns described after on the evolution of Acrochordiceratidae.

### Genus *Columboceras* Bucher

#### Figure 2

\* 2002 *Columboceras* Bucher, p. 281 (type *C. inflatum* Bucher, 2002, p. 282).

*Type species.* *Columboceras inflatum* Bucher, 2002, p. 282, pl. 1, figs 5–6 from the Toad Formation (British Columbia).

*Diagnosis.* Small-sized acrochordiceratid characterized by depressed, somewhat inflated whorl section, moderately involute coiling, fine, straight and prorsiradiate ribs, sharp plicate ribbing, and absence of tuberculation or faint nodes where ribs branch off. Suture line and adult shell not known (maximum known shell diameter of 21 mm).

*Composition of the genus.* Type species only.

*Occurrence.* The genus is only known from the *Paracrochordiceras americanum* Zone (early Anisian, Middle Triassic) in the Toad Formation of British Columbia.

### Genus *Bradyia* Bucher

#### Figure 2

\* 2002 *Bradyia* Bucher, p. 282 (type *B. cameronense* Bucher, 2002, p. 282).

*Type species.* *Bradyia cameronense* Bucher, 2002, p. 282, pl. 1, fig. 35, text-fig. 4 from the Toad Formation (British Columbia).

*Diagnosis.* Small to medium-sized acrochordiceratid distinguished by rounded whorl section, moderately evolute coiling, fine, straight and prorsiradiate ribs, subdued plicate ribbing, presence of constrictions, absence of tuberculation, and a subammonitic suture line with deeply indented and broad lateral lobe. The presence of constrictions makes this genus very distinct among Acrochordiceratidae. Adult shell morphology not known (maximum known shell diameter of ca. 60 mm).

*Composition of the genus.* Two species belong to this genus: *Bradyia cameronense* Bucher, 2002 (p. 282, pl. 1, fig. 35, text-fig. 4); and *Acrochordiceras coyotense* Bucher, 1992 (p. 152, pl. 6, figs 17–21).

*Occurrence.* The genus is known in the *Paracrochordiceras americanum* Zone (early Anisian, Middle Triassic) from the Toad Formation of British Columbia and

in the *Acrochordiceras hyatti* Zone (middle Anisian, Middle Triassic) from the Prida Formation of north-west Nevada (Humboldt Range).

### Genus *Acrochordiceras* Hyatt

#### Figure 2

\* 1877 *Acrochordiceras* Hyatt, p. 124 (type *A. hyatti* Meek, 1877, p. 124).

. 1907 *Haydenites* Diener, p. 72 (type *H. hatschekii* Diener, 1907, p. 72).

. 1916 *Silesiacrochordiceras* Diener, p. 101 (type *Ammonites (Acrochordiceras) damesii* Noetling, 1880, p. 334).

. 1934 *Epacrochordiceras* Spath, p. 401 (type *Acrochordiceras portisi* Martelli, 1906, p. 132).

*Type species.* *Acrochordiceras hyatti* Meek, 1877, p. 124, pl. 11, fig. 5a [only].

*Diagnosis.* Large-sized acrochordiceratid characterized by compressed to depressed shell, moderately evolute to involute coiling, rounded and low-arched venter, abrupt umbilical shoulders, slightly sinuous to straight, rectiradiate ribs, plicate ribbing, a single row of tubercles from which may arise several ribs, presence of parabolic nodes on inner whorls, and ceratitic to subammonitic suture line with smoothly crenulated saddles and deeply indented lobes. Mature body chamber with a smooth venter, simple ribs bearing marginal swellings, and subquadragonal whorl section. Adult shell diameter up to ca. 250 mm.

*Composition of the genus.* Monnet et al. (2010) thoroughly revised the genus and considered that *Acrochordiceras* contains only four valid species: *Ammonites (Acrochordiceras) damesii* Noetling, 1880 (p. 334); *Acrochordiceras carolinae* Mojsisovics, 1882 (p. 141); *Acrochordiceras hyatti* Meek, 1877 (p. 124); and *Haydenites hatschekii* Diener, 1907 (p. 72).

*Occurrence.* The genus *Acrochordiceras* ranges throughout the entire middle Anisian (Middle Triassic; Fig. 2). It occurs mainly in North America (Nevada) and the Tethys (Alps, Bosnia, Turkey, Himalayas, South China).

### Genus *Globacrochordiceras* nov.

#### Figure 2

*Type species.* *Globacrochordiceras transpacificum* gen. et sp. nov.

*Diagnosis.* As for the type species.

*Derivation of name.* Genus name refers to the globular whorl shape with an almost closed umbilicus and group affinity of the fossil.

*Composition of the genus.* Type species only.

*Occurrence.* As for the type species.

*Description.* As for the type species.

*Remarks.* The genus *Globacrochordiceras* is a typical acrochordiceratid with its plicate ribbing, its roughly rounded high-oval whorl section, and its subammonitic suture line. From a general point of view, *Globacrochordiceras* differs from all other acrochordiceratids by its very involute coiling and its overhanging umbilical wall.



Another acrochordiceratid genus occurred in the late Spathian (Early Triassic): *Pseudacrochordiceras* Tozer, 1994a. Three genera of Acrochordiceratidae (Fig. 2) existed during the early Anisian (Middle Triassic): *Paracrochordiceras* Spath, 1934; *Columboceras* Bucher, 2002; and *Bradyia* Bucher, 2002. Finally, a last additional genus occurred in the middle Anisian: *Acrochordiceras* Hyatt, 1877.

*Pseudacrochordiceras* is a large-sized, depressed, moderately evolute, strongly ribbed shell with a ceratitic suture line. *Globacrochordiceras* is thus morphologically very close to *Pseudacrochordiceras* and differs by having more involute coiling, overhanging umbilical wall, weaker ribs, and more complex suture line with deeply indented lobes.

*Paracrochordiceras* is a small-sized, evolute, subquadrate and depressed shell with sharp to subdued plicate ribbing, absence of tuberculation (except discrete lateral parabolic nodes on innermost whorls), and ceratitic suture line. Therefore, *Globacrochordiceras* differs from *Paracrochordiceras* by having very involute coiling, subtriangular whorl section, overhanging umbilical wall, and larger adult shell diameter.

*Columboceras* is a small-sized, depressed, subcircular, moderately evolute, finely ribbed shell without tuberculation. Although morphologically relatively close, *Globacrochordiceras* differs from *Columboceras* by having subtriangular whorl section, overhanging umbilical wall, thinner ribs, and significantly larger adult shell diameter.

*Bradyia* is a small-sized, non-tuberculated, evolute, subcircular shell with a subammonitic suture line and characterized by constrictions. Hence, *Globacrochordi-*

*ceras* differs from *Bradyia* by subtriangular whorl section, involute coiling, overhanging umbilical wall, larger adult shell diameter, and absence of constrictions.

*Acrochordiceras* covers a large morphological spectrum because of its long-term evolutionary trends during the middle Anisian (see Monnet et al. 2010, 2012). It is a medium- to large-sized shell with moderately evolute to involute coiling, rather subquadrate, compressed to depressed whorl section, ceratitic to subammonitic suture line, and the presence of one row of tubercles. Therefore, *Globacrochordiceras* differs from *Acrochordiceras* by subtriangular whorl section, more involute coiling, overhanging umbilical wall, and absence of tuberculation.

### *Globacrochordiceras transpacificum* gen. et sp. nov.

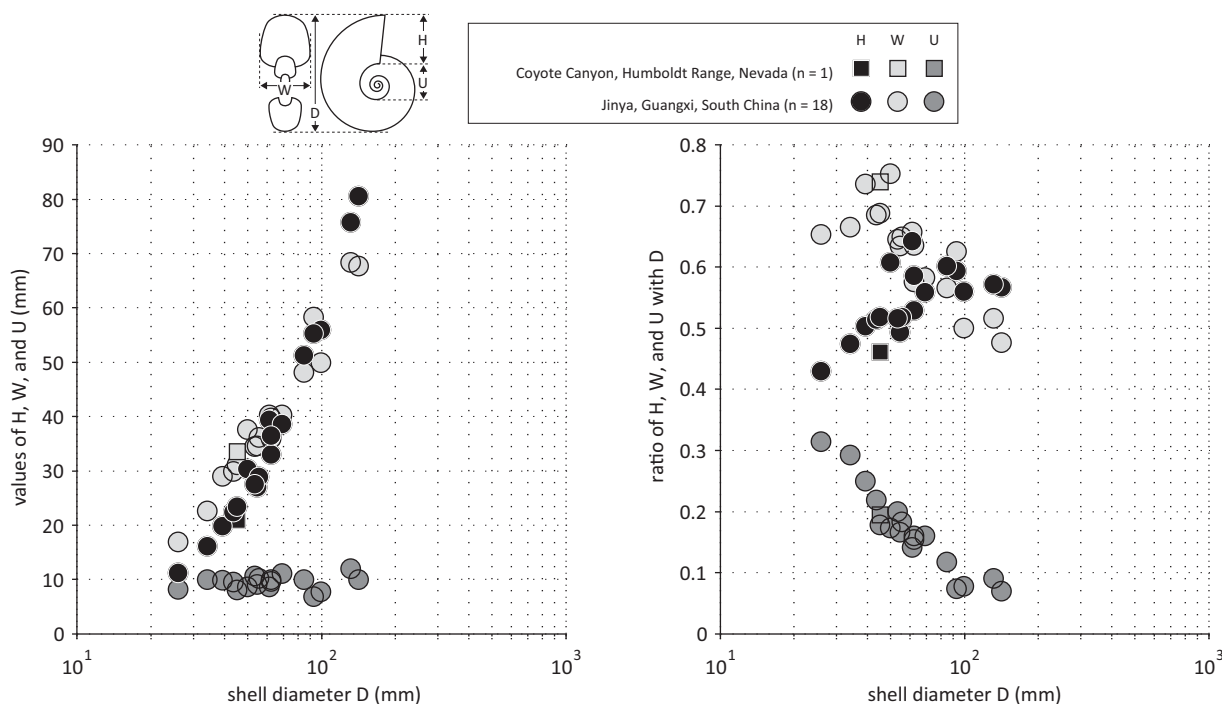
Figures 3–9

**Holotype.** PIMUZ 29402 (Figs 4B, 7C–E), Loc. JIN 78, Jinya (Guangxi, South China); *Neopopanoceras haugi* Zone (late Spathian, Early Triassic).

**Diagnosis.** Acrochordiceratid showing the typical plicate ribbing (rounded ribs enlarging when crossing the venter without interruption) and characterized by very involute coiling (increasing through ontogeny), overhanging and deep umbilical wall, absence of tuberculation, and globular to subtriangular whorl section. Mature body chamber with subdued ribbing. Adult suture line subammonitic with deeply indented lobes. Adult shell diameter up to ca. 150 mm.

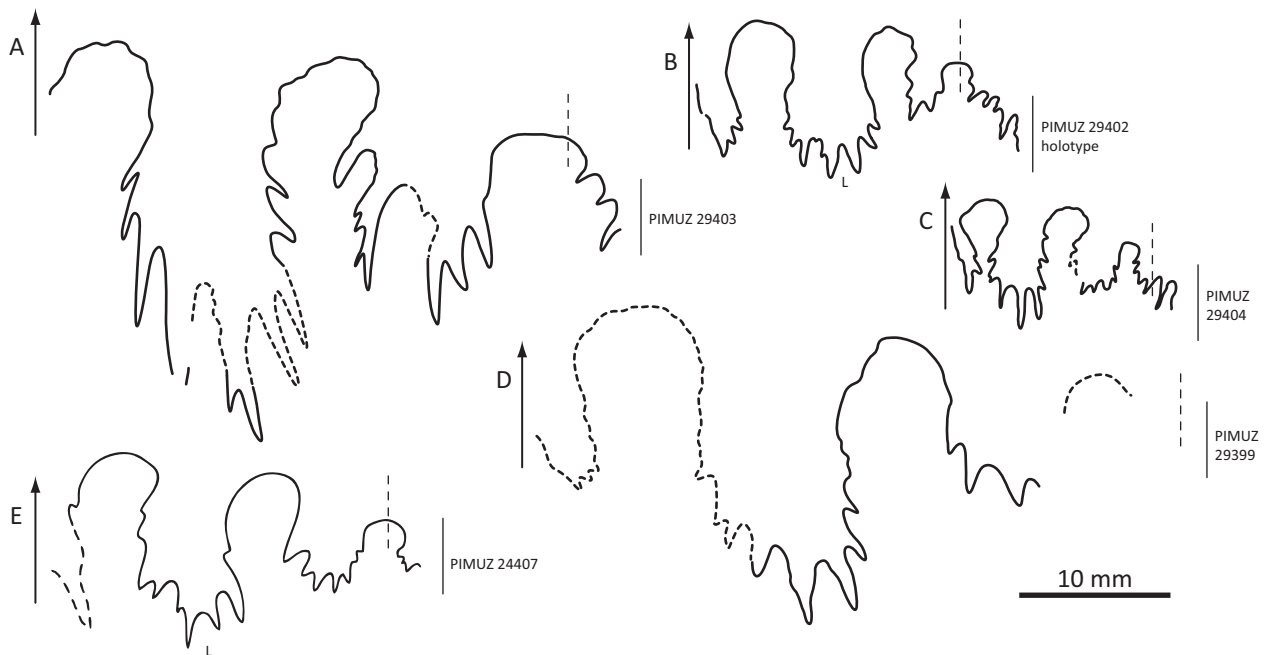
**Derivation of name.** Species name refers to the occurrence of the species on both West and East sides of Panthalassa.

**Material.** Nineteen measured specimens from Jinya (Guangxi, South China) (samples: JIN 71 and JIN 78) and from the northern Humboldt



**Figure 3.** Measurements of the classical geometrical parameters of the ammonoid shell for *Globacrochordiceras transpacificum* gen. et sp. nov. from Guangxi (South China) and Nevada (USA). D, shell diameter; H, whorl height; U, umbilical diameter; W, whorl width.



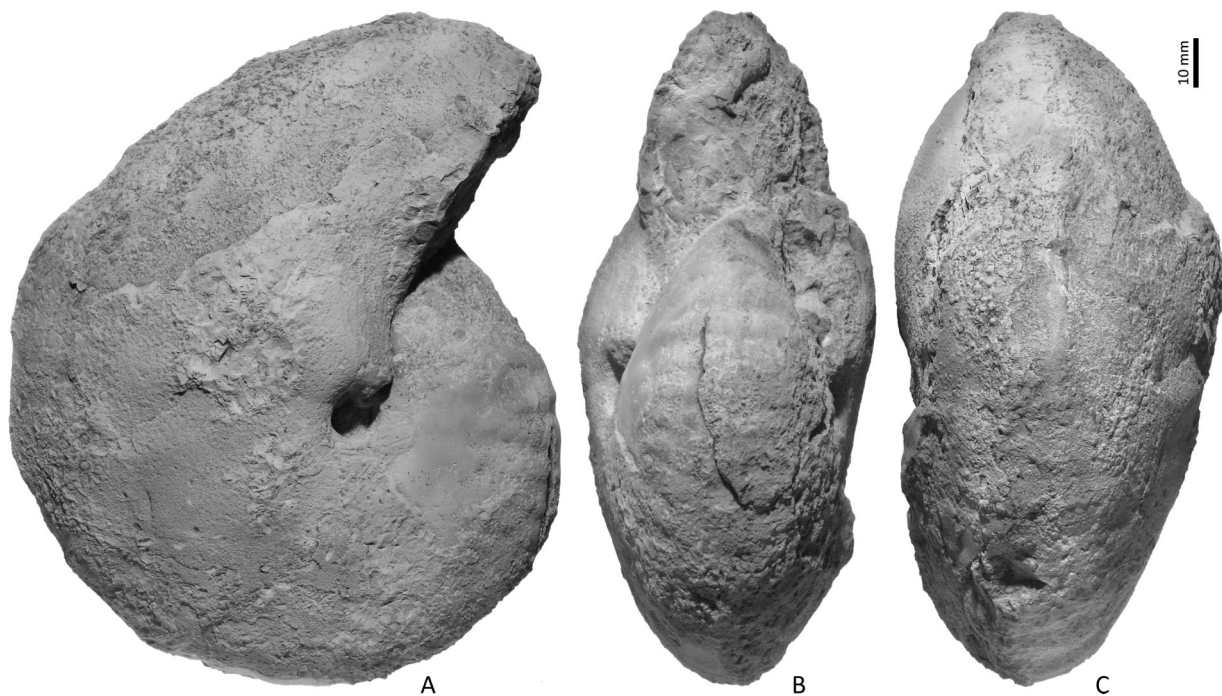


**Figure 4.** Suture lines of *Globacrochordiceras transpacificum* gen. et sp. nov. from the *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic);  $\times 2$ . **A.** PIMUZ 29403, loc. JIN 71, Jinya (Guangxi, South China); **B.** PIMUZ 29402, loc. JIN 78, Jinya (Guangxi, South China), holotype; **C.** PIMUZ 29404 (suture reversed), loc. JIN 71, Jinya (Guangxi, South China); **D.** PIMUZ 29399, loc. JIN 78, Jinya (Guangxi, South China); **E.** PIMUZ 24407 (suture reversed), loc. HB 110, northern Humboldt Range (Nevada, USA).

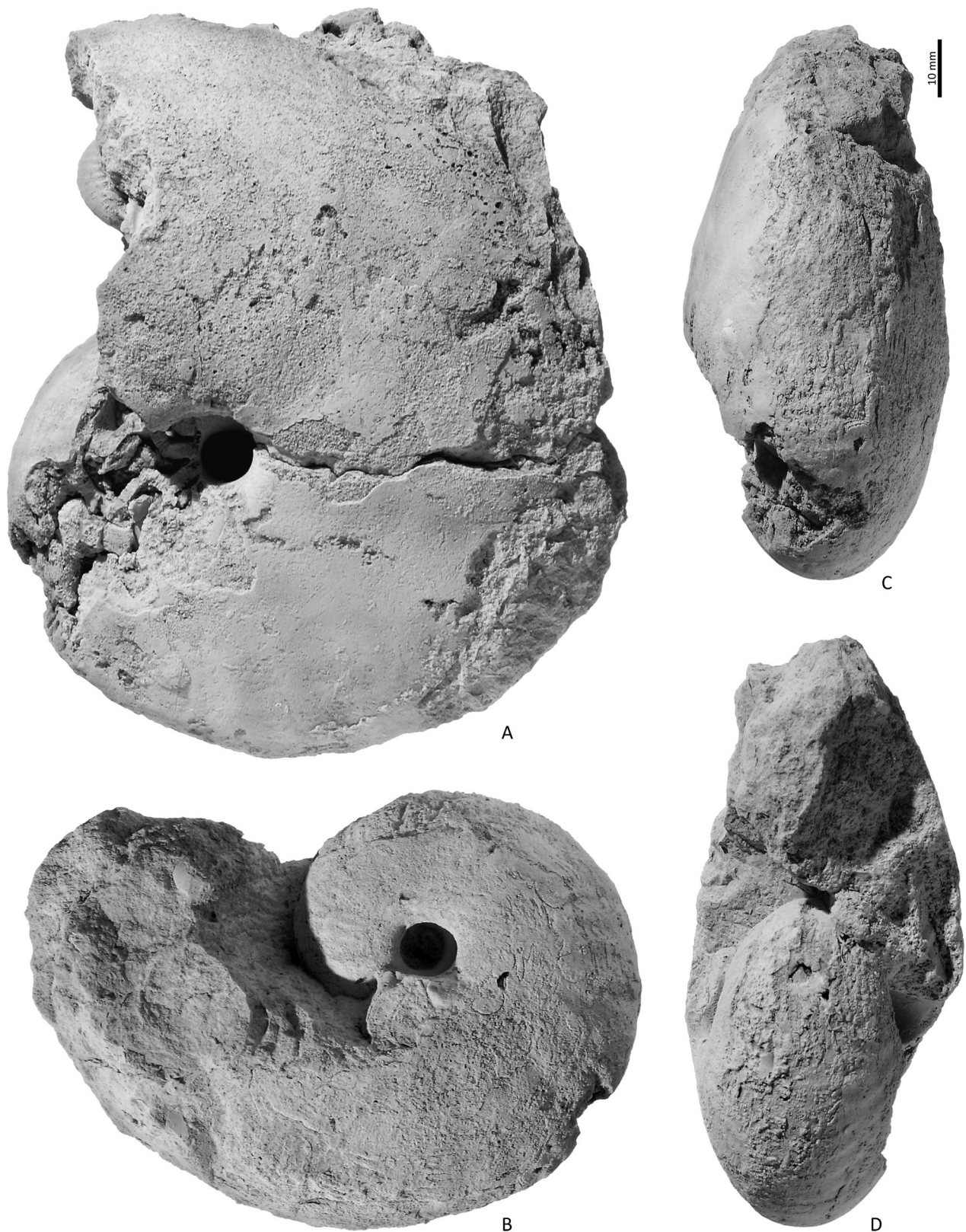
Range (Nevada, USA) (sample: HB 110). The four classical geometrical parameters of the ammonoid shell (shell diameter  $D$ , whorl height  $H$ , whorl width  $W$ , and umbilical diameter  $U$ ) describe the quantitative morphological range of the species (Fig. 3).

**Occurrence.** The species occurs in the *Neopopanoceras haugi* Zone (late Spathian, Early Triassic) from the

NW Guangxi (South China) and from the northern Humboldt Range (Nevada, USA). The species, although scarcely known, shows a distribution restricted to low latitudes. Note that although the genera *Globacrochordiceras* and *Pseudacrochordiceras* both occur in the *haugi* Zone, they did not actually co-exist in time and



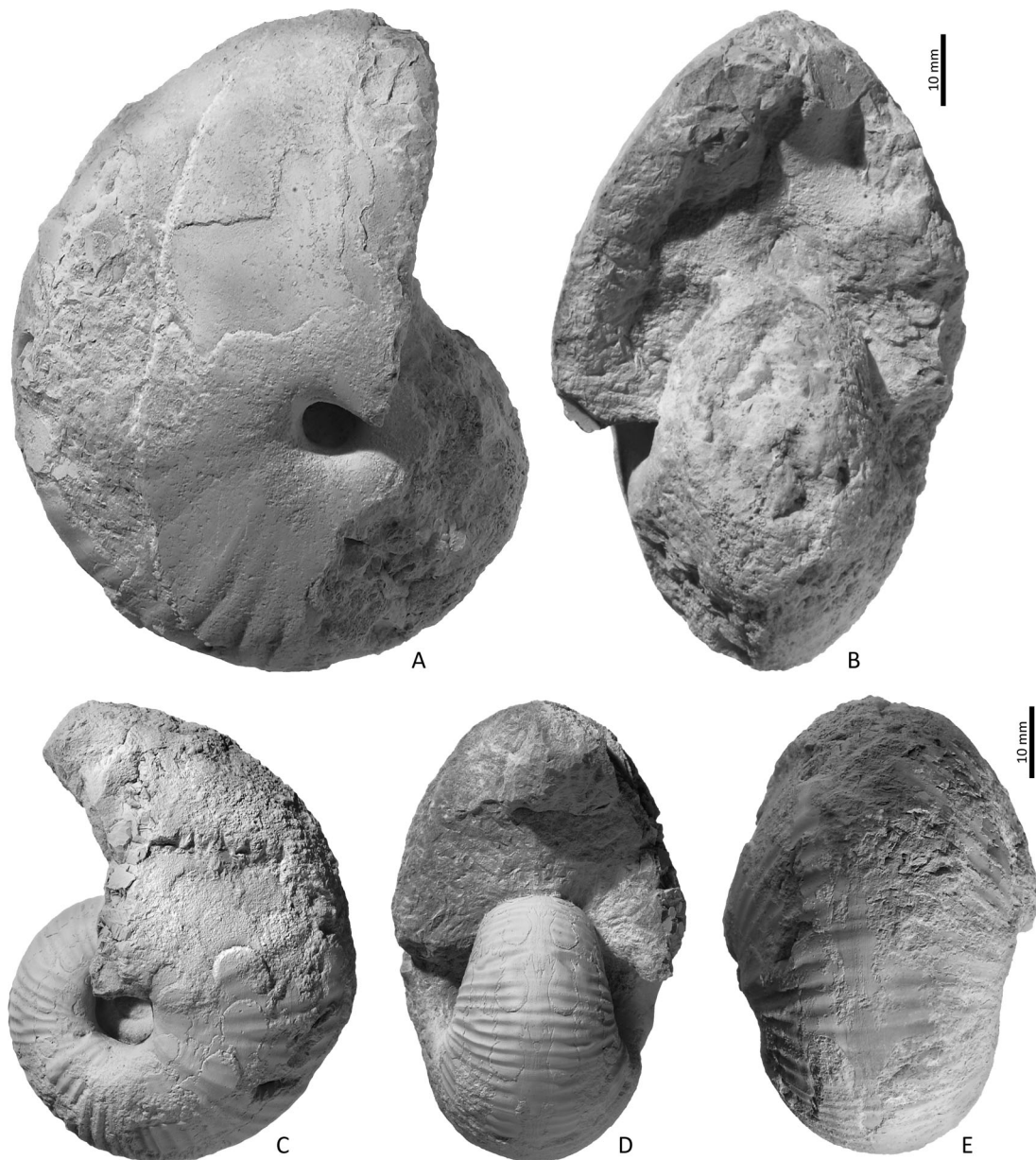
**Figure 5.** *Globacrochordiceras transpacificum* gen. et sp. nov. **A–C.** PIMUZ 29399, sample JIN 78, Jinya, Guangxi (South China); *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic); mature specimen.



**Figure 6.** *Globacrochordiceras transpacificum* gen. et sp. nov. A–D. PIMUZ 29400, sample JIN 71, Jinya, Guangxi (South China); *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic); submature specimen;  $\times 1$ .

space. In the northern Humboldt Range, which is the single area where the two genera are both present, *Globacrochordiceras* occurs in strata slightly older, and thus represents the oldest described member of the family.

Noteworthy, *Globacrochordiceras transpacificum* displays a peculiar distribution in space and time. The species is restricted to the low-palaeolatitude intertropical belt in both east and west sides of the wide ocean

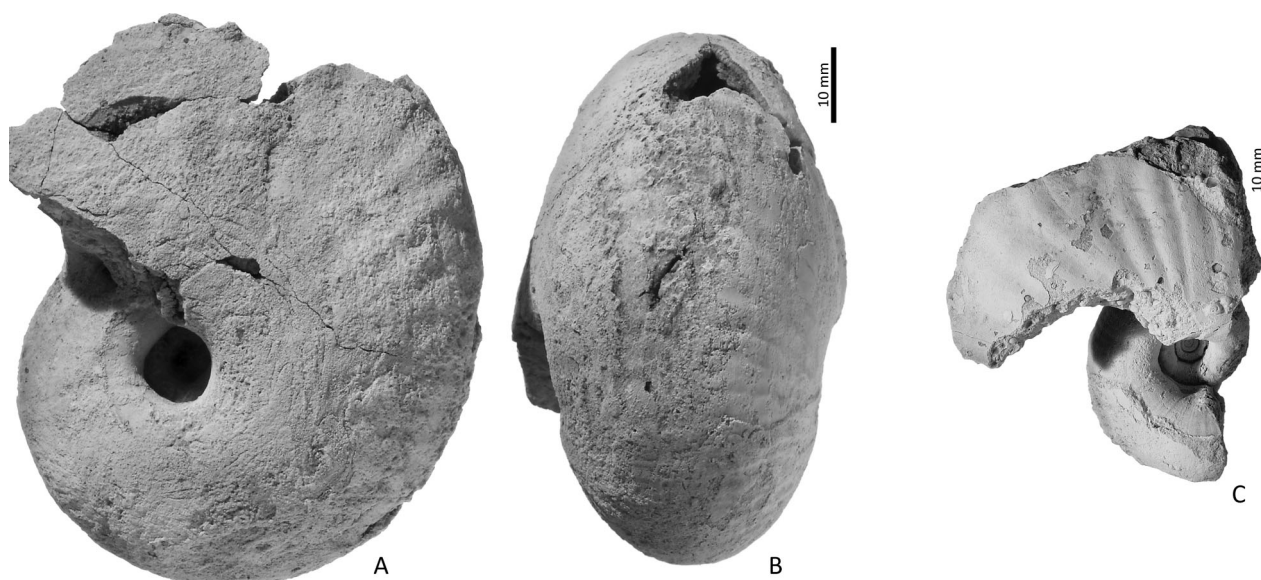


**Figure 7.** *Globacrochordiceras transpacificum* gen. et sp. nov. **A–B.** PIMUZ 29401, sample JIN 78, Jinya, Guangxi (South China); *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic); **C–E.** PIMUZ 29402, sample JIN 78, Jinya, Guangxi (South China); holotype; *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic).

Panthalassa (Fig. 1). A trans-Panthalassic distribution like that of *Globacrochordiceras* is striking, but in fact is frequent among Early and Middle Triassic ammonoids. For instance, Monnet et al. (2008) and Brayard et al. (2009a) described several ammonoid genera having such a peculiar palaeogeographical distribution. These taxa occurring on both east and west equatorial sides of Panthalassa suggest that ammonoid dispersal by oceanic currents was relatively frequent and that faunal exchange between both sides was intense during the Early and Middle Triassic. Furthermore, these genera generally have a short time-range and thus are crucial for highly detailed long-distance correlations. This intertropical distribution probably resulted from the interplay of several factors (see Brayard et al. 2009a)

such as a juvenile planktonic phase of ammonoids (see De Baets et al. 2012), possible active long-distance migration of adults (see Brayard & Escarguel 2013), thermal constraints on the life habitat of ammonoids, intense westward equatorial oceanic currents, and the presence of terranes as stepping stones within the intertropical belt (Brayard et al. 2009b). However, the exact contribution of each of these factors remains to be investigated.

**Description.** Shell coiling characterized by a regular increase of shell involution through ontogeny, from moderately involute inner whorls to involute mature whorls with a very narrow umbilicus. Whorl section changes from slightly depressed inner whorls to rela-



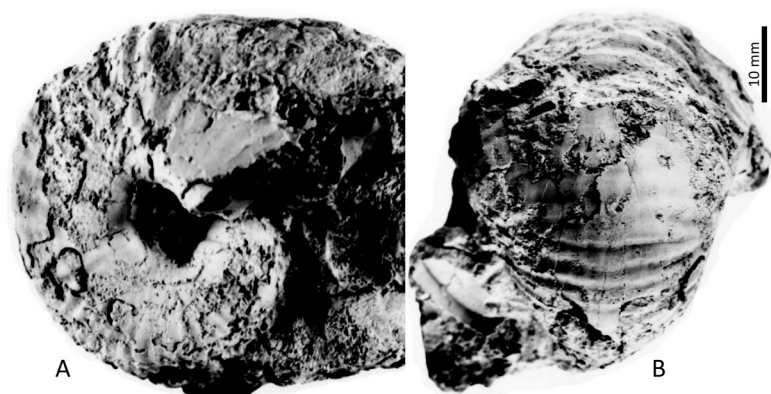
**Figure 8.** *Globacrochordiceras transpacificum* gen. et sp. nov. **A–B.** PIMUZ 29403, sample JIN 71, Jinya, Guangxi (South China), *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic); **C.** PIMUZ 29404, sample JIN 71, Jinya, Guangxi (South China), *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic).

tively compressed outer whorls; shell invariably high-whorled, high-oval with a large rounded venter, rounded indistinct ventral shoulders, rounded flanks with maximum whorl width near the umbilicus, narrow rounded umbilical shoulders, and deep overhanging umbilical wall. Ornamentation composed only by thin, numerous, straight to slightly sinuous, rectiradial ribs that cross the venter without interruption and typically increase in strength from the umbilicus to the venter (the so-called plicate ribbing). Ribs usually single, but sometimes branching dichotomously at mid-flank. On the mature body chamber, ribs become sparser and decrease in strength near the venter without crossing the venter. Suture line subammonitic with weakly indented, rounded, narrow, elongated saddles, and deeply crenulated lobes with the first one being deeper and larger than the first saddle (Fig. 4).

## Discussion

### Evolutionary history of Acrochordiceratidae during the Anisian

Monnet et al. (2012) recently analysed in detail the long-term morphological evolution of Acrochordiceratidae during the Anisian. Their study analysed quantitatively and statistically the morphological changes of the acrochordiceratid shell, based on large collections (more than 700 specimens) from North America. This study showed that (1) the monophyletic clade of Acrochordiceratidae underwent a significant increase (possibly with several steps) of its adult shell diameter (i.e. Cope's rule), (2) the lineage also showed an evolute to involute evolutionary trend (i.e. an increase of shell involution), and (3) the clade furthermore experienced an increase of indentation of its suture line. Multiple ex-



**Figure 9.** *Globacrochordiceras transpacificum* gen. et sp. nov. **A–B.** PIMUZ 24407, sample HB 110, Coyote Canyon (Humboldt Range), Nevada (USA); *Neopopanoceras haugi* Zone (upper Spathian, Early Triassic).



amples of similar morphological trends in ammonoid shells have already been illustrated and discussed (e.g., Haas 1942; Guex 1973, 1992, 2006; Thierry 1982; Bayer & McGhee 1984; Kennedy & Wright 1985; Dommergues et al. 1989; Dommergues 1990; Klug et al. 2005; Monnet et al. 2011, 2012; De Baets et al. 2012).

The increasing body size of the studied lineage conforms with Cope's rule, known as the widespread tendency of animal groups to evolve toward larger body size (Newell 1949; Rensch 1960; Gould 1966). Size increase is commonly interpreted in terms of adaptive advantages such as increased defence against predation, increased food competition, increased success in mating, increased individual longevity and/or better energy use, among others (Stanley 1973; Brown & Maurer 1986; Hone & Benton 2005). For ammonoids, several authors illustrated and discussed examples of increasing ammonoid shell size (Stanley 1973; Hallam 1975; Thierry 1982; Guex 2003; Dommergues et al. 2002; Monnet et al. 2011, 2012; De Baets et al. 2012).

The increasing shell involution (i.e. protracted closure of the umbilicus by increasing overlap of the conch whorls) is also the most commonly described long-term morphological trends for ammonoids (see references above, as well as Hyatt 1889; Schindewolf 1940; Erben 1966; De Baets et al. 2009, 2012). Several studies interpreted such trends as the result of adaptive selection, which favoured more involute shell shapes for their improved hydrodynamics by drag reduction and increased manoeuvrability (Schmidt 1930; Raup 1967; Chamberlain 1976; Saunders & Shapiro 1986; Elmi 1991, 1993; Jacobs 1992; Jacobs & Chamberlain 1996; Klug & Korn 2004).

The increasing suture indentation (frilling) is also a common pattern of ammonoid evolution, especially at large taxonomic ranks (Boyajian & Lutz 1992; Saunders et al. 1999; Allen 2006). The classical morpho-functional interpretation (often called the Buckland hypothesis) is that increasing suture indentation leads to forms adapted to deeper water depth, because it is supposed to provide buttressing against hydrostatic pressure on the phragmocone (Buckland 1836; Pfaff 1911; Saunders 1995; De Blasio 2008; and references inside). However, this function of the septal folding remains controversial (Saunders 1995; Olóriz et al. 2002; Lewy 2002) and constructional constraints complicate its interpretation (see discussion in Monnet et al. 2011) leading to the idea that the evolution of the suture indentation of ammonoids exceeds their functional needs or limits.

The protracted changes in shell morphology of Acrochordiceratidae are robust and non-random (Monnet et al. 2012) and can be interpreted at first sight as being constrained by the persistent, common selection pressure on this mostly anagenetic lineage with relatively moderate evolutionary rates during an ecologically stable period. As discussed by Monnet et al. (2011), such trends in ammonoid shell (which acts as

a buoyancy apparatus) could reflect that their morphology is mainly controlled by adaptive and constructional constraints.

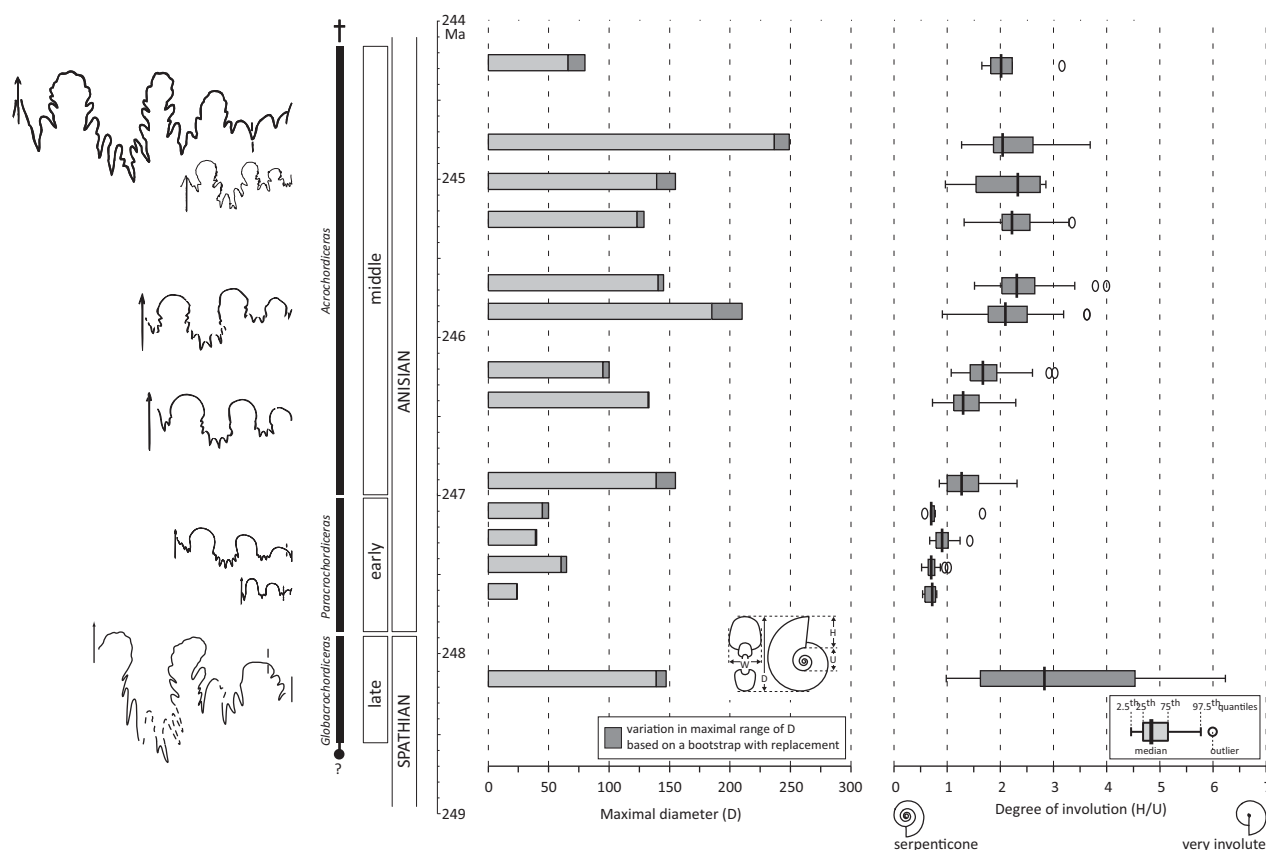
### Evolutionary jump of Acrochordiceratidae at the Early/Middle Triassic boundary

A persistent directed evolution toward larger adult shell diameter, more involute coiling and more indented suture line thus characterize the evolutionary history of Acrochordiceratidae during the Anisian (Monnet et al. 2012). The family is known to disappear at the middle/late Anisian boundary (Monnet et al. 2008), but its earlier morphological and taxonomic history in the Spathian (Early Triassic) is poorly documented. Indeed, the oldest record of Acrochordiceratidae dates back to the late Spathian with the rare occurrence of *Pseudacrochordiceras inyoense* in the *Neopopanoceras haugi* Zone of California and Nevada (Smith 1914; Silberling & Wallace 1969; Tozer 1994a; Guex et al. 2010; this study). With the discovery and herein description of the new genus *Globacrochordiceras* from Nevada and South China, the long-term morphological changes in Acrochordiceratidae can be more completely evaluated (Fig. 10).

On the one hand, the acrochordiceratids of the late Spathian (*Globacrochordiceras* and *Pseudacrochordiceras*) are large-sized (ca. 150 mm in shell diameter), high-whorled, involute to moderately evolute shells. These genera are restricted to the late Spathian and do not range across the Early/Middle Triassic boundary. On the other hand, the acrochordiceratids of the early Anisian (*Paracrochordiceras*) are small-sized (ca. 70 mm), very evolute shells. Hence, early Anisian forms stand in sharp contrast with older late Spathian morphologies. Spathian acrochordiceratids were evidently not part of the long-term morphological trends documented in the Anisian (Fig. 10).

Strikingly, late Spathian forms closely resemble those of the late middle Anisian found at the end of the previously described evolutionary trends of the family. Therefore, the evolutionary history of Acrochordiceratidae is characterized by a marked and probably rapid (see below) change of shell morphology at the Spathian/Anisian (Early/Middle Triassic) boundary (Figs 10, 11). Then, this abrupt morphological change ("evolutionary jump", *sensu* Guex 1992) of Acrochordiceratidae is followed by a protracted shift (spanning ca. 4 Myr) of the shell morphology until the end of the middle Anisian (Figs 10, 11). At the end of this latter morphological shift, the general morphology of Acrochordiceratidae is close, but not identical, to the original morphology of the group.

Due to common various possible biases of the fossil record, the documented morphological evolutionary jump may be at first regarded as spurious (see Raup & Crick 1982). However, these biases are minimized thanks to a roughly equal amount of outcrops available



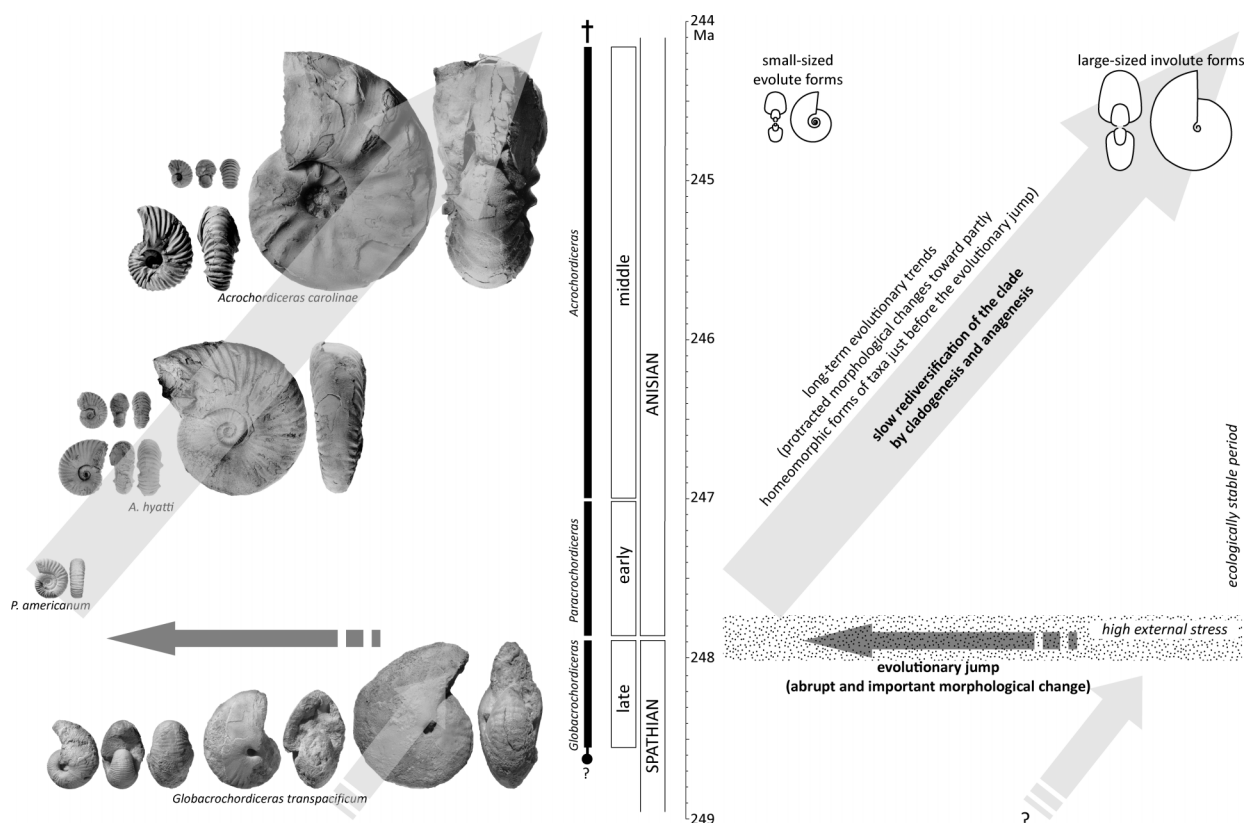
**Figure 10.** Evolution of suture shape, maximum shell diameter and degree of involution for Acrochordiceratidae during the late Spathian to the middle Anisian. Figure modified (after figs 4, 5, and 8 in Monnet et al. 2012) by adding Spathian data. See Monnet et al. (2012) for more details.

in the same basin for both the Spathian and the Anisian, a comparable sampling intensity throughout the studied interval, and similar relative abundances of preserved ammonoids. Furthermore, the possible influence of facies changes recorded at the Spathian/Anisian boundary (see below) is also reduced. Indeed, several authors discussed the possible relationships between ammonoid shell shape and facies (Jacobs et al. 1994; Olóriz et al. 1997; Kawabe 2003; Wilmsen & Mosavina 2011; further references in Monnet et al. 2011) but without a clear consensus. In the northern Humboldt Range, the depositional environment of strata of *haugi* Zone age does not significantly differ from that of the younger Anisian faunas (i.e. mixed siliclastic and carbonate outer platforms). In Guangxi, the depositional environment of strata of *haugi* Zone age also indicates an outer platform setting, but a very predominantly carbonate one. Hence, the presence of *Globacrochordiceratidae* is apparently independent from the amount of clastic input in those outer platform settings. Similarly, occurrences of *Acrochordiceratidae* range from the exclusively carbonate Hallstatt limestone in Europe to the mudstone of Guangxi. Therefore, the documented shape changes through time are not mirrored by any horizontal facies dependence, making these changes essentially of evolutionary significance and unrelated to facies variations. Furthermore, shell shapes resembling *Paracro-*

*chordiceratidae* existed in the latest Spathian (e.g. *Eodanubites*; see Guex et al. 2010) and forms converging with *Globacrochordiceratidae* persisted in the early Anisian (e.g. *Columbisculites*, *Isculites*; see Bucher 1989; Tozer 1994b). Hence, the jump in morphology does not relate to the lack of certain facies around the Spathian/Anisian boundary since other taxa with similar shell shapes are present, if one accepts the underlying assumption that some link between facies and shell morphology can be established.

This morphological evolutionary jump of Acrochordiceratidae around the Early/Middle Triassic boundary is probably much faster than the protracted evolutionary trend of the family documented during the Anisian (estimated to last ca. 4 Myr). The available radio-isotopic ages for this time interval (see Ovtcharova et al. 2006 and Galfetti et al. 2007b) enable to estimate that this morphological jump lasted ca. 0.4 Myr.

The morphological evolutionary jump of Acrochordiceratidae documented around the Early/Middle Triassic boundary represents a peculiar pattern of evolution of ammonoids. Guex (1992, 2000, 2001, 2006) illustrated and discussed several such evolutionary jumps from a qualitative point of view. This author pointed out that these evolutionary jumps are characterized by the appearance of forms, which are partly homeomorphic with remote ancestors of their own lineage and inter-



**Figure 11.** Sketch of the evolutionary history of shell morphology of Acrochordiceratidae. The lineage displays a sudden and drastic morphological change (evolutionary jump) at the Spathian/Anisian (Early/Middle Triassic) boundary probably triggered by a global regressive event and a global carbon isotope excursion. Then, the family displays a long-term morphological shift toward larger shells with more involute coiling and more indented suture line during a relatively ecologically stable period. The clade disappears at the middle/late Anisian boundary with forms close, but not identical, to the original Spathian ones. This kind of morphological evolutionary jump seems to be a frequent evolutionary pattern in ammonoids and at the origin of numerous ammonoid lineages. All figures are at the same scale.

preted these newly evolved homeomorphic taxa as being atavistic. In this context, the abrupt morphological evolutionary jump between *Globacrochordiceras* and *Paracrochordiceras* at the Spathian/Anisian (Early/Middle Triassic) boundary may correspond to a generalized morphological reset of long-term trends (called proteromorphosis by Guex 2001), which cannot be explained by normal paedomorphic transformations (see Landman 1988).

### Stress-induced evolutionary jumps in ammonoids

Guex (1992, 2001, 2006) argued that episodes of strong environmental stress are at the origin of many new ammonoid lineages by promoting the abrupt appearance of significantly different forms by means of such evolutionary jumps. Indeed, stressful environments are well known to affect the normal development of organisms and to induce morphological variation and large phenotypic changes, as well as stronger phenotypic selection favouring different morphotypes (Parsons 1993; Hoffmann & Parsons 1997; Bijlsma & Loeschcke 1997; West-Eberhard 2003, 2005; Hallgrímsson & Hall 2005; Badyaev 2005; Badyaev et al. 2005). For example,

Rutherford & Lindquist (1998) demonstrated that mutant heat shock protein Hsp90 was responsible for a great variety of inheritable “abnormal” forms of *Drosophila*. This suggests that an external stress (e.g., temperature) can uncover morphological variants for selection to act upon. Hence, in the fossil record, the abrupt appearance of morphologically distant organisms concomitant with intense environmental changes could result from such processes. Jablonski et al. (1983) argued also that many evolutionary novelties occurred in the more stressed nearshore environments. Among cephalopods, size reductions are well known to occur under stressful environments (Shimer 1908; Spath 1919; Kummel 1948; Mignot et al. 1993; Urlichs 2012), but there are exceptions. The phenomenon of miniaturization is widespread among many organisms and is frequently associated with evolutionary morphological novelties (Hanken & Wake 1993), which are not related to simple paedomorphic transformations (Landman et al. 1991). Noteworthy, in highly stressed and widely fluctuating environments a punctuated evolutionary pattern is likely to happen (Parsons 1993). The morphological evolutionary jump of Acrochordiceratidae documented around the Early/Middle Triassic boundary may therefore represent such a case of evolution. Note-



worthy, similar patterns of macroevolution have been described in other groups such as radiolarians (Guex et al. 2012) and foraminifers (Desmares et al. 2008).

For palaeontologists, the major evidence of extreme environmental changes is the occurrence of extinction periods. Noteworthy, the Early/Middle Triassic is associated with a drastic diversity (taxonomic richness) dropdown and a high turnover at the family level for ammonoids (see Brayard et al. 2009c). It coincides also with the first renewal of gymnosperm flora after the end-Permian mass extinction (Kürschner & Herengreen 2010). Furthermore, in north-west Nevada, deposition of outer platform anoxic facies of the upper Spathian Tobin Formation was interrupted abruptly at the Early/Middle Triassic boundary by deltaic deposits of the Dixie Valley Formation (see Nichols & Silberling 1977; Bucher 1989). Open platform sedimentation resumed in the lower Anisian, with deposition of the Fossil Hill Member. Similarly, in South China, the Early/Middle Triassic boundary shows a drastic change in the mode of sedimentation from carbonate-dominated to siliciclastic-dominated depositional environments (Galfetti et al. 2008). These sedimentary events coincide with a second-order sequence boundary (transgressive–regressive cycle) recognized worldwide and mark a global and major sea-level change (Haq et al. 1987; Embry 1997; Gianolla & Jacquin 1998; Egorov & Mørk 2000; Hermann et al. 2011). The Early/Middle Triassic boundary also records a worldwide and pronounced positive excursion in carbon isotopes (Atudorei & Baud 1997; Payne et al. 2004; Korte et al. 2005; Galfetti et al. 2007a, 2007b; Tanner 2010; Hermann et al. 2011). Hence, the Spathian/Anisian (Early/Middle Triassic) boundary is associated with significant global and stressful environmental changes, which affected the evolution of organism lineages. Acrochordiceratidae survived this event by generating a descendant (*Paracrochordiceras*) whose morphology stands in sharp contrast with older forms (*Globacrochordiceras*, *Pseudacrochordiceras*) (Figs 10, 11). Further study will aim at identifying such evolutionary jumps in other ammonoid lineages around the Early/Middle Triassic boundary. The exact or most important stressors that may have played a role in the morphological evolutionary jump documented for Acrochordiceratidae remain to be identified. However, this awaits additional data and analyses especially on temperature and nutrient levels around the Spathian/Anisian boundary and on the phenotypic impact and inheritance of these factors on Recent cephalopods. Indeed, temperature, nutrient availability and ocean acidification among others are well known to impact shell ontogeny and morphology of extant molluscs with accretionary growth (see Boletzky 2003; Przeslawski 2004; Boyle & Rodhouse 2005; Pecl & Jackson 2008; De Baets et al. 2012; Tamburi & Martin 2012; Melatunan et al. 2013; Dorey et al. in press; Mattoo et al. in press; and references inside), although these changes are not systematic (see Schifano 1982; Gutowska et al. 2008) and not necessarily inheritable.

## Conclusions

This study describes a new genus of Acrochordiceratidae (Ammonoidea, Cephalopoda), namely *Globacrochordiceras*, which records the oldest known member of the family. *Globacrochordiceras* is characterized by plicate ribbing (rounded ribs which strengthen when crossing the venter without interruption), increasing involution through ontogeny, overhanging and deep umbilical wall, absence of tuberculation, globular to subtriangular whorl section, and subammonitic adult suture line. This new taxon occurs in the *Neopopanoceras haugi* Zone (late Spathian, Early Triassic) of Nevada (USA) and Guangxi (South China).

This new genus highlights a peculiar pattern of ammonoid macroevolution, which is the evolutionary reaction of ammonoid lineages when exposed to heavy environmental stresses. On the one hand, the evolutionary history of the family consisted of long-term morphological trends (increases of adult size, degree of involution and indentation of the suture line) during the early and middle Anisian. On the other hand, the morphology of the Spathian *Globacrochordiceras* and *Pseudacrochordiceras* stands in sharp contrasts with the Anisian *Paracrochordiceras* and thus illustrates a case of an evolutionary jump of Acrochordiceratidae at the Early/Middle Triassic boundary. This drastic morphological change coincided with stressful environments as reflected by a global second-order regression accompanied by a global carbon isotope excursion.

## Acknowledgements

We greatly appreciated the help of Thomas Galfetti for fieldwork and ammonoid sampling. Rosemarie Roth and Markus Hebeisen provided technical support for photography and preparation. We acknowledge stimulating discussions with Jean Guex about this topic over the past years. We thank the two reviewers, Kenneth De Baets and Kevin Bylund, for their constructive comments and suggestions. The Swiss National Foundation supported this study (project n°135446). AB is also supported by the Région Bourgogne and the CNRS INSU Intervie.

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