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AMMONOIDS FROM THE ZHUGANPO MEMBER OF THE FALANG FORMATION AT NIMAIGU AND THEIR RELEVANCE FOR DATING THE XINGYI FOSSIL-LAGERSTÄTTE (LATE LADINIAN, GUIZHOU, CHINA)

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Abstract. We herein document the various ammonoid faunas, of which 8 are newly described taxa, recently collected from the Falang Formation at Nimaigu (Wusha) near Xingyi (Guizhou, South China) and also define their biostratigraphy, correlation and age. The sampled interval includes the Zhuganpo Member, which contains the world famous Xingyi Fossil-Lagerstätte, and the lowermost part of the overlying Wayao Member. Ammonoids are quite abundant, but preservation is usually very poor. New genera *Yangites*, *Haoceras* and *Sinomeginoceras* are described on the basis of four new species. The new subfamily Haoceratinae (family Trachyceratidae) is erected to accommodate *Haoceras* and *Sinomeginoceras*. *Xenoprotrachyceras*, *Detoniceras*, *Ptychites*, *Trachyceras* and *Clionitites* are also recognized, together with a specimen attributed with doubt to *Parasturia*.

Most of the faunas are endemic and typical representatives of Upper Ladinian ammonoid zones have not been recognized. A new local biostratigraphic scale is proposed, consisting of the *Haoceras xingyiense* zone, *Trachyceras* beds and *Trachyceras multituberculatum* zone, in stratigraphic order.

The *Trachyceras* beds and the *Trachyceras multituberculatum* zone are attributed to the Lower Carnian, but most of the bio-chronostratigraphic analysis is focused on the *Haoceras xingyiense* zone, because it directly overlies the vertebrate-bearing interval. Correlation of the new biozone is discussed and its stratigraphic position is referred, at least in part, to the lower Sutherlandi Zone of the North American scale. This correlation pinpoints the age of the Xingyi Fossil-Lagerstätte as middle Late Ladinian, which until now had been a matter of debate for 30+ years.

Introduction

The Xingyi Fossil-Lagerstätte in Guizhou (South China), which yielded the first marine reptile *Keichousaurus hui* described from China (Young 1958), has for the last decade yielded abundant Triassic marine reptiles (Li et al. 2002; Li & Rieppel 2004; Cheng et al. 2006; Rieppel et al. 2006, 2008; Li 2007; Zhao et al. 2009; Jiang et al. 2011; Cheng et al. 2012; Ji et al. 2012) and fishes (Su 1959; Liu et al. 2003; Jin 2006; Tintori et al. 2012, 2013a, 2013b). This Fossil-Lagerstätte continues to provide a rich record of ichthyosaurs, sauropterygians, thalattosaurs, *Tanystropheus*, *Macrocnemus* and other marine reptiles and fishes, which complements the rich Triassic marine vertebrate record of the Luoping, Panxian and Guanling Fossil-Lagerstätten, all distributed over a distance of about 200 km from eastern Yunnan to Guizhou.

The Xingyi Fossil-Lagerstätte is preserved within the Zhuganpo Member of the Falang Formation, whose widely occurring outcrops range from the Dingxiao District to the Wusha District (Xingyi City, Guizhou Province) and extend westward to Fuyuan and Luoping counties (Yunnan Province).

The Nimaigu locality (Wusha District) was selected in 2009 for extensive excavation to recover vertebrates, utilizing a scientifically based bed-by-bed collecting technique. Most of the excavation was carried out between 2010 and 2013, and many new taxa were found in addition to species already known from the area. New discoveries from this excavation include the shastasaurid ichthyosaur *Guizhouichthyosaurus* (Ji et al. 2012) and a new species of *Qianichthyosaurus* (Yang et al. 2013), both of which were previously known only

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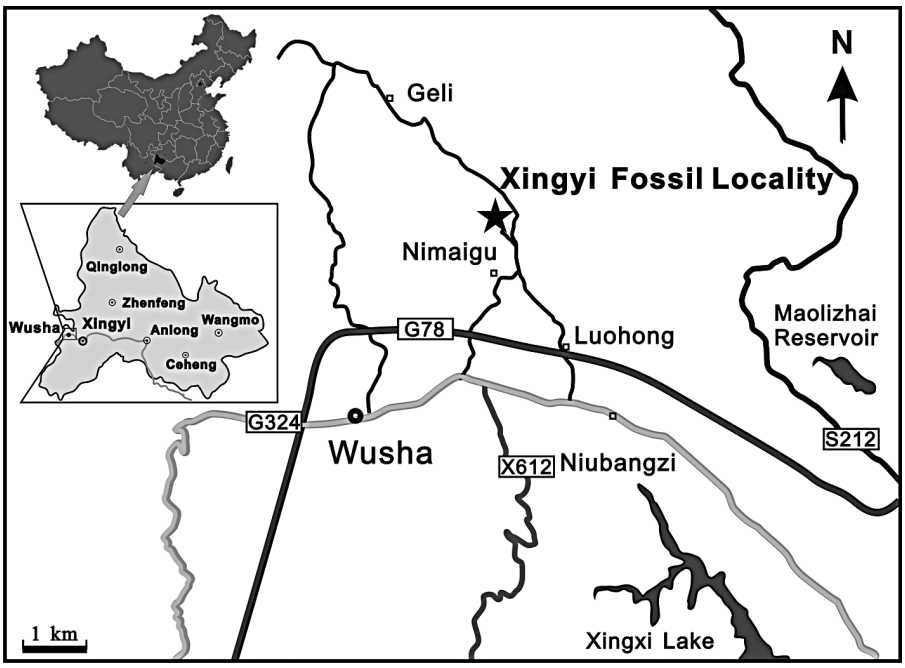


Fig. 1 - Location map of the fossil locality at Nimaigu village, Wusha town, Xinyi City, Qianxinan Buyei and Miao Autonomous Prefecture, Guizhou Province.

from the Late Triassic Guanling Fossil-Lagerstätte, and a new species of pistosauroid sauropterygian, as well as several new species of fishes (Lin et al. 2011; Tintori et al. 2012, 2013a, 2013b).

In the past, invertebrate fossils have been frequently reported from the Falang Formation in the Xingyi area, but up until the recent excavation paleontologists were mostly attracted by the extraordinary abundance of vertebrates collected from several localities. Consequently, the age of the Xingyi Fossil-Lagerstätte has never been precisely defined, and the literature is rather confusing. Young (1958), in his description of *Keichousaurus hui*, suggested a Late Ladinian age for the vertebrate-bearing level, and this age was later supported by Li (2006). In contrast Wang (1983) suggested an Early Ladinian age for the Zhuganpo Member of the Falang Formation, based on the occurrence of the ammonoid *Xenoprotrachyceras primum*, a species interpreted as being closely related to *Ceratites reitzi* Boeckh, 1872 from the Western Tethys, which at that time was considered to be of Early Ladinian age (now regarded as Late Anisian, e.g., Brack et al. 2005). A much younger Carnian age (Late Triassic) was instead proposed by Wang et al. (1998) who identified the conodont *Paragondolella polygnathiformis* from a sample collected 3.0 m above the *Keichosaurus* bearing bed, but Wang et al. (2001), in a later general overview of the vertebrate localities of Guizhou, again assigned a Ladinian age to the Xingyi vertebrate fauna.

In order to accurately determine the age of the Xingyi Fossil-Lagestätte and to better understand its faunal diversity, the recent excavation at Nimaigu also included sampling for ammonoids of the whole sequence from the Zhuganpo Member to the overlying basal part of the Wayao Member of the Falang Formation (Fig. 2 and 3). Ammonoid occurrences were found to be relatively common, but their preservation often is not very good. A total of 338 specimens were collected and in this work we describe the better preserved portion of this collection.

Geographic and stratigraphic setting

The Nimaigu section (Wusha district; Fig. 1) is close to Xingyi City in southwest Guizhou Province, about 320 km SW of Guiyang City, the capital of Guizhou. Coordinates for the site are 25°09'52"N and 104°47'19"E and its elevation is about 1491 m.

The Xingyi area is located on the southwestern Yangtze carbonate platform, according to the Bureau of geology and mineral resources of Guizhou province (1987). Triassic rocks are widespread in this area and the thickness of the entire sequence exceeds 5600 m. The sedimentary succession exposed at the Nimaigu section consists of part of the Middle Triassic Yangliujing Formation, overlain by the Zhuganpo and Wayao Members of the Falang Formation.

The upper part of Yangliujing Formation consists of thick-bedded dolomite, while the Falang Formation consists mainly of gray, dark gray, medium-bedded and thin micritic limestones, nodular micritic limestones, argillaceous limestones, sandy limestones and marls.

Zhuganpo Member. This member is characterized lithologically by dark-gray to gray, medium-bedded micritic limestones, nodular micritic limestones and argillaceous layers. The marine vertebrate fauna documented

Fig. 2 - View of the fossil locality, taken in 2013. A) General view of the quarry showing the complete exposure of the studied succession, B) view of the lower and middle part of the section. Numbers refers to key beds. Vbb: vertebrate-bearing beds. See Fig. 3 for log.

in the literature as the Xingyi Fauna is preserved in this member and consists of reptiles and fishes.

Wayao Member. This unit consists of dark gray calcareous clay rocks interbedded with thin to medium thick nodular micritic limestones, marls, bioclastic limestones and sandy limestones. In the Guanling area this member yields the well-known Carnian (Late Triassic) Guanling Biota, consisting of marine reptiles (Li 1999, 2000; Li & Rieppel 2002; Li et al. 2008; Liu 1999; Cheng et al. 2007; Yin et al. 2000; Jiang et al. 2004, 2005) and invertebrates including spectacular crinoids attached to floating wood (Jiang et al. 2005; Wang et al. 2008).

The Nimaigu section near Wusha

Section (Fig. 2 and 3) is about 48 m thick and is well exposed in the recently excavated quarry. Its lithologic description is as follows (from top to bottom; see Fig. 3):

Wayao Member of the Falang Formation

8) Dark gray, medium to thin-bedded marls, intercalated with shales; 5.6 m, but the succession continues upward;

– conformity

Zhuganpo Member of Falang Formation

7) Dark gray, thick bedded limestone, top of beds laminated. Bed numbers 227-238, 3.8 m.

6) Gray, medium bedded flint zebra limestone intercalated with thick bedded limestone. Bed numbers 194-226, 8.8 m.

5) Gray, thick-medium bedded limestone, interbedded with medium bedded argillaceous banded limestone. Bed numbers 170-193, 6.6 m.

4) Dark gray, medium bedded flint zebra lime-

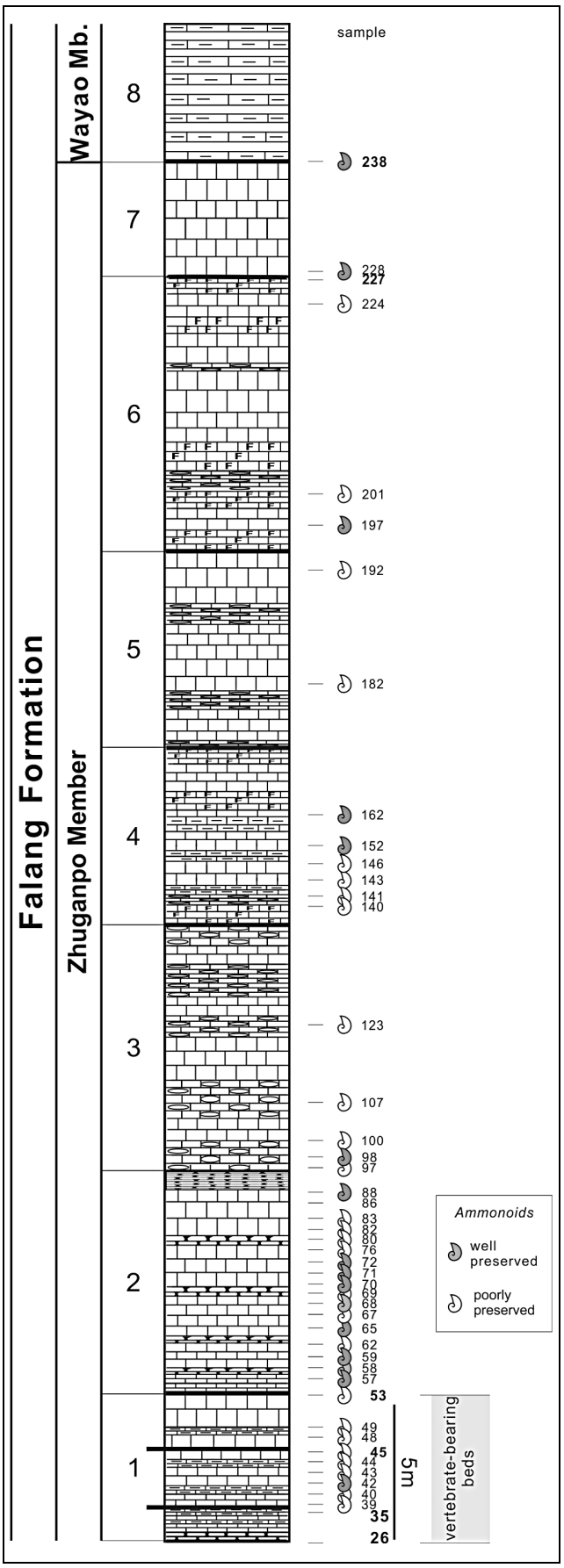


Fig. 3 - Lithostratigraphy of the studied section showing position of the vertebrate-bearing interval and the ammonoid samples.

stone intercalated with argillaceous banded limestone. Bed numbers 139-169, 6.5 m.

3) Dark gray, medium-thin bedded argillaceous banded limestone intercalated with gray medium- thick limestone. Bed numbers 97-138, 9.7 m.

2) Gray, medium-thin bedded limestone, intercalated with medium-thin bedded nodular limestone. Bed numbers 54-96, 7.7 m.

1) Vertebrate-bearing interval. Medium-thin bedded argillaceous banded limestone, marl and nodular limestone intercalated with medium-thick limestone. Bed numbers 26-53, 5.4 m. Interval is subdivided into:

1-3) Gray, medium-thick bedded limestone intercalated with dark gray medium-thin bedded marl. Bed numbers 45-53, 1.8 m.

1-2) Medium bedded limestone intercalated with marl. Bed numbers 35-44, 2.5 m.

1-1) Dark gray, thin bedded limestone intercalated with argillaceous banded limestone; the base of this layer is marked by a thin bedded nodular limestone. Bed numbers 26-34, 1.1 m.

– Cover, bottom of excavation

Taxonomic results

Most of the 338 specimens collected are completely flattened or small in size. Although they do document the common occurrence of ammonoids in the Xingyi intraplatform basin, they are of no practical value in terms of taxonomic analysis. Only 55 specimens are sufficiently well preserved for taxonomic study. However, only a portion of this group consists of complete specimens showing the suture line. These specimens are suitable for detailed taxonomic analysis, which resulted in their classification to the species level. Other specimens are incomplete, consisting of half whorls or even quarter whorls, sometimes partially included in the rock matrix. When preservation or completeness permits, these specimens are classified to the genus level, but a more accurate assignment is most often not possible. Bio- and chronostratigraphy is obviously influenced by taxonomy, and taxa in open nomenclature or with uncertain generic attribution are considered to be of secondary importance in defining biostratigraphic units.

Most specimens were collected from intervals 1 and 2 of the section. Several specimens from these intervals exhibit a combination of ventral shape, spiral ornamentation and suture line that is very unusual with respect to known Ladinian ammonoids in China and elsewhere in the world. In order to accommodate these specimens, four new species, three new genera and one new subfamily are here described (see Systematic paleontology).

Systematic paleontology (MB and XZ)

Family-group taxonomy follows that of Tozer, 1994, which updates that published in 1981 (Tozer 1981a).

Comparison with reference collections. The classification of the collection from Nimaigu has been facilitated by the familiarity of one of the authors (MB) with type collections housed in Padova University (Italy), Institute fur Palaeontologie of the Vienna University and Geologische Bundesanstalt (Austria), Geological Survey of Canada in Vancouver and Ottawa and Smithsonian (Washington, USA). The type collection from South China, housed at the Nanjing Institute for Geology and Paleontology, Academia Sinica, has been examined jointly by MB and XZ.

Repository of specimens. Specimens described in this paper are housed in the Geological Museum of the Peking University, Paleontological collection, Yiheyuan Str. 5, Haidian District, Beijing 100871, P.R. China.

Acronyms. GMPKU: Geological Museum of the Peking University. NIGPAS: Nanjing Institute for Geology and Paleontology, Academia Sinica.

Numbering of specimens. Each specimen mentioned in the text is identified by both registration number (e.g., GMPKU-P-....) and collection number. The latter, in parenthesis, indicates locality, year of collection, bed number and the individual number of the specimen (e.g., ws2012-42-1: 1st specimen from bed 42, collected in 2012 at Wusha (the district that includes Nimaigu). Specimens from NIGPAS are identified only by their museum numbers.

Dimensions. D= diameter; H= max. whorl height in D; h= min. whorl height in D; U= umbilical width in D; W= whorl width in H; SGR= (H-h)/h x 100. All measurements are in mm. SGR is in percent. Measurements in italics represent partly damaged specimens. The position of nodes and of subdivision of ribs on the flank relative to the umbilical margin, is expressed as in term % of whorl height (H).

Occurrence. The stratigraphic record of the taxa is referred to the new local zonation described in the chapters following the Systematic paleontology.

Superfamily Ceratitoidea Mojsisovics, 1879

Family Ceratitidae Mojsisovics, 1879

Subfamily Nevaditinae Tozer, 1994

Genus *Xenoprotrachyceras* Wang, 1983

Type species: *Xenoprotrachyceras primum* Wang, 1983

Xenoprotrachyceras cf. **primum** Wang, 1983

Pl. 1, fig. 1a-b

Material: Only one specimen GMPKU-P-3071 (ws2012-59-11).

Description. The relatively large-sized specimen is preserved only as a half whorl that is partially included in matrix. The venter and one nearly complete flank are exposed and matrix covers a small portion part of the periumbilical border that is not visible in Pl. 1, fig. 1a.

Coiling is almost evolute and the whorl section tends to be rather thick.

Ornamentation consists of ribs and two rows of nodes. Ribs are straight to slightly convex on the flank (Pl. 1, fig. 1a) from the inner part of the flank to 75% of H, at the position of the first row of nodes, from which they suddenly project forward until they end at the ventral node. Most ribs are primary, but two intercalatory ribs are visible at the beginning of the preserved part of the whorl.

Nodes are arranged in two rows, one at about 75% of H and the other in ventral position (Pl. 1, fig. 1b). Ventral nodes are oblique. Center of venter is depressed, but not deeper than spaces between ventral nodes. In the middle of the flank some ribs tend to exhibit a very weak, radially elongated thicknening.

Suture line is not visible.

Discussion. Attribution of specimen GMPKU-P-3071 (ws2012-59-11) to the monotypic genus *Xenoprotrachyceras* Wang, 1983 is based not only on its large size, almost evolute coiling and thick whorl section, but more importantly on its style of ribbing, number of rows of nodes and their position. These features have been directly checked by comparison with the type specimens housed in NIGPAS. Ribbing, which is well visible on the original figures by Wang (1983, pl. 1, fig. 12), is slightly convex, at least from the umbilical border to the first row of nodes. This feature is unknown in the Trachyceratidae and Paraceratitinae. The types also show a gentle radial thickening of the ribs at the middle of the flank, a single row of nodes at the forward-projecting point of the ribs and a second row of nodes adjacent to the ventral furrow.

The whorl section of the holotype of *X. primum* is quite thick (see also Wang 1983, pl. 1, fig. 11) with parallel flanks and rather distinct shoulders. However, since the Namaigu specimen consists only of a whorl fragment with one flank and the venter preserved, it is not possible to make a full comparision with the type specimen, but its whorl section does not appear to be subtrapezoidal. As regard the suture line, this feature is not visible on the specimen from Nimaigu, then no comparison is possible with the subammonitic suture of the holotype of *X. primum* (Wang 1983, fig. 1d).

Attribution to *X. primum* by confronta is justified even though the available specimen is only a whorl fragment and some slight differences are present with respect to the type specimens of *X. primum*. The first row of nodes of the holotype of *X. primum* (NIGPAS 155596) is located almost exactly on the shoulder, while this row appears to be slightly offset from the shoulder in the specimen from Nimaigu. Rib spacing is slightly denser on the Nimaigu specimen, which shows 15 ribs in about 130°, while the same number of ribs is distributed over nearly half a whorl on the holotype.

Specimen GMPKU-P-3071 differs from specimens attributed to *Detoniceras* sp. A by its almost evolute coiling, thicker whorl section and number of rows of nodes. *Detoniceras* sp. A, is more involute, its whorl section is subtrapezoidal with a narrow venter and it has 4 to five rows of nodes. Aside from these differences, *X.*

cf. *primum* and *Detoniceras* sp. A do possess some similar ornamentation features. The sudden change of course of the ribs on the outer part of the flank occurs in both taxa, but the ribs are convex in *X.* cf. *primum* and sinuous in *Detoniceras* sp. A. The very weak radial thickening of the ribs that occurs in *X.* cf. *primum* is similar to the well developed inflation of the ribs of *Detoniceras* sp. A.

Occurrence. The monotypic genus *Xenoprotrachyceras* is known only from Guizhou, where it was collected from the Zhuganpo Member of the Falang Formation (Wang 1983). *X. primum* was selected by Wang as the index fossil for a zone he considered to be Lower Ladinian. The specimen here attributed to *X.* cf. *primum* was collected from the lower part of the *Haoceras xingyiense* zone (Upper Ladinian) of Xingyi.

Genus *Detoniceras* Manfrin & Mietto, 1991

Type species: *Detoniceras rex* Manfrin & Mietto, 1991

Detoniceras sp. **A**

Pl. 1, fig. 2a-b, 3a-c

Material: Two specimens: GMPKU-P-3077 (ws2012-72-2) and GMPKU-P-3079 (ws2012-88-3).

Description. The two specimens consist only of internal molds of body chamber whorl fragments (~1/4 whorl). They are preserved in three dimensions, with undeformed whorl section and ventral side.

Coiling is involute with a compressed subtrapezoidal whorl section whose maximum width is located at about 1/3 of whorl height. The venter is flat and quite narrow (Pl. 1, fig. 2a and 3b) and its width is slightly less than 30% of maximum whorl width.

Ornamentation consists of ribs and spiral rows of nodes. Ribs on specimen GMPKU-P-3079 are more sinuous and more forward projected on the outer part of the flank than those of specimen GMPKU-P-3077. Ribs commonly branch quite low on the flank, between the umbilical node and 20% of H. Most ribs are primary, while intercalatory ribs are rare. The latter start at about 20% of H.

Specimen GMPKU-P-3079 exhibits five rows of nodes. The first is located on the umbilical margin, the second consists of a radially elongated thickning of ribs at about 50% of H, the third consists of relatively strong, rounded nodes at about 80% of H, at the position where the ribs project forward, the fourth consists of very weak nodes located in the middle of the narrow space between the third row and the ventral shoulder, and the fifth, located in a ventrolateral position, consists of weak slightly radially elongated nodes. Specimen GMPKU-P-3077 has nodes very similar to those of the previous specimen, except it lacks the fourth row.

Discussion. The available specimens are attributed to *Detoniceras* Manfrin & Mietto, 1991 based on their compressed whorl section, flat venter not crossed by ribs and ornamentation consisting of ribs and several rows of nodes (4 in the type species *Detoniceras rex* Manfrin & Mietto, 1991). Given that this combination of features is very rare in Ladinian ammonoid lineages, the specimens can be attributed to *Detoniceras* with reasonable confidence even though their suture line is not known. The morphological flat venter feature is typical of the latest Anisian *Nevadites* Smith, 1914, and of the Early Carnian *Boreotrachyceras* Konstantinov, 2012. However, assignment to these genera is not considered because, apart from their different age, *Nevadites* is generally much more evolute with a rather thick whorl section and a gently rounded umbilical border, while *Boreotrachyceras* includes in its variability a weakly furrowed venter (Konstantinov 2012: pl. fig. 3, fig. 2c, 3c). *Boreotrachyceras* also exhibits 6 to 9 rows of nodes on adult specimens (Konstantinov 2012) and, even more important, is a member of the Boreal province, which from the Anisian to the Carnian, was never connected to the Tethys Realm (see Tozer 1981b; Dagys 1988).

Xenoprotrachyceras Wang, 1983, may also be compared with the specimens from Nimaigu. However, this genus is characterized by slightly evolute coiling and a thick whorl section with a distinctive ventro-lateral shoulder. In this regard, *Xenoprotrachyceras* is very similar to the late Ansian *Reitziites* Brack & Rieber, 1993. The venter of *Xenoprotrachyceras*, despite the rather poor preservation of the holotype, appears to be furrowed and not flattened.

At the species level, the two specimens from Nimaigu are left in open nomenclature because their incomplete fragmentary nature limits comparison with other species of *Detoniceras*. Species from the Western Tethys usually have a distinct lateral node, often spiny (e.g. *Detoniceras rex* Manfrin & Mietto, 1991, *D. svilajanus* Balini, Jurkovšek and Kolar-Jurkovšek, 2006 and possibly *D. tetranodosum* [De Toni, 1914])

Occurrence. Specimens here described were collected from beds 72 and 88 of the Xingyi section, which are included in the new *Haoceras xingyiense* zone, Upper Ladinian.

In the Tethys realm, *Detoniceras s.s.*, namely with flat venter such as in the type species, is known from the Southern Alps and the Dinarids. *Detoniceras rex* Manfrin & Mietto, 1991 has been found in the Val Vela Limestones from a level that yields a conodont assemblage referred by Manfrin & Mietto (1991) to the Archelaus Zone. *Detoniceras tetranodosum* (De Toni, 1914) was collected from a fissure filling within a car-

bonate platform with ammonoids of the Gredleri and Archelaus zones (Manfrin & Mietto 1991). *Detoniceras* sp. ind. from the Cunardo Formation of western Southern Alps was referred to the Archelaus Zone (Calabrese & Balini 1995). In the Dinarids, *Detoniceras svilajanus* Balini, Jurkovšek & Kolar- Jurkovšek, 2006 was found in levels yielding conodonts of the Hungaricus assemblage zone. Taken together, these occurrences are consistent with a Late Ladinian age for *Detoniceras s.s.*

Genus *Yangites* n. gen.

Type species: *Yangites densicostatus* n. gen n. sp.

Derivatio nominis: The genus is dedicated to prof. Yang Shouren, who has worked on Triassic biostratigraphy in south China since 1980. He provided us with some most useful stratigraphic scales based on ammonoids, bivalves and conodonts.

Diagnosis: Large sized ammonoids with very involute coiling of the inner whorls, with outer whorl becoming slightly less involute due to significant egression that starts much before the beginning of the mature body chamber. Compressed whorl section with flat to very slightly depressed venter, not crossed by ribs. Ornamentation consists of dense ribs and two to four rows of nodes. Ribs are wavy in cross section. Two rows of nodes in ventral and ventrolateral position are always present, to which very weak umbilical and/or lateral nodes are sometimes added. Suture line with three saddles on the lateral side. The tops of the saddles are rounded, but their sides are more or less indented, depending on the species.

Composition of the genus: *Yangites densicostatus* n. gen. n. sp. (type) and ?*Bulogites langdaiensis* Wang, 1983.

Remarks on the selection of the type species. The holotype of ?*Bulogites langdaiensis* Wang, 1983, which is much more complete than the type series of *Yangites densicostatus* n. gen. n. sp., is crucial for understanding the nature of coiling of the inner whorls of the new genus *Yangites*. However, the new genus is described with *Y. densicostatus* as the type species because Wang's species lacks precise stratigraphic position within a measured section. For a morphological comparison of the two species, see the discussion regarding *Y. densicostatus* n. sp.

Comparison to other genera. *Yangites* n. gen. is similar to *Detoniceras* Manfrin & Mietto, 1991 in that they both have a flat venter, but it is distinguished by its weaker nodes, stronger ribbing and more indented suture line. The nodes of *Detoniceras*, especially those on the flank, are often spiny (cf. *D. rex* Manfrin & Mietto, 1991 and *D. svilajanus* Balini, Jurkovšek & Kolar-Jurkovšek, 2006), while the ribs are usually rather weak. In contrast, the ribbing of *Yangites* is quite well sculptured and in cross section is very wavy. With regard to the wavy nature of its ribbing, *Yangites* is very similar to the Middle Anisian *Bulogites* Arthaber, 1912 and Wang's (1983) original assignment of *Yangites langdaiensis* to *Bulogites* with question mark, is fully understandable. Aside from their very different stratigraphic position, *Bulogites* differs from *Yangites* by its wider, convex venter and in the position of its nodes. In addition to the rows of nodes in the umbilical position and ventrolateral position (shoulder) that are always present, *Bulogites* usually exhibits one or very rarely two rows in a lateral position, with the 2nd row at about 60% of H (cf. the type species *Bulogites multinodosus* [Hauer, 1892]). *Yangites* n. gen. is characterized by ventrolateral and ventral nodes, of which the latter never occur in *Bulogites*.

Taxonomic position at family and subfamily rank. Ornamentation consisting of ribs and several rows of nodes is quite common in Ladinian and Carnian ammonoids. This combination of features is typical of members of the subfamily Nevaditinae Tozer, 1994 (Late Anisian to Ladinian) of the family Ceratitidae Mojsisovics, 1879, and of genera of the subfamilies Arpaditinae Hyatt, 1900 (Ladinian), Protrachyceratinae Tozer, 1971 (Ladinian) and Trachyceratinae Haug, 1894 (Ladinian to Carnian) of the family Trachyceratidae Haug, 1894.

The new genus *Yangites* is easily distinguished from genera of the subfamily Arpaditinae by its lack of ventral keel bordering its flat to slightly depressed venter. Ornamentation on several genera of the subfamily Protrachyceratinae includes several rows of nodes, but the venter of representatives of this subfamily is always rather deeply furrowed. Ornamentation consisting of several rows of nodes can also be found in the subfamilies Nevaditinae and Trachyceratinae, but the two groups differ quite notably in the nature and shape of the venter. *Yangites* n. gen. is here attributed to Nevaditinae because of its flat to slightly depressed venter at the mature stage. Representatives of Trachyceratinae during ontogeny may exhibit a significant variation in the shape of the venter and in the occurrence of nodes (e.g., *Muensterites* Mojsisovics, 1893, *Maclearnoceras* Tozer, 1963 and *Zestoceras* Tozer, 1994: see Tozer 1994); however, a flat to depressed venter has never been reported from any growth stage in the members of this subfamily. Members of Trachyceratinae usually have a furrowed venter, even though the furrow may change in depth or even disappear during ontogeny. This is typical for *Maclearnoceras* Tozer, 1963, whose inner whorl furrow eventually disappears during ontogeny, leaving a convex venter that is crossed by undisturbed ribs.

Occurrence and age. The new genus *Yangites* is known only from Guizhou (South China). Wang assigned the species *Y. langdaiensis* (Wang 1983) to the *Xenoprotrachyceras primum* zone, which he considered to be Lower Ladinian because of the morphological affinities of the index species *X. primum* with the species *Reitziites reitzi*. Re-examination of Wang's data (see Regional biostratigraphic framework chapter) leads

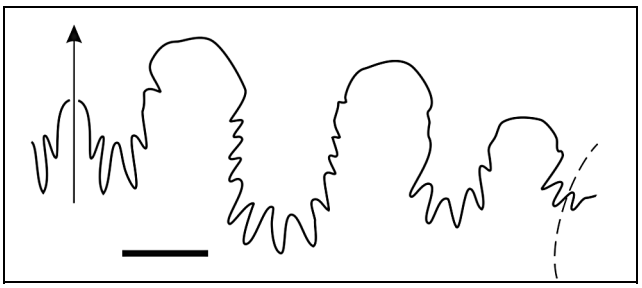


Fig. 4 - Suture line of *Yangites densicostatus* n. gen. n. sp., holotype, GMPKU-P-3085 (ws2012-152-1). Bar scale is 5 mm.

to the conclusion that his biostratigraphy is not based on documented stratigraphic sections and also, the taxa of the zone lack independent calibration. Moreover *X. primum* and *R. reitzi* are homeomorphic species and they most likely are not coeval. The species *Y. densicostatus* is known only from the Nimaigu section, where it ranges from the *Haoceras xingyiense* zone up to a position about midway to the overlying *Trachyceras* beds. This positioning leads to a Late Ladinian age assignment.

Yangites densicostatus n. gen. n. sp.

Pl. 1, fig. 4a-b, 5, 6a-b; Fig. 4

Derivatio nominis: the name emphasizes the dense ribbing.

Stratum typicum and locus typicus: Bed 152, Zhuganpo Member, Falang Formation, Nimaigu section (Xingyi, Guizhou).

Type series: The new species is described on the basis of the holotype GMPKU-P-3085 (ws2012-152-1) (Pl. 1, fig. 4; Fig. 4), and two paratypes: GMPKU-P-3070 (ws2012-59-10) and GMPKU-P-3072 (ws2012-65-2).

Diagnosis: Very compressed *Yangites*, with two to four rows of nodes and deeply indented but ceratitic, suture line.

Description. All type specimens are preserved as internal molds and each consists only of a little more than one quarter whorl. Holotype GMPKU-P-3085 (ws2012-152-1) and paratype GMPKU-P-3072 (ws2012-65-2) are also slightly compacted. The holotype and paratype GMPKU-P-3070 are phragmocone fragments and paratype GMPKU-P-3072 is body chamber fragment.

Coiling appears to be slightly evolute, at least at the mature stage of growth, as inferred by the size of the available specimens. Their diameter is estimated to be between 80 mm (paratype GMPKU-P-3070) and 85 mm for the other two types. For GMPKU-P-3070, the umbilical diameter (U) is about 32 mm in and H is about 26 mm.

The whorl section is compressed and appears to be subrectangular, with the two flanks converging only very slightly to the venter. Venter is bordered on both sides by ventral nodes and it is not crossed by ribs. The shape of the venter of the holotype varies from slightly concave to almost flat, while it is distinctly depressed in paratype GMPKU-P-3072.

Ornamentation consists of dense ribs, wavy in cross section, and rows of nodes, variable in number. Ribs are slightly sinuous, sometimes nearly biconcave as seen on the holotype. Primary ribs are more frequent than intercalatory and bifurcated ribs. Intercalatory ribs begin at about 1/3 of H, whereas bifurcate ribs appear to arise slightly closer to the umbilical margin.

All ribs bear one node in the ventrolateral position and one where the rib ends in the ventral position. In addition to these rows, the holotype exhibits two additional rows of weak nodes in the umbilical and lateral position. Those nodes in the lateral position are located at about 65% of H and are sliglthy radially elongated. The holotype bears 13 ventral nodes in a quarter whorl, while paratype GMPKU-P-3072 bears 15 in a comparable position. For paratype GMPKU-P-3070, it is possible to count only the ventrolateral nodes (13).

The suture line (Fig. 4) consists of three lateral saddles. Denticles are very deep in the bottom of the lobes. The sides of the lobes are indented about 2/3 of the way to the tops of the saddles by gradually smaller denticles. The tops of the saddles are rounded.

Discussion. The lack of umbilical and lateral nodes on the two paratypes is here considered to simply represent a wide intraspecific variability. These two types of nodes are actually very weak on the holotype.

Yangites densicostatus n. gen. n. sp. differs from *Yangites langadiensis* (Wang, 1983) by its more compressed whorl section and slightly more indented suture line. These differences have been verified by examination of the type specimens of *Y. langdaiensis* (Wang) housed in the Museum of the Paleontological Institute of the Academia Sinica in Nanjing. The type series of *Y. langdaiensis* consists of the holotype NIGPAS 15059 and two paratypes. Paratype NIGPAS 15060 is actually too small to be considered a valid representative of this taxon, and specimen NIGPAS 15061, a fragment similar in size to the holotype, exhibits a much thicker whorl section than the holotype, which documents a rather wide variation in this character of Wang's species.

Occurrence and age. *Yangites densicostatus* n. gen. n. sp., which is a rather long ranging species, is documented in beds 59, 65 and 152 of the Nimaigu section, from the lower part of the *Haoceras xingyiense* zone to a position about midway to the overlying *Trachyceras* beds. This positioning leads to a late Late Ladinian age assignment.

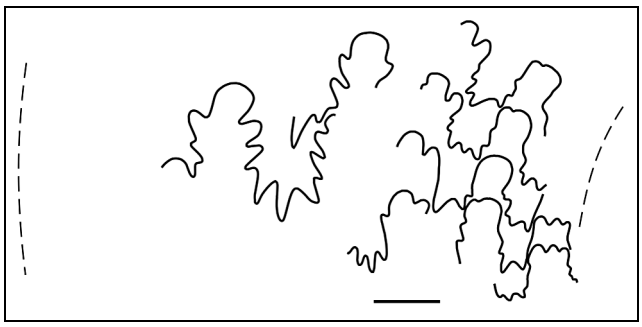


Fig. 5 - Suture line of ?*Parasturia* sp., GMPKU-P-3060 (ws2012-42-1). Bar scale is 5 mm.

Superfamily Ptychitoidea Mojsisovics, 1882

Family Sturiidae Kiparisova, 1958

Genus *Parasturia* Spath, 1951

Type species: *Meekoceras emmerichi* Mojsisovics, 1882

?Parasturia sp.

Fig. 5

Material: One specimen: GMPKU-P-3060 (ws2012-42-1).

Description. One very involute poorly preserved specimen, probably smooth, from bed 42 of the studied section is tentatively referred to *Parasturia* Spath, 1951. The ammonitic suture line (Fig. 5) consists of five saddles on the flank.

Remarks. Preservation of this specimen is very poor and it is partly included in rock matrix from which it cannot be separated. Although many Middle Triassic ammonoids are characterized by involute coiling and a nearly smooth surface, the available specimen is the lowermost sample of the collection and was collected within the vertebrate-bearing interval. Thus, even a tentative identification is justified.

The suture line (Fig. 5) with its simple denticles and barely indented third, fourth and fifth saddles essentially excludes any relationship with Arcestidae, Joannitidae and Ptychitidae as well as *Sturia* Mojsisovics, 1882 and *Psilosturia* Diener, 1916. It bears some resemblance to that of *Beyrichites* Waagen, 1895 (family Ceratitidae) and also to *Parasturia* Spath, 1951. We tentatively assign it to *Parasturia* because this genus is known from the Ladinian (Arkell et al. 1957; Tozer 1981a; Manfrin et al. 2005), while *Beyrichites* is Anisian in age (Arkell et al. 1957; Tozer 1981a; Krystyn et al. 2004). Incomplete preservation of the suture prevents a definite generic assignment.

Occurrence. Specimen was collected from bed 42, which lies in the middle part of the vertebrate bearing interval, about 3.5 m below the lower boundary of the *Haoceras xingyiense* zone.

Family Ptychitidae Mojsisovics, 1882

Genus *Ptychites* Mojsisovics, 1875

Type species: *Ammonites rugifer* Oppel, 1865

Ptychites sp. **A**

Pl. 1, fig. 7a-c; Fig. 6

Material: One specimen only: GMPKU-P-3086 (ws2012-152-3).

Description. The specimen is small and is preserved as an internal mold of a half whorl of phragmocone. Its coiling is involute and its whorl section is depressed such that the general shape of the shell resembles a cadicone. The surface is smooth and lacks constrictions. The suture line (Fig. 6) is ammonitic with deeply indented saddles, and the more developed denticles of the lobes are triple pointed.

Remarks. The specimen is assigned to Ptychitidae for its very typical suture line with triple-pointed indentitions in the deepest part of the lobes. Such indentitions can be found in quite a large number of genera of this family, including the medium-sized slightly compressed to slightly depressed *Ptychites* Mojsisovics, 1875, *Aristoptychites* Diener, 1916, *Arctoptychites* Archipov, Korchinskaya and Tozer, 1994, the large sized, very compressed *Flexoptychites* Spath, 1951 and *Lanceoptychites* Balini, 1998.

The specimen is a juvenile, but with a D of about 20 mm. At this size, Ptychitidae usually exhibit the beginning development of mature features in the whorl section and venter. In this respect, the depressed whorl section with the wide rounded venter of the Nimaigu specimen suggests a closer relationship with *Ptychites* than to *Aristoptychites* and *Arctoptychites*. The whorl section of *Aristoptychites* is subtriangular and slightly compressed, whereas in *Arctoptychites* the inner whorls that correspond in size to the available specimen from Nimaigu show a blunt ventral ridge and a rostrum. With respect to known stratigraphic ranges, however, the at-

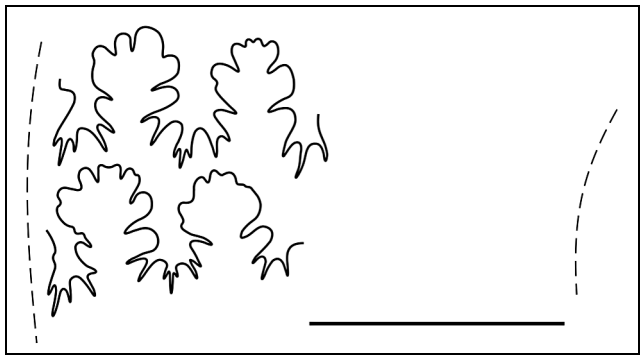


Fig. 6 - Suture line of *Ptychites* sp. A, specimen GMPKU-P-3086 (ws2012-152-3). Bar scale is 5 mm.

tribution to *Ptychites* implies the extension of the range of the genus from the Lower to the Upper Ladinian.

As regards comparison with other species of *Ptychites*, the available specimen differs from many of them by its very depressed whorl section and lack of ribs. Only *P. hamatus* Tozer, 1994, from the Upper Anisian-Lower Ladinian of British Columbia is somewhat similar to the Nimaigu specimen with its nearly smooth surface and depressed whorl section. The available specimen most likely represents a new species, but the lack of information regarding the mature shell and body chamber prevents comparison with existing species of *Ptychites*. For this reason the specimen is left in open nomenclature.

Occurrence. Specimen was collected from level 152 of the studied section, which lies in the middle of the interval between the *Haoceras xingyiense* zone and the *Trachyceras* beds. *Yangites densicostatus* occurs at the same level. It represents the youngest record of *Ptychites* known from the Bithynian (Middle Anisian) to the Illyrian (Upper Anisian) of the Tethys (Krystyn et al. 2004) and the Middle Anisian to Lower Ladinian of North America (Tozer 1994).

Superfamily Clydonitoidea Hyatt, 1877
Family Trachyceratidae Haug, 1894

Preliminary remarks. The Trachyceratidae is one of the most important ammonoid families of the Ladinian and Carnian, not only for the large number of genera but also because it includes many taxa with high chronostratigraphic significance. The structure of the family is complex and has been updated several times by some of the most experienced specialists of the 20th century. In this work we refer to the structure provided by Tozer in his last monograph (1994), following more than 30 years of work devoted to the revision of Triassic Ammonoidea for the Treatise on Invertebrate Paleontology. This work was never published as such, but the structure of Triassic ammonoid Orders he conceived for the Treatise was included in his 1994 monograph. For this work, we divide the family Trachyceratidae Haug, 1894 into four subfamilies: Protrachyceratinae Tozer, 1971, Arpaditinae Hyatt, 1900, Trachyceratinae Haug, 1894 and Sirenitinae Tozer, 1971.

Subfamily Haoceratinae n. subfam.

Type genus: *Haoceras* n. gen.

Diagnosis: Small to medium sized, densely ribbed Trachyceratidae with relatively few rows of nodes and deeply indented, nearly subammonitic suture line consisting of three elongated to linguoid saddles on the flank. Lobes with deep denticles in the central part, tops of the saddles rounded to wavy. Venter narrow, furrowed, not crossed by ribs and bordered by nodes. Ventral nodes simple, not double pointed.

Composition: *Haoceras* n. gen. (type) and *Sinomeginoceras* n. gen.

Remarks on the composition of the subfamily. The new subfamily is purposely described with narrow variability with limits for two reasons. First, our knowledge of Ladinian and Carnian ammonoids from South China is seriously lacking and this paper is a first contribution to its revision. Second, we do not want to add a new "basket"-like subfamily to the already complex structure of Trachyceratidae.

The new genus *Yangites* is not included in the new subfamily because of its flat to slightly depressed venter and suture line with saddles having rounded tops.

Langdaiceras Wang, 1983 has a suture line similar to that of *Haoceras* n. gen. and *Sinomeginoceras* n. gen. with its deeply indented sides and elongated-linuoid outline (Wang 1983, fig. 1c). However, the coiling of *Langdaiceras* is evolute, adult specimen size is large and, more importantly, the venter is flat to slightly convex.

PLATE 1

Upper Ladinian ammonids from Zughanpo Member of the Falang Formation.

Fig. 1 - *Xeoprotrachyceras* cf. *primum*, specimen GMPKU-P-3071 (ws2012-59-11) in part included in the rock matrix, 1a, lateral view, 1b, slightly oblique view under different light.

Fig. 2 - *Detoniceras* sp. A, specimen GMPKU-P-3077 (ws2012-72-2), fragment of body chamber, 2a, ventral view, 2b, lateral view.

Fig. 3 - *Detoniceras* sp. A, specimen GMPKU-P-3079 (ws2012-88-3), fragment of body chamber, 3a, lateral view, 3b, ventral view, 3c oblique view of shoulder and venter.

Fig. 4 - *Yangites densicostatus* n. gen. n. sp., holotype GMPKU-P-3085 (ws2012-152-1), fragment of phragmocone, 4a, lateral view, 4b, ventral view).

Fig. 5 - *Yangites densicostatus* n. gen. n. sp., paratype GMPKU-P-3070 (ws2012-59-10), phragmocone, lateral view

Fig. 6 - *Yangites densicostatus* n. gen. n. sp., paratype GMPKU-P-3072 (ws2012-65-2), fragment of body chamber, 6a, lateral view, 6b, ventral view.

Fig. 7 - *Ptychites* sp. A, specimen GMPKU-P-3086 (ws2012-152-3), fragment of phragmocone, 7a, ventral view, 7b, aperturral view, 7c, lateral view.

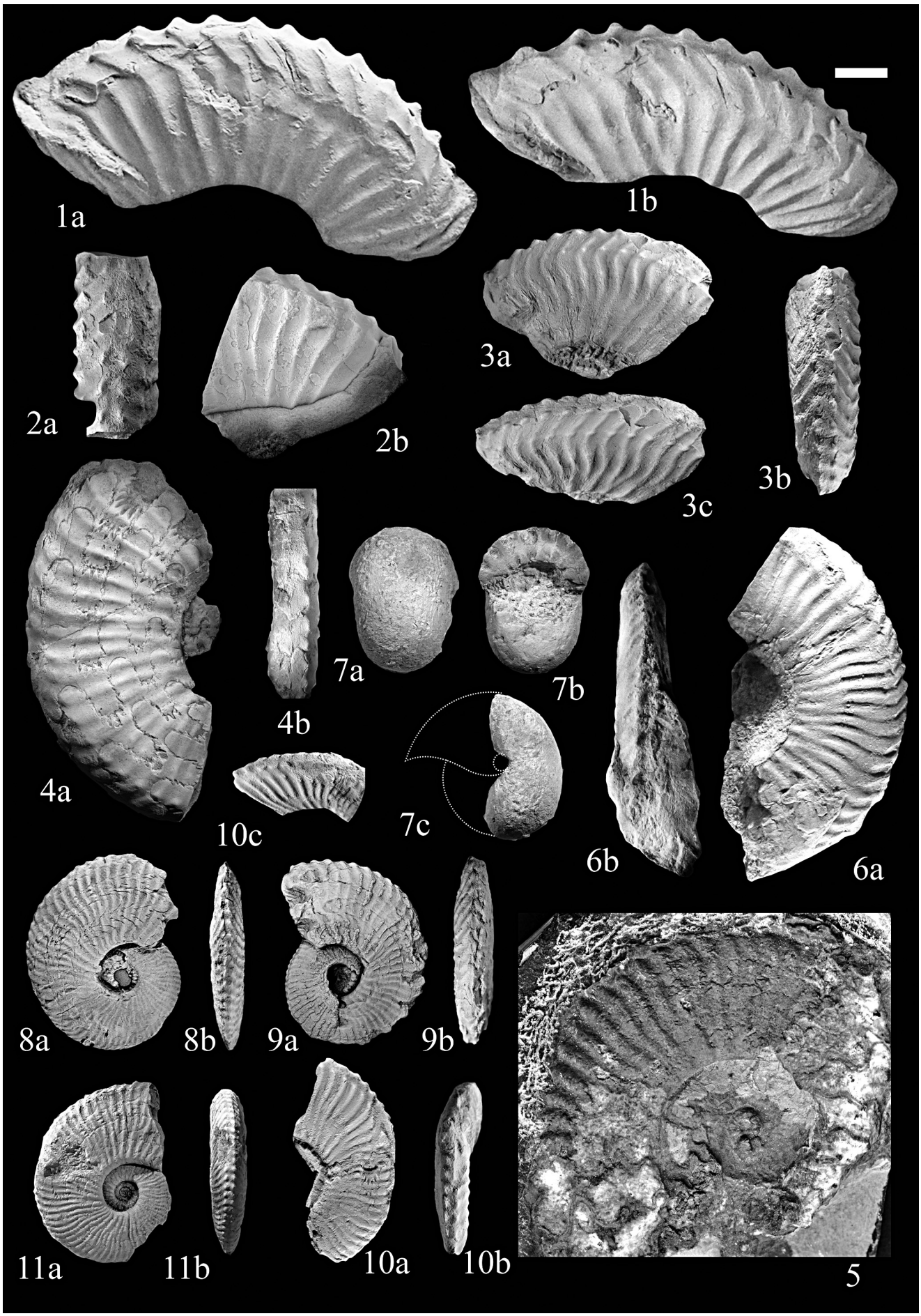
Fig. 8 - *Sinomeginoceras wangi* n. gen. n. sp., holotype GMPKU-P-3075 (ws2012-70-1), phragmocone, 8a, lateral view, 8b, ventral view.

Fig. 9 - *Sinomeginoceras wangi* n. gen. n. sp., paratype GMPKU-P-3073 (ws2012-68-2), 9a, lateral view, 9b, ventral view.

Fig. 10 - *Sinomeginoceras wangi* n. gen. n. sp., paratype GMPKU-P-3080 (ws2012-98-2), 10a, lateral view, 10b, ventral view.

Fig. 11 - *Sinomeginoceras xingyiense* n. gen. n. sp., holotype GMPKU-P-3076 (ws2012-71-1), 11a, lateral view, 11b, ventral view.

All specimens whitened with ammonium chloride except Fig. 5. Bar scale is 1 cm for all specimens.


1a
1b
2a
2b
3a
3b
3c
4a
4b
5
6a
6b
7a
7b
7c
8a
8b
9a
9b
10a
10b
10c
11a
11b

Comparison to other subfamilies. The new subfamily is erected to accommodate *Haoceras* n. gen. and *Sinomeginoceras* n. gen., which show a combination of features that do not conform with present subdivisions of the family Trachyceratidae.

Subfamily Protrachyceratinae Tozer, 1971 includes taxa with furrowed venters bordered by simple nodes, but their ornamentation is characterized by many rows of nodes as well as ribs. The suture line of some members of this subfamily is ceratitic (e.g. *Eoprotrachyceras* Tozer, 1980), but it is much more commonly distinctly ammonitic (e.g. *Protrachyceras* Mojsisovics, 1893, *Neoprotrachyceras* Krystyn, 1978 and *Spirogmoceras* Silberling, 1956). The elongated outline of the saddles of *Protrachyceras* resemble the linguoid outline of the saddles of Haoceratinae, which suggests that this genus may be the ancestor of the new subfamily.

Subfamily Trachyceratinae Haug, 1894, in Tozer's view (1994), shows a very wide composition, in some respects too wide (see Mietto et al. 2008, p. 396). This subfamily includes genera with dense ribbing and only a few rows of nodes or without any nodes (e.g. *Maclearnoceras* Tozer, 1963, *Frankites* Tozer, 1971 *Zestoceras* Tozer, 1994). These taxa (part of the subfamily Anolcitinae Mietto, Manfrin, Preto & Gianolla, 2008) are quite similar to *Haoceras* n. gen. and *Sinomeginoceras* n. gen. in ornamentation, but differ in their very simple ceratitic suture line with rounded saddles and simple indented lobes. Indented suture lines are characteristic of other Trachyceratinae such as *Trachyceras* Laube, 1869 and *Austrotrachyceras* Krystyn, 1978, but in these genera the saddles are strongly and deeply indented to the top and the number of rows of nodes is high (from 8-9 to more than 12), and their ventral nodes are double pointed.

The only other subfamily that can be compared with Haoceratinae n. subfam. is Arpaditinae Hyatt, 1900. This subfamily, which also includes genera with dense ribbing and only a few rows of nodes (e.g. *Meginoceras* MacLaern, 1930), is distinguished from Haoceratinae by its two ventral keels, often nodose. The coiling of Arpaditinae expands slowly and its suture line is very often ceratitic, especially in Ladinian genera.

Occurrence and age. Haoceratinae are known only from the Late Ladinian of Guizhou, China.

Genus *Haoceras* n. gen.

Type species: *Haoceras xingyiense* n. gen. n. sp.

Derivatio nominis: The genus is dedicated to Prof. Wei-cheng Hao, an ostracod specialist and former director of the Geological Museum of PKU, who since 1999, has been the mentor for research on the Triassic vertebrate localities of South China.

Diagnosis: Medium sized Trachyceratidae with slightly involute to slightly evolute coiling, a compressed whorl section and a furrowed venter. Ornamentation consists of two rows of nodes and dense ribbing. Ribs often branch at the umbilical node and always end on the venter with an obliquely elongated node. Deeply indented, nearly subammonitic suture line with three elongated saddles exposed on the lateral side. Tops of saddles rounded. Deep denticles in the middle part of the lobes. Lateral lobe indented on both sides, at least up to 2/3 of the distance to the top of the 1st and 2nd saddle.

Composition of the genus: Type species only.

Discussion. *Haoceras* n. gen. shares with *Sinomeginoceras* n. gen. a nearly subammonitic suture line with rather elongated saddles and deeply indented lobes. Apart from its similar suture line, *Haoceras* differs from *Sinomeginoceras* in many other features, such as in its nearly evolute coiling, larger size, less compressed whorl section, and the presence of a second row of nodes in an umbilical position.

Within the Trachyceratinae, the genera most similar to *Haoceras* n. gen. are *Zestoceras* Tozer, 1994, *Maclearnoceras* Tozer, 1963 and *Frankites* Tozer, 1971, all of which are characterized by dense ribbing. The most important difference between these genera and *Haoceras* is in the suture line, which for the three taxa is ceratitic with broad rounded saddles and small indented lobes, whereas *Haoceras* has rather narrow, elongated saddles and deeply indented lobes.

Aside from the suture line, *Zestoceras* differs from *Haoceras* in having a convex ventral side that is not furrowed. *Maclearnoceras* has a furrow, but only on its innermost whorls. These whorls are characterized by 5 rows of nodes, while the ornamentation on the outer whorls consists only of ribs that cross the venter. *Frankites* tends to be larger, and is more involute. It lacks nodes and exhibits a perculiar pattern of ribbing that consists of flat ribs with complex branching.

The more similar Arpaditinae are *Meginoceras* McLearn, 1930 and *Liardites* Tozer, 1963. These two genera are distinguished by a ceratitic suture line with broad, rounded saddles and relatively few denticles located only in the central part of the lobes. In addition to these features, the furrow of *Meginoceras* is bordered by two nodose keels, while *Liardites* lacks nodes but exhibits ribs that bifurcate nearer to the venter instead of the umbilical margin.

Occurrence and age. The new genus *Haoceras* is known only from the Nimaigu section (Guizhou, South China) where it ranges from the base to the top of the *Haoceras xingyiense* zone. Its age is estimated to be middle to Late Ladinian.

Haoceras xingyiense n. sp.

Pl. 2, fig. 1a-b, 2a-b, 3a-b, 4a-b, 5, 6a-b, 7a-b, 8a-b; Fig. 7a-c

Derivatio nominis: Named for Xingyi, the most important town in the area, which also lends its name to the vertebrate fauna preserved in the Zhugampo Member of the Falang Formation.

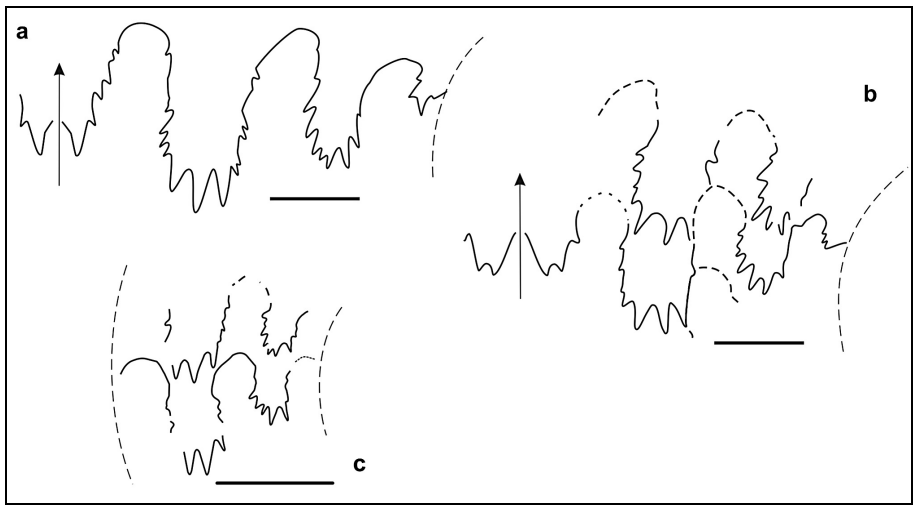


Fig. 7 - Suture lines of *Haoceras xingyiense* n. gen. n. sp. a) external suture of the holotype GMPKU-P- 3066 (ws2012-59-1); b) external suture of paratype GMPKU-P- 3068 (ws2012-59-7); c) suture line of paratype GMPKU-P-3078 (ws2012-88-1) between venter and periumbilical margin. Bar scale is 5 mm.

Stratum typicum and locus typicus: Bed 59, Zhuganpo Member, Falang Formation, Nimaigu section (Xingyi, Guizhou) from which the holotype and three of the paratypes were collected.

Type series: The new species is described on the basis of the holotype GMPKU-P- 3066 (ws2012-59-1) and ten paratypes: GMPKU-P- 3067 (ws2012-59-5), GMPKU-P- 3068 (ws2012-59-7), GMPKU-P- 3069 (ws2012-59-8), GMPKU-P- 3061 (ws2012-57-1), GMPKU-P- 3062 (ws2012-57-2), GMPKU-P- 3063 (ws2012-57-4), GMPKU-P- 3064 (ws2012-58-1), GMPKU-P- 3065 (ws2012-58-2), GMPKU-P- 3074 (ws2012-68-4), GMPKU-P- 3078 (ws2012-88-1).

Diagnosis: As for the genus.

Description. All specimens consist only of phragmocones. Coiling is slightly involute (H>U), but in few specimens it appears to be slightly evolute (e.g. GMPKU-P- 3069 [ws2012-59-8] and GMPKU-P-3078 [ws201288-1]). This is especially true for the very innermost whorls visible on the holotype GMPKU-P-3066 (ws2012-59-1) and on the paratype GMPKU-P-3078 (ws2012-88-1).

The coiling rate is very low in most of the specimens, with SGR lower than 60%.

Whorl section is compressed with H/W usually between 1.5 and 2.0. Venter is furrowed, but furrow does not appear to be deeper than the space between ribs.

Ornamentation, consisting of ribs and two rows of nodes in the umbilical and ventral positions, does not change throughout ontogeny.

Ribs are rectiradiate to very slightly prorsiradiate and sinuous, organized into primary, intercalatory and bifurcate types. Primary ribs start at the umbilical node, sometimes in couples from the same node. Intercalatory and bifurcate types start quite low on the flank, between 20 and 40% of H. Ribbing is typically wavy, with interspaces between ribs that are as wide as the ribs or slightly narrower. Rib spacing, however, varies quite notably from specimen to specimen. Most specimens exhibit a rib frequency between 24 to 28 per half whorl, but for specimen GMPKU-P- 3068 (ws2012-59-7) the number of ribs is 22 in 110° (equivalent to 36 ribs in 180°). This specimen is considered to be a densely ribbed variant.

Nodes are located on the umbilical margin and the venter. Those on the umbilical margin are quite rounded and more or less prominent, depending on the specimen. Their number varies between 12 and 15 per half whorl. Ventral nodes are oblique, with an angle of about 70° (GMPKU-P- 3064 [ws2012-58-1] and GMPKU-P- 3063 [ws2012-57-4]: Pl. 2, fig. 6). Every rib ends with a ventral node.

Suture line consists of three elongated saddles on the flank. Lobes are deeply indented with the lateral lobe indented for 2/3 of its height (Fig. 7b-c) or almost to the top of the 1st saddle (the holotype: Fig. 7a).

Dimensions (mm)

Specimen	D	H	U	h	W	U/D	H/W	SGR
ws2012-59-1 holotype	58.2	23	22	13.2	11.4	0.37	2.01	74.24
ws2012-57-2	60.5	24	20.4	16.10	-	0.33	-	49.06
ws2012-57-1	50.1	18.6	17.5	14	11.7	0.34	1.58	32.85
ws2012-59-5	52	20.1	17.1	14.8	11.2	0.32	1.79	35.81
ws2012-68-4	31.2	14.2	9.5	7.5	7.6	0.30	1.86	89.33
ws2012-59-8	30	11	12	7.0	8-0	0.4	1.37	57.14
ws2012-88-1	30	10.3	11	8.7	6.8	0.36	1.51	18.39

Discussion. Very few species are comparable to *Haoceras xingyiense* n. sp. This new species, with its complex nearly subammonitic suture line, is similar to that of *Sinomeginoceras wangi* n. gen. n. sp. and *S. xingyiense* n. gen. n. sp., but these two species differ by several features already emphasized in the discussion section for the new genus *Haoceras*.

Well developed periumbilical nodes occur in *Protrachyceras longjiangense* Wang & He, 1976, but this species has thicker whorls and ornamentation typical of *Protrachyceras,* consisting of three to five rows of nodes (respectively on the holotype NIGPAS 29275

and the paratype NIGPAS 29276), as well as a ceratitic suture line (Wang & He 1976, fig. 28c). Very little similarity can be found with species of *Zestoceras* (cf. Tozer 1994), which are characterized by a ceratitic suture, convex ventral side at a mature stage and a lack of periumbilical nodes.

Occurrence and age. The species, which serves as the index fossil for the Late Ladinian *H. xingyiense* zone, is rather common in the Nimaigu section and has been collected from beds 57, 58, 59, 68 and 88.

Genus *Sinomeginoceras* n. gen.

Type species: *Sinomeginoceras wangi* n. gen. n. sp.

Derivatio nominis: The compound name emphasizes the occurrence in China and its similarity with *Meginoceras* McLearn, 1930.

Diagnosis: Rather small, very involute and very compressed Trachyeceratidae, with very narrow venter. Ornamentation consists of one row of ventral nodes and very dense ribbing. The nodes, small and paired on both sides of the venter, may be rounded or oblique, depending on the species. The very narrow venter varies slightly between species, depending on the shape of ventral nodes. Usually the venter is furrowed, but on occasion the paired ventral nodes are so close that they appear to be in contact.

Suture line with three saddles on the lateral side. The 1st and 2nd saddle are elongated and usually wavy until the top. The lateral lobe is wider than the 1st saddle and both sides are indented for at least half of the distance from the base of the lobe to the top of the saddle. The central part of each lobe is indented by deep, elongated denticles.

Composition of the genus: *Sinomeginoceras wangi* n. gen. n. sp. (type) and *S. xingyiense* n. gen. n. sp.

Discussion. The new genus *Sinomeginoceras* displays a combination of features that is peculiar within the family Trachyceratidae. Its suture line is similar to *Haoceras*, but it differs by the features discussed in the new genus *Haoceras*. Morphologically, *Sinomeginoceras* n. gen. is similar to some Arpaditinae and Trachyceratinae, but its suture line is significantly different from these taxa.

The Arpaditinae genus most similar to *Sinomeginoceras* is *Meginoceras* McLearn, 1930 with its small size, involute coiling, dense ribbing, small ventral nodes and narrow sulcate venter. Separation of the two genera is easily accomplished on the basis of their suture lines. All species of *Meginoceras* have ceratitic suture lines with broad rounded saddles and very simplified small denticles limited to the deepest part of the lobes. The suture line of *Sinomeginoceras* is instead characterized by narrow elongated wavy and almost subammonitic 1st and 2nd saddles and by deeply indented lobes. Apart from its suture line, *Sinomeginoceras* differs from *Meginoceras* by its more compressed whorl section (H/W>2.8 vs. 1.33 to 1.77 for *Meginoceras* [Tozer 1994]) and the lack of raised ventral nodose keels (e.g. the type species *M. meginae* McLearn, 1930).

Another Arpaditinae that may be compared with *Sinomeginoceras* n. gen. is *Liardites* Tozer, 1963. This genus (Tozer 1994) lacks ventral nodes and, again, has a very simple ceratitic suture line with broad, rounded saddles.

Trachyceratinae exhibiting similarities with *Sinomeginoceras* n. gen. include *Zestoceras* Tozer, 1994, *Maclearnoceras* Tozer, 1963 and *Frankites* Tozer, 1971. These genera, however, share the same type of ceratitic suture line with broad, rounded saddles and small indentitions of the lobes. *Sinomeginoceras* is also distinguished from these genera by the paired ventral nodes on its venter.

The venter of *Zestoceras* is crossed by ribs and is not furrowed. Moreover, ventral nodes occur only on the phragmocone.

Maclearnoceras is characterized by tuberculate and furrowed innermost whorls, but the nodes and furrow disappear during ontogeny and the mature venter is convex and crossed by ribs.

The venter of *Frankites* is furrowed and also crossed by weakened ribs. However, it has no ventral nodes and the ribbing is very typical, being flat and with complex branching (see Tozer 1994; Balini 2008 and Mietto et al. 2008).

Occurrence and age. *Sinomeginoceras* n. gen. is known only from the Nimaigu section (Guizhou, China) where it ranges from slightly above the base of the *Haoceras xingyiense* zone to just above the top of the zone. Its age is Late Ladinian.

Sinomeginoceras wangi n. gen. n. sp.

Pl. 1, fig. 8a-b, 9a-b, 10a-b; Fig. 8a-b

Derivatio nominis: The new species is named in honor of prof. Wang Yi-gang, who dedicated 30 years to the study of Chinese Triassic ammonoids.

Stratum typicum and locus typicus: Bed 70, Zhuganpo Member, Falang Formation, Nimaigu section (Xingyi, Guizhou).

Material: Species description is based on the holotype and three paratypes. Holotype: GMPKU-P-3075 (ws2012-70-1). Paratypes: GMPKU-P-3094 (ws2012-68-1), GMPKU-P-3073 (ws2012-68-2) and GMPKU-P-3093 (ws2012-68-3). Specimen GMPKU-P-3080 (ws2012-98-2) is doubtfully attributed to the species and is not included in the type series.

Diagnosis: *Sinomeginoceras* with obliquely elongated, paired ventral nodes separated by a furrow.

Description. Specimens are all preserved as internal molds of the phragmocone. Coiling of the inner whorls tends to be very involute, but it gradually becomes egressive at a diameter that varies slightly from specimen to specimen. For the holotype GMPKU-P-3075 (ws2012-70-1), the umbilical egression begins at a diameter of about 25-26 mm, while in the paratype GMPKU-P-3073 (ws2012-68-2) it starts at about 19-20 mm. The latter specimen is slightly elliptized with σ2 exactly in the direction of this D, but this deformation

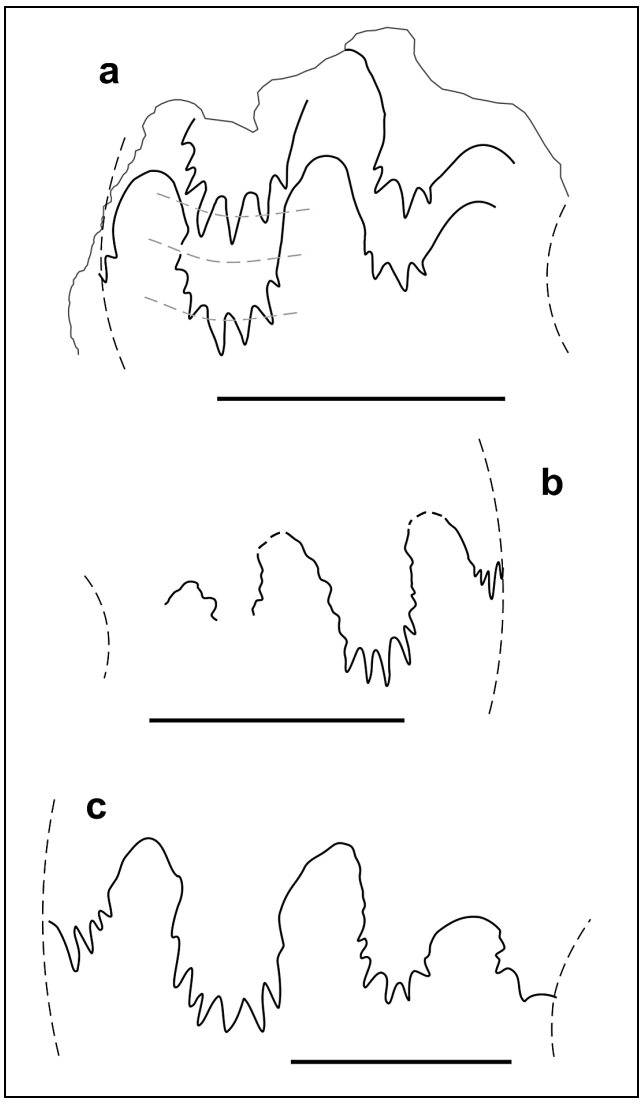


Fig. 8 - Suture lines of *Sinomeginoceras* n. gen. a) *S. wangi* n. gen. n. sp., holotype GMPKU-P-3075 (ws2012-70-1); b) paratype GMPKU-P-3073 (ws2012-68-2); c) *S. xingyiense* n. gen. n. sp., holotype GMPKU-P-3076 (ws2012-71-1). Gray dashed lines on a) show the outline of ribs that slightly deform the largest denticles of the lateral lobe. Bar scale is 5 mm.

cannot justify of the significant difference in the beginning of the egression with respect to the holotype.

Very compressed whorl section (H/W from 1.96 to 2.08) with flanks slowly converging to the extremely narrow venter. Ventral width is about 1.5-1.7 mm at H = 14 mm for the holotype.

Ribs are prosiradiate, just slightly sinuous. Course is nearly straight until the middle part of the flank, where they become a little more rounded and project forward slightly. Primary ribs are accompanied by frequent secondary and intercalatory ribs. Branching point is quite low on flank (~20% of H), while intercalatory ribs usually start around 30-40% of H, depending on the specimen. Ratio of total ribs/primary ribs in a quarter of whorl is always >2. Holotype GMPKU-P-3075 (ws2012-70-1) has a total of 17 ribs with 7 primaries and paratype GMPKU-P-3073 (ws2012-68-2) has 14 ribs with 6 primaries.

Every rib ends with a ventral node. Ventral nodes are always paired and oblique. Paratype GMPKU-P-3073 (ws2012-68-2) exhibits more elongated nodes than the holotype. Nodes of each pair are not connected, but are separated by a distinct furrow. Holotype has about 32 nodes per half whorl at a diameter of ~37 mm.

Suture line (Fig. 8a-b) consists of three saddles on lateral side, with the 1st and 2nd slightly wavy until the top. All specimens, even those whose suture line is not figured, show features typical of the new genus emphasized in its diagnosis, namely the lateral lobe wider than the 1st saddle, the deeply indented lobes and the indentitions affecting the sides of the lobes for about 50% of height. In this respect, Fig. 8a and 8b represent the two extreme variants, those with indentation high up on the saddle side and those with very little indentation.

Dimensions

Specimen	D	H	U	W	U/D	H/W	H/U
ws2012-70-1 holotype	37.0	17.0	10.0	4.8	0.27	3.54	1.7
ws2012-68-2	36.2	14.9	9.8	5.0	0.27	2.98	1.52

Discussion. *Sinomeginoceras wangi* n. gen. n. sp. is more abundant in the collection than *S. xingyiense* n. sp. Hence, it has been selected as type of the genus because it is better known, especially regarding its variability. The main difference with respect to *S. xingyiense* n. gen. n. sp. is in the shape of the ventral nodes, which are oblique and elongated in *S. wangi* and rounded in *S. xingyiense*.

S. wangi n. sp. shows some similarity with respect to its ventral side with some Canadian *Meginoceras* taxa described by Tozer (1994) from Meginae subzone 3 and the overlying Maclearni Zone. *Meginoceras aylardi* (McLearn) and *M. effervescens* (Tozer), lack raised keels and they appear close to *S. wangi* n. gen. n. sp. Raised keels actually occur in the older forms of *Meginoceras* (including the type *M. meginae* [McLearn]) from Meginae subzone 1 and 2. The separation of these species and *S. wangi* n. gen. n. sp. is based on features already emphasized in the Discussion of the genus.

Occurrence and age. The species is definitely documented within the upper part of the Late Ladinian *Haoceras xingyiense* zone (beds 68 and 70) of the Nimaigu section (Guizhou, South China). The upper boundary of its range probably occurs just above the

top of this biozone, in level 98, from which specimen GMPKU-P-3080 (ws2012-98-2) was collected.

Sinomeginoceras xingyiense n. gen. n. sp.

Pl. 1, fig. 11a-b; Fig. 8c

Derivatio nominis: The name celebrates the town of Xingyi that lends its name to the famous vertebrate fauna collected from the Zhuganpo Member of the Falang Formation in the surroundings of Wusha.

Stratum typicum and locus typicus: Bed 71, Zhuganpo Member, Falang Formation, Nimaigu section (Xingyi, Guizhou).

Type series: Holotype only: GMPKU-P-3076 (ws2012-71-1).

Diagnosis: *Sinomeginoceras* with small, rounded and paired ventral nodes.

Description. Available specimen preserved as an internal mold of the phragmocone, it is not compacted, but very slightly elliptized. Coiling is involute, with umbilical egression starting at about 15 mm of H.

Whorl section highly compressed (H/W=2.8), maximum width very close to periumbilical margin and flanks very slowly converging to very narrow venter, which is only about 1.2 mm wide at H ~13 mm. Venter is not truly furrowed because the paired ventral nodes are so close they appear to be in contact.

Ribbing very dense, consisting of sinuous-falcoid, prorsiradiate, primary, intercalatory or secondary ribs very similar to *S. wangi* n. sp. Primary ribs more common than other types and for 1/4 whorl the ratio of total ribs/primary ribs is 18/11. Primary ribs may be simple or begin in bundles at periumbilical margin. This is slightly more common in first half of last preserved whorl. Intercalatory and bifurcated ribs start at about 30% of H.

Ventral nodes are small, rounded and paired. Their high frequency (34 nodes in half whorl at D = 36 mm) reflects the dense ribbing.

Suture line (Fig. 8c) exhibits three saddles on flank. First and 2nd are elongated and wavy to the top. Relative size of 1st saddle and lateral lobe, and pattern of indentitions closely match *S. wangi* n. sp.

Dimensions

Specimen	D	H	U	W	U/D	H/W	H/U
ws2012-71-1 holotype	36.3	16.8	10.1	6.0	0.27	2.8	1.66

Discussion. *Sinomeginoceras xingyiense* n. gen. n. sp. differs from *S. wangi* n. gen. n. sp. mainly in the shape of the ventral nodes, which are rounded in the former species and oblique in the latter. Other differences are very small, such as the egression that starts at a slightly smaller diameter in *S. xingyiense*.

Occurrence and age. Species was collected from level 71 of the Nimaigu section, which is within the *Haoceras xingyiense* zone, Late Ladinian.

Subfamily Trachyceratinae Haug, 1894

Genus *Trachyceras* Laube, 1869

Type species: *Ceratites aon* Münster, 1834

Trachyceras sp. ind.

Pl. 2, fig. 9, 10

Material: Two specimens: GMPKU-P-3088 (ws2012-197-1) and GMPKU-P-3089 (ws2012-228-1).

Description. Both specimens are very poorly preserved. GMPKU-P-3088 (ws2012-197-1) is preserved only on one side while GMPKU-P-3089 (ws2012-228-1) is flattened, consisting only of an impression in the matrix. Ribs are flat, especially those of GMPKU-P-3088, and bear simple, well rounded subspiny nodes. Spiral rows of nodes number at least 10 for GMPKU-P-3088 and about 12 for GMPKU-P-3089. Venters of both specimens is not preserved and suture lines are not visible.

Remarks. The two specimens most probably are not conspecific since the ribbing of specimen GMPKU-P-3089 (ws2012-228-1) is more dense than that of GMPKU-P-3088 (ws2012-197-1). Given the lack of information regarding the suture line and ventral features, we tentatively attribute the two specimens to *Trachyceras* Laube, 1869 based on their flat ribs that bear rounded nodes and of the high number of spiral rows of nodes. The ribs of *Daxatina* Strand, 1929 (see Tozer 1994) are not as flat as those of *Trachyceras* Laube, 1869, while *Protrachyceras* Mojsisovics, 1893 has a lower number of spiral rows of nodes (e.g. six in the type species *Trachyceras archelaus* [Laube, 1869]).

Occurence. Specimens were collected from beds 197 and 228 in the upper part of the Nimaigu section, below the FO of *Trachyceras multituberculatum* Hsü. Both levels belong to the Lower Carnian *Trachyceras* beds.

Trachyceras multituberculatum Hsü, 1940

Pl. 2, fig. 11, 12a-b

1940 *Trachyceras multituberculatum* Hsü, p. 170.

v 1983 *Trachyceras multituberculatum* - Wang, p. 159, pl.1, fig. 3-4.

2003 *Trachyceras multituberculatum* - Hao et al., p. 434, pl. 2, fig. 1-3.

2003 *Trachyceras multituberculatum* - Xu et al., pl. 1, fig. 2,3; pl. 2, fig. 6; pl. 3, fig. 5, 11; pl. 4, fig. 2

2003 *Trachyceras multituberculatum* - Wang et al., pl. 1, fig. 2.

Stratum typicum and locus typicus: Type specimen was collected by Hsü (1940) from the Wayao Member of the Falang Formation at Zhenfeng, Guizhou, China.

Material: Three specimens: GMPKU-P-3090 (ws2012-238-1), GMPKU-P-3091 (ws2012-238-2) and GMPKU-P-3092 (ws2012-238-3).

Description. The three available specimens are completely flattened, but still retain the test. Whorl section and ventral side are not preserved, and the suture line is not exposed. Coiling is involute and ornamentation consists of very flat ribs and multi-pointed nodes that are typical for the species.

Flat ribs are very narrow at umbilical margin; they gradually become very wide on the flank, but inter-space between ribs does not change. On external part of flank, ribs are 4-5 times wider than at umbilical margin; hence, this explains the relatively low frequency of ribs. Specimen GMPKU-P-3092 (ws2012-238-3) bears 8 to 9 ribs per quarter whorl, larger specimen GMPKU-P-3090 (ws2012-238-1) bears 9 ribs, while similarly sized GMPKU-P-3091(ws2012-238-2) bears between 9 to 10 ribs. Paired ribs commonly start at umbilical nodes and very rarely branch at middle of flank. Intercalatory ribs begin at this position. Course of ribbing is sinuous-falcoid, but with a wide convex-forward middle part that is well visible on Pl. 2, Fig. 11.

Nodes are organized in rows of simple nodes on inner part of flank, while rows on outer part consist of triple-pointed nodes, elongated in direction of coiling.

Specimen GMPKU-P-3092 (ws2012-238-3) (Pl. 2, fig. 12), even if small, most represents organization of nodes. It exhibits the umbilical strong, spiny nodes that are another typical feature of *T. multituberculatum*, followed by three rows of simple nodes and five rows of triple-pointed nodes. Specimen GMPKU-P-3091 (ws2012-238-2)(not figured), of a larger size, exhibits some strong umbilical nodes, but the compaction prevents an exact count of the rows of nodes. At least two rows of single nodes appear to be present together with two or three rows of triple-pointed nodes. Flattened and incomplete specimen GMPKU-P-3090 (ws2012-238-1) is attributed to *T. multituberculatum* only on the basis of its very wide, flat ribs.

Dimensions

Specimen	D	H	U	h	W	U/D
ws2012-238-3	25.0	-	7.1	-	-	0.28

Discussion. Attribution of the specimens to *Trachyceras multituberculatum* Hsü, 1940 is relatively easy because of the very typical features for this species. Flat ribs, multi-pointed nodes and strong, spiny umbilical nodes are usually visible even on flattened specimens. The stable synonymy of *T. multituberculatum* reflects the straight-forward identification of the species.

As reported by Wang (1983), who selected the lectotype and re-described the species, the multi pointed nodes of the more external rows may be become four- to five-pointed on larger specimens. At about 17.5 mm of H, the lectotype NIGPAS 15571 (Wang 1983: pl. 1, fig. 4), which was examined by us, exhibits one row of umbilical spines followed by two rows of simple nodes, in turn followed by one row of extremely small multi-pointed nodes, and then three rows of four-pointed nodes, the last located on the venter. About one quarter whorl later, the nodes of the 6th row becomes five-pointed.

No information regarding the suture line of this unusually ornamented species is available in the literature and our examination of Hsü and Wang's collections housed at NIGPAS confirms this lack of knowledge.

Occurrence and age. *Trachyceras multituberculatum* was collected from level 238 of the studied section. This species is known only from Guizhou (South China), where it has been reported at several localities (Hsü 1940; Wang 1983; Hao et al. 2003; Xu et al. 2003; Wang et al. 2003; Wang et al. 2009). Wang (1983) selected the species as the index fossil of the *T. multituberculatum* zone, which is of Early Carnian age (Wang 1983; Wang et al. 2003).

Family Clionititidae Arabu, 1932

Genus *Clionitites* Strand, 1929

Type species: *Clionites angulosus* Mojsisovics, 1893

Clionitites sp. ind.

Pl. 2, fig. 13a-b

Material: One specimen GMPKU-P-3087 (ws2012-162-1).

Description. Small sized specimen is preserved as a three dimension internal mold of the phragmocone. It is characterized by involute coiling (H/U is 1.22), and a slightly compressed, semioval whorl section (H/W is 1.58). Flanks gradually converge to the venter, which although not well preserved, does not appear to have a furrow.

Ribbing is gently wavy and consists of slightly sinuous, nearly straight primary ribs with some bifurcation very close to umbilical margin. Intercalatory ribs occur very rarely, starting at about 30% of H. All ribs end with a weak ventral node. Venter is not crossed by ribs and appears nearly flat. A total number of 19 ribs per half whorl can be counted. Suture line is ceratitic with three saddles on lateral side.

Dimensions

Specimen	D	H	U	W	U/D	H/W
ws2012-162-1	12.1	4.9	4.0	3.1	0.33	1.58

Discussion. The available specimen was collected from a level much younger than those yielding *Haoceras xingyiense* n. gen. n. sp., *Sinomeginoceras wangi* n. gen. n. sp. and *S. xingyiense* n. gen. n. sp. Hence, it cannot be interpreted as an inner whorl of one these three new species. Apart from its different stratigraphic origin, the specimen from level 162 differs from the inner whorls of the three new species by its wavy gentle ribbing. The ribbing of of *H. xingyense* is much more distant, whereas for *S. wangi* and *S. xingyiense,* it is much denser.

Its involute coiling, suboval whorl section and ribs ending with a ventral node suggest attribution to the "basket" genus *Clionitites* Strand, 1929. The taxonomy of this genus is rather complex (cf. Johnston 1941: 449; Spath 1951: 50; Balini et al. 2000: 41; Mietto et al. 2008: 396-397) and a wide variety of species, ranging in age from Late Ladinian to Early Norian has been referred to this genus. The small size of the available specimen prevents a full attribution at the species level. It appears to be closer to species of *Clionitites* whose venter lacks a true furrow, but instead exhibits a mere interruption of ribs at the ventral nodes. As regards coiling, species of *Clionitites* from the Upper Ladinian and lowermost Carnian are usually very evolute (e.g. *Clionites wheeleri* Johnston, 1941; *C. barwicki* Johnston, 1941; *C. reesidei* Johnston, 1941; *Clionitites callazonensis* Tozer, 1994), but within the wide group of species attributed to *Clionitites* there are also taxa whose coiling is slightly involute, such as "*Ceratites" busiris* Münster, 1834 and "*Ceratites" basileus* Münster, 1841.

Occurrence. Specimen was collected from level 162 of the Nimaigu section, which lies in the interval between the *Haoceras xingyiense* zone and the *Trachyceras* beds.

Regional biostratigraphic framework of the Xingyi ammonoid faunas

The collection from the Nimaigu section is much larger than any other collection from Guizhou conducted in the past. Moreover, it results from a strict bed-by-bed sampling of a well exposed succession, whereas most previous collections were made without the support of detailed stratigraphic measurements (e.g. Wang 1983). Consequently, correlation of the new bed-by-bed data with the local bio-chronostratigraphic scale available from the literature implies a need for its revision.

The only reference scale available for the bio-chronostratigraphy of Ladinian to Carnian sediments of Guizhou is that proposed by Wang (1983) in a comprehensive taxonomic and stratigraphic review of several ammonoid findings dating back to the early 20th century (Mansuy 1912; Hsü 1940, 1944), which was also based on new data collected by Wang himself. Wang defined three zones (Fig. 9), namely the *Xenoprotrachyceras primum*, *Protrachyceras deprati* and *Trachyceras multituberculatum* zones, documented in three members of the Falang Formation. Not one of these zones was supported by a stratigraphic section, but each was based on a faunal list of taxa. Thus, they can be regarded to as Oppel Zones sensu Hedberg (1976). More recently, Wang's bio-chronostratigraphy was applied by Hao et al. (2003) and Xu et al. (2003) without the benefit of a detailed stratigraphic framework, and by Wang

PLATE 2

Upper Ladinian and Lower Carnian ammonids from Zughanpo and Wayao members of the Falang Formation.

Fig. 1 - *Haoceras xingyiense* n. gen. n. sp., holotype GMPKU-P-3066 (ws2012-59-1), phragmocone, 1a, lateral view, 1b, ventral view.

Fig. 2 - *Haoceras xingyiense* n. gen. n. sp., paratype GMPKU-P-3067 (ws2012-59-5), phragmocone, 2a, lateral view, 2b, ventral view.

Fig. 3 - *Haoceras xingyiense* n. gen. n. sp., paratype GMPKU-P-3068 (ws2012-59-7), phragmocone, 3a, lateral view, 3b, ventral view.

Fig. 4 - *Haoceras xingyiense* n. gen. n. sp., paratype GMPKU-P-3069 (ws2012-59-8), 4a, lateral view, 4b, ventral view.

Fig. 5 - *Haoceras xingyiense* n. gen. n. sp., GMPKU-P- 3061 (ws2012-57-1), phragmocone, lateral view.

Fig. 6 - *Haoceras xingyiense* n. gen. n. sp., paratype GMPKU-P-3063 (ws2012-57-4), 6a, lateral view, 6b, ventral view.

Fig. 7 - *Haoceras xingyiense* n. gen. n. sp., paratype, GMPKU-P-3074 (ws2012-68-4), specimen with test, 7a, lateral view, 7b, ventral view.

Fig. 8 - *Haoceras xingyiense* n. gen. n. sp., paratype GMPKU-P-3078 (ws2012-88-1), phragmocone, 8a, lateral view, 8b, ventral view.

Fig. 9 - *Trachyceras* sp. ind., specimen GMPKU-P-3088 (ws2012-197-1).

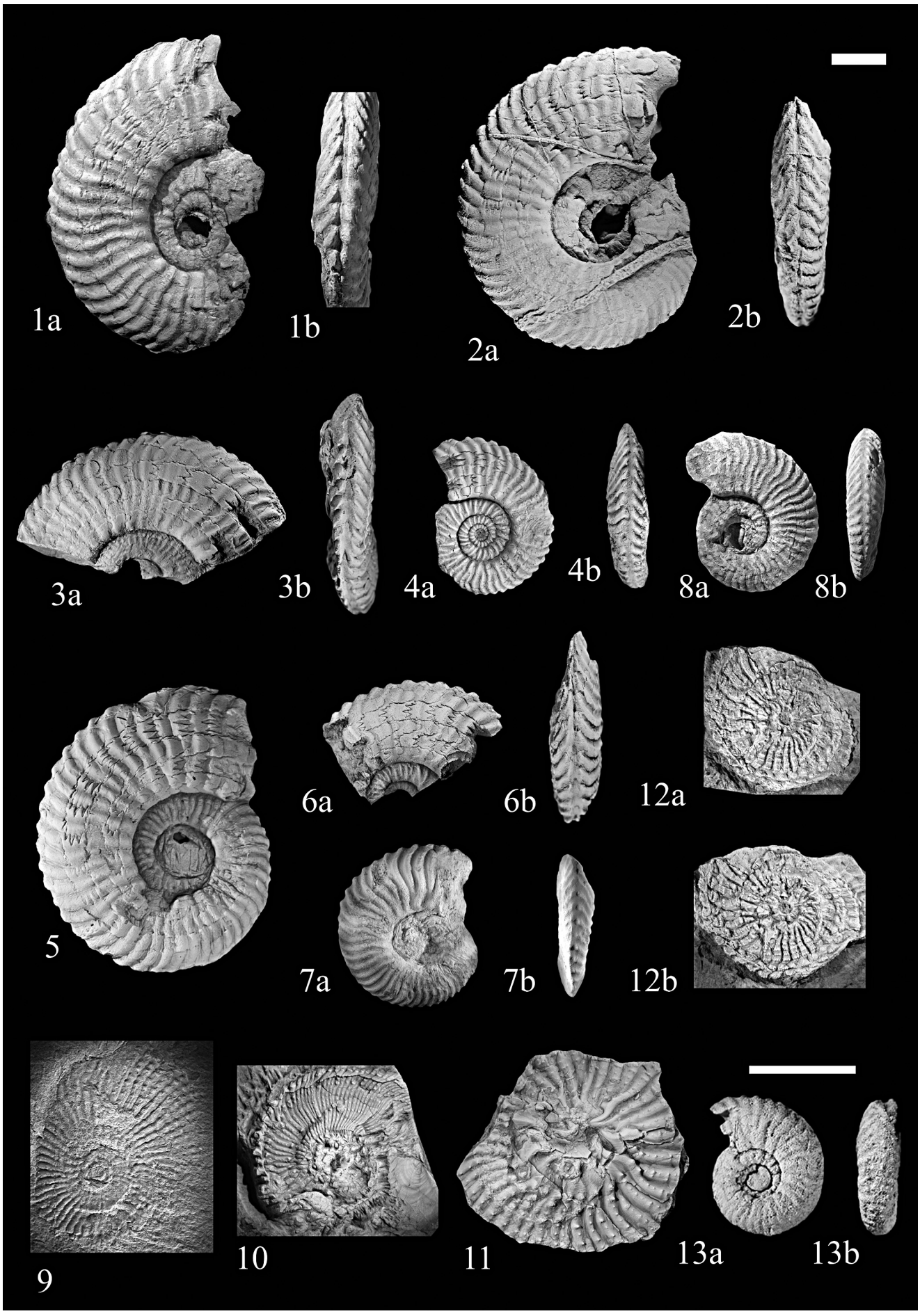
Fig. 10 - *Trachyceras* sp. ind., specimen GMPKU-P-3089 (ws2012-228-1).

Fig. 11 - *Trachyceras multitubertulatum* Hsü, 1940, specimen GMPKU-P-3090 (ws2012-238-1).

Fig. 12 - *Trachyceras multitubertulatum* Hsü, 1940, specimen GMPKU-P-3092 (ws2012-238-3), 12a, lateral view, 12b, same view but under different light.

Fig. 13 - *Clionitites* sp. ind., specimen GMPKU-P-3087 (ws2012-162-1), 13a, lateral view, 13b, ventral view.

All specimens whitened with ammonium chloride. Bar scale is 1 cm for all specimens. Long bar is for Fig. 13, short bar for all the other figures.


1a
1b
2a
2b
3a
3b
4a
4b
8a
8b
5
6a
6b
12a
7a
7b
12b
9
10
11
13a
13b

Lithostratigraphy		Wang, 1983	
		Zone	Faunal list
Falang Formation	Longchang Mb.	*Trachyceras multituberculatum*	*Trachyceras multituberculatum* (8)
	Laishike Mb.	*Protrachyceras deprati*	*Protrachyceras pseudoarchelaus* (2), *P. deprati* (9), *P. costulatum* (2), *P. mutabile* (2), *P. guizhouense* (2), *Proarcestes* sp.
	Zhuganpo Mb.	*Xenoprotrachyceras primum*	*Xenoprotrachyceras primum* (3), *Langdaiceras pateriformis* (2), ?*Bulogites langdaiensis* (3)

Fig. 9 - Bio-chronostratigraphic scale of the Ladinian/Carnian of Guizhou from Wang (1983). Taxonomic classification is as shown in original paper. The number of specimens classified by Wang is shown in brackets. Specimens are housed in the Nanjing Institute for Geology and Paleontology, Academia Sinica.

et al. (2003), who provided a range chart for the succession exposed at Guanling. This chart included conodonts and ammonoids documenting the *Trachyceras multituberculatum* Zone.

New zonation of the Zhuganpo Member at the Nimaigu section

Biostratigraphic analysis of the studied succession is obviously influenced by the quality of the available collection. As emphasized in the Taxonomc results chapter, two groups of taxa have been identified (Fig. 10). The first consists of taxa fully classified at the species level on the basis of well preserved specimens. The second group, whose importance is relatively minor, consists of taxa in open nomenclature or taxa whose attribution is uncertain, even at the genus level.

The faunas were mainly collected from the Zhuganpo Member (Fig. 10), but they do display some affinities with the *Xenoprotrachyceras primum* Zone of Wang (1983; Fig. 9). Two elements of the *X. primum* Zone have been identified, namely *Xenoprotrachyceras*, represented however, by only one specimen referred by confronta to *X. primum*, and *Yangites xingyiensis* that is congeneric with *Y. langdaiensis* (Wang, 1983). *Langdaiceras pateriformis* has not yet been found at Nimaigu.

Elements common to the *Protrachyceras deprati* Zone have not been found at Nimaigu, but the upper part of the section can be referred to the *Trachyceras multituberculatum* Zone because of the occurrence of the index species. In this general framework and taking into account the range chart (Fig. 10), we suggest the exclusion of the *X. primum* Zone, at least at the local scale and instead erect the discrete biostratigraphic subdivision, namely the *Haoceras xingyiense* biozone for the Nimaigu section (Fig. 10). This subdivision is independent from Wang's chronostratigraphy for the lower and middle part of the section.

• *Haoceras xingyiense* biozone. This biozone is here conceived as a range zone encompassing the interval from bed 57 to bed 88 of the Nimaigu section (Fig. 10). In addition to the zonal index ammonoid, faunal composition includes *Sinomeginoceras wangi* n. gen. n. sp., *S. xingyiense* n. sp., *Detoniceras* sp. A, *Yangites densicostatus* n. gen. n. sp. and *Xenoprotrachyceras* cf. *primum*. However, *S. wangi* n. sp. and *Y. densicostatus* n. sp. also occur above the *H. xingyiense* biozone. This biozone is correlative, at least in part, with the *X. primum* Zone of Wang (1983).

• *Trachyceras* beds. The genus *Trachyceras* is found below the FO of *T. multituberculatum*, in beds ranging from 197 to 228 (Fig. 10). This interval is herein referred to as an informal biostratigraphic unit, namely the *Trachyceras* beds, which requires additional work in order to be recognized as a formal biozone. Better preserved material is necessary to clarify the taxonomic position of this earliest *Trachyceras* that undoubtedly differs from *T. multituberculatum*.

• *Trachyceras multituberculatum* biozone. This range biozone, whose lower boundary is placed at bed 238 (Fig. 10), is based on the occurrence of *T. multituberculatum*, which serves as the index ammonoid. This taxon is also documented from several other localities in Guizhou.

The intervals below the *H. xingyiense* biozone (beds 26 to 56) and between the top of this biozone and the FO of *Trachyceras* (beds 89 to 196) are left unassigned because ammonoid occurrences are quite rare. Moreover, the few specimens thus far collected are in open nomenclature, and their attribution to ?*Parasturia*, *Ptychites* and *Detoniceras* is only tentative.

An alternative biostratigraphic subdivision for the Nimaigu section would utilize *Yangites densicostatus* as a marker of a range biozone. However, this option is considered unwise because *Y. densicostatus* is quite rare in the section, being represented by only three specimens. Moreover, even though the lower part of the range of *Y. densicostatus* includes a rich fauna, its upper part does not.

The much greater abundance of *H. xingyiense* and the relatively rich accompanying faunal assemblage makes this biozone potentially recognizable in other sections.

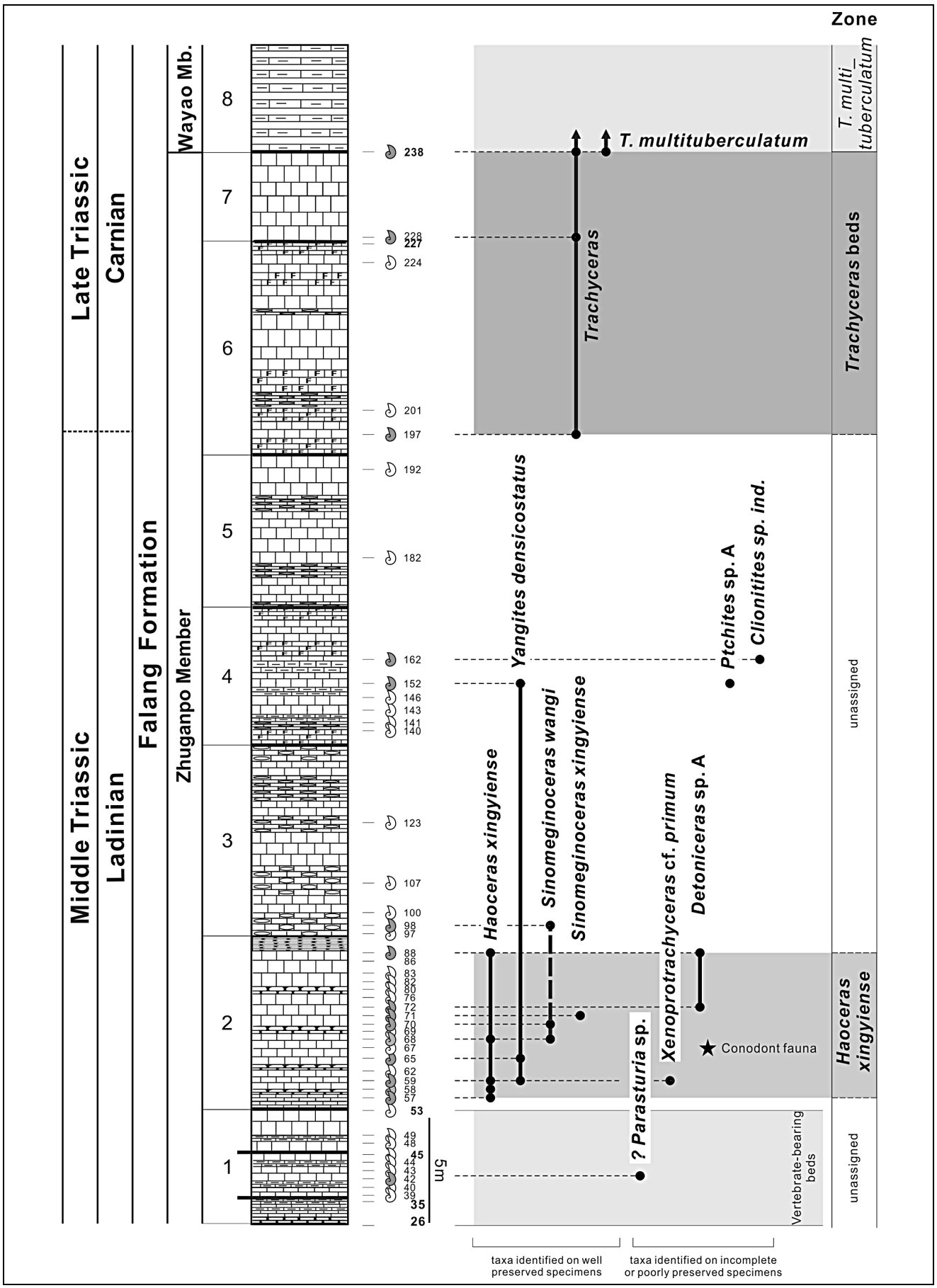


Fig. 10 - Ammonoid range chart and biostratigraphic classification of the Falang Formation at the Nimaigu section. Star shows position of the conodont fauna described by Wang et al. (1998).

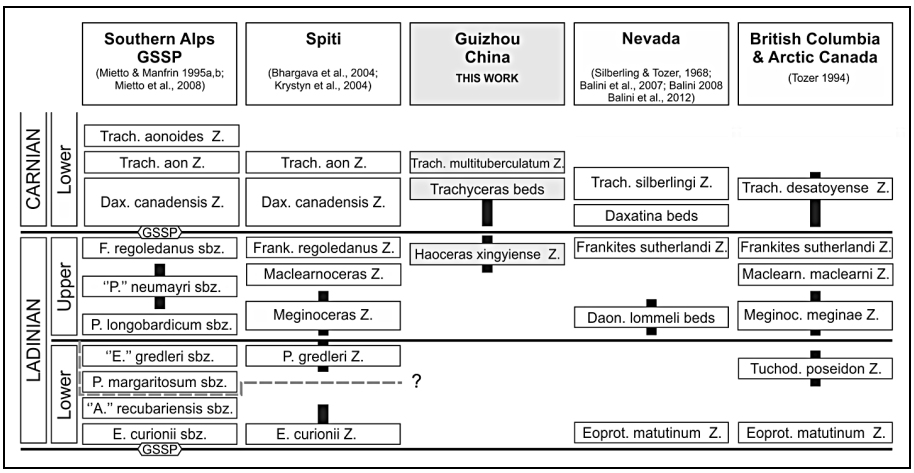


Fig. 11 - Correlation chart of the new local biostratigraphic scale with the Upper Ladinian-Lower Carnian ammonoid scales from the Tethys Realm and North America. The Lower/Upper Ladinian boundary in the Southern Alps (bold line) is based on Brack & Rieber (1993). The solution preferred by Mietto & Manfrin (1995a, b), represented by the gray dashed-line, is lower, with the boundary between the "*Anolcites*" *recubariensis* and *Protrachyceras margaritosum* subzones.

Correlation of the local biostratigraphy with Tethys and North America

A wealth of integrated Upper Ladinian/Lower Carnian bio-chronostratigraphic data published in the last 15 years has resulted from investigations of the Ladinian/Carnian Working Group of the Subcommission on Triassic Stratigraphy, aimed at the definition of the GSSP of the Carnian stage. These studies have significantly improved resolution of ammonoid chronostratigraphic scales from different regions (Fig. 11) and also greatly refined the regional correlation based on ammonoids, conodonts and daonellids. The abundance of recent, well-constrained data from Tethys and Panthalassa greatly facilitates discussion of the new biostratigraphical correlation proposed for the Nimaigu section, even though the significant number of endemic taxa places some limitations on its usefulness.

The Ladinian/Carnian boundary at Nimaigu

Our inveastigation at Nimaigu has shown that *Trachyceras multituberculatum* is not the earliest *Trachyceras* in Guizhou; instead, the earliest *Trachyceras* is documented in the underlying *Trachyceras* beds. Attribution of the *Trachyceras* beds to the Carnian is without doubt, since *Trachyceras* is an undisputed Carnian genus (Tozer 1967, 1981a, 1981b, 1994; Silberling & Tozer 1968; Urlichs 1974, 1977, 1994; Krystyn 1978; Mietto & Manfrin 1995a, 1995b; Gaetani 1995; Balini et al. 1998, 2001; Broglio Loriga et al. 1999; Balini & Jenks 2007; Mietto et al. 2008, 2012; Balini et al. 2012). It is worth noting that representatives of *Trachyceras* from the *Trachyceras* beds have a more simplified ornamentation with respect to that of *T. multituberculatum* and that a similar pattern of ornamentation can also be found in theTethyan *Trachyceras*. In the Tethyan successions, the most complex ornamentation is exhibited by *Trachyceras* taxa of the second Carnian zone (Aon Zone: *Trachyceras aon* with double pointed nodes on the shoulder [Urlichs 1994] and *Brotheotrachyceras* Urlichs, 1994), while those from the first Carnian zone (Canadensis Zone) never have double or multi-pointed nodes on the flanks. This similarity suggests correlation of the *Trachyceras multituberculatum* zone at Nimaigu with the Aon Zone of the Tethys realm (Fig. 11).

The report of the conodont *Paragondolella polygnathiformis* 3 m above the vertebrate-bearing interval (sample Xy14: Wang et al. [1998]) at Nimaigu is not very helpful for identification of the base of the Carnian, because the specimen figured by Wang et al. (pl 1, fig. 6) is not *P. polygnathiformis sensu strictu*, but, as reported in the caption, is a transition *P. polygnathiformis-P. nodosa*. This identification has been confirmed by A. Nicora (pers. comm., 2014). It is also worth mentioning that the FO of *P. polygnathiformis s.s.* is quite diachronous, being recorded in the lowermost part of the first Carnian zone at GSSP Prati di Stuores (Canadensis Zone: Mietto et al. 2008; 2012) and at South Canyon in Nevada (Balini et al. 2007; Orchard and Balini 2007; *Daxatina* beds in Balini et al. 2012), while it occurs within the Upper Ladinian Sutherlandi Zone in Spiti (Krystyn et al. 2004).

Correlation and age of the Haoceras xingyiense zone

This correlation is more complex and at present we can only hypothesize that the zone is probably correlative, at least in part, with the lower Sutherlandi Zone of North America (Fig. 11). This conjecture is based on a number of considerations discussed below, which are in part speculative.

1) A lack of definite Carnian ammonoids below the FO of *Trachyceras*. Aside from the new taxa, which thus far are endemic, the ammonoids collected below the *Trachyceras* beds are typical of the Ladinian, with the exception of *Clionitites*. This genus, which is more common in the Carnian, actually has its FO below the

Upper Ladinian in Nevada (Balini, 2008; pers. obs. MB).

2) Lack of ammonoids representative of the Upper Ladinian zones. The Zhuganpo Member at Nimaigu did not yield ammonoids representative of the three Upper Ladinian zones, namely the Meginae, Maclearni and Sutherlandi zones of the North American scale (Tozer 1967, 1994; Silberling & Tozer 1968; Fig. 11) that are also documented in the Tethyan successions (Mietto & Manfrin 1995a, 1995b; Bhargava et al. 2004; Krystyn et al. 2004; Mietto et al. 2008; Fig. 11).

3) Stratigraphic significance of *Detoniceras*, ?*Parasturia* and *Ptychites*. *Parasturia* and *Ptychites* have never been found in beds younger than Early Ladinian. However, the occurrence of these taxa at Nimaigu is based on the attribution of a few very poorly preserved specimens and this datum cannot be considered as reliable evidence of an Early Ladinian age for the *H. xingyiense* zone. On the contrary, *Detoniceras s.s.* is known from the Late Ladinian (Manfrin & Mietto 1991; Calabrese & Balini 1995; Balini et al. 2006).

4) The new genera *Haoceras* and *Sinomeginoceras*, which represent the bulk of ammonoid occurrences in the *H. xingyiense* zone, are morphologically very similar to *Meginoceras*, especially to its youngest representatives (see Systematic paleontology). However, the morphological similarity of these taxa does not imply that the *H. xingyiense* zone is coeval with the Meginae Zone of North America.

5) The occurrence of the transitional conodont *Paragondolella polygnathiformis – P. nodosa* from a sample 3 m above the vertebrate-bearing interval (Wang et al. 1998), i.e., within the *H. xingyiense* zone, suggests a possibly younger age, because this species has never been reported from beds older than the Sutherlandi Zone. This datum may suggest the Sutherlandi Zone as a possible age for the *H. xingyiense* zone.

6) If condonts are consistent with a correlation of the *Haoceras xingyiense* zone with the Sutherlandi Zone, then the lack of *Frankites* is quite unusual. *Frankites* ranges from the base of the Upper Ladinian Sutherlandi Zone (= Regoledanus Zone, Fig. 11) to the lower part of the Lower Carnian *Daxatina canadensis* Zone, and is one of the best markers for Late Ladinian zonations, being very common from the western Tethys to Tethys Himalaya and North America. *Frankites* is also facies-independent, having been documented in Hallstatt-like red limestones from the Northern Alps and Greece (e.g. Mojsisovics 1893; Krystyn 1983), in marls of the Wengen and San Cassiano formations in the Southern Alps (e.g. Mojsisovics 1882; Mietto & Manfrin 1995; Balini et al. 2000), in dark gray limestones of Tethys Himalaya and North America (e.g. Krystyn et al. 2004; Balini 2008), as well as in the siltstones and dark gray limestones of central Nevada (respectlively: Silberling & Tozer 1968: 36 and Waller & Stanley 2005; Balini et al. 2007 and Balini 2008). The apparent non-occurrence of *Frankites* in the Nimaigu section is herein interpreted to be due to paleobiogeographic reasons.

7) Reliability of *Xenoprotrachyceras primum* Wang, 1983 as a marker for the Lower Ladinian. Only one specimen of *Xenoprotrachyceras* has been found at Nimaigu, within the beds of the *H. xingyiense* zone. However, since the genus *Xenoprotrachyceras* and the species *X. primum* lack independent chronostratigraphic calibration, their original attribution to the Early Ladinian (Wang, 1983) is not reliable. Wang assigned *X. primum* (and the genus) to the Lower Ladinian because of its similarity to *Trachyceras reitzi* Boeckh, 1872. The morphological similarity of *X. primum* and *Reitziites reitzi* (Boeckh, 1872; revised by Brack & Rieber 1993) is great in terms of coiling, whorl section and ornamentation; however, their suture lines are very different. *Reitziites reitzi* has a ceratitic suture line (Brack & Rieber 1993, fig. 17e-f), while that of *X. primum* is ammonitic (Wang 1983; pers. obs. MB on the type, 2013). Moreover, the net result of the recent selection of the base Ladinian GSSP (cf. Brack et al. 2005) has been to move the Anisian/Ladinian boundary up slightly, such that the position of *Reitziites reitzi* is now restricted to the second to the highest zone of the Upper Anisian (Brack et al. 2005).

Conclusions

The systematic study of the ammonoids collected bed-by-bed in 2010-2013 from the Zhuganpo Member of the Falang Formation at Nimaigu (Xingyi) has resulted in the recognition of nine genera, including the newly described genera *Yangites*, *Haoceras* and *Sinomeginoceras.* These new genera and the genus *Trachyceras* are represented by five species, of which four are new. The identification of *Xenoprotrachyceras* cf. *primum*, notwithstanding its open nomenclature, is the first report of *Xenoprotrachyceras* from a bed-by-bed sampled section. The genera *Detoniceras*, *Ptychites* and *Clionitites* are left indeterminate at the species level, while the identification of *Parasturia* is uncertain even at the generic level. The faunal analyses lead to the following conclusions:

– Most of the faunas are new and endemic.

– The index ammonoids of the Ladinian zones (e.g. *Meginoceras*, *Maclearnoceras* and *Frankites*) are not represented in the collections.

– A new local biostratigraphic scale is proposed, consisting of the *Haoceras xingyiense* zone, *Trachyceras* beds and *Trachyceras multituberculatum* zone, in stratigraphic order.

– The chronostratigraphic assignment of the *Trachyceras* beds and the *T. multituberculatum* zone to the Lower Carnian is based on the premise that *Trachyceras* has always been regarded as an undisputed marker for the Carnian.

– Correlation and age of the *Haoceras xingyiense* zone. Due to the abundance of endemic taxa, the level of confidence in the correlation and age of the *Haoceras xingyiense* zone is low. Based on the stratigraphic position of the Carnian taxa and the re-examination of conodonts, we suggest that the new zone is at least in part equivalent to the lower part of the Sutherlandi Zone of the North American scale.

Based on the above data we assign a middle Late Ladinian age to the Xingyi Fossil-Lagerstätte recorded in a 5.6 m thick stratigraphic interval about 0.6 m below the base of the *Haoceras xingyiense* zone.

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