

# Middle Ordovician actinocerid nautiloids (Cephalopoda) from Xainza County, Tibet, western China, and their paleogeographic implications

Xiang Fang,<sup>1,2</sup> Tingen Chen,<sup>1</sup> Clive Burrett,<sup>3,4</sup> Yongsheng Wang,<sup>5</sup> Yonggui Qu,<sup>5</sup> Chunzi Zheng,<sup>5</sup> Yunbai Zhang,<sup>1</sup> Yuandong Zhang,<sup>1\*</sup> and Wenjie Li<sup>1,2</sup>

<sup>1</sup>CAS Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China (xfang@nigpas.ac.cn), (chenten40@163.com), (ybzhang@nigpas.ac.cn), (ydzhang@nigpas.ac.cn), (wjli@nigpas.ac.cn)

<sup>2</sup>University of Chinese Academy of Sciences, Beijing 100049, China

<sup>3</sup>School of Physical Sciences, University of Tasmania, Tasmania 7001, Australia (cfburrett@gmail.com)

<sup>4</sup>Palaeontological Research and Education Centre, Mahasarakham University, Mahasarakham 44150, Thailand

<sup>5</sup>Jilin Institute of Geological Survey, Changchun 130061, China (jlwangysh@163.com), (596089519@qq.com), (zheng\_czi@163.com)

Abstract.—Actinocerid nautiloids from the Lhasai Formation in the Xainza region are studied systematically for the first time. The nautiloids are identified as Middle Ordovician in age based on stratigraphic correlations with those from North China, Sibumasu, North Australia (northern Gondwana), and North America (Laurentia). A cluster analysis shows strong affinities between the actinocerid nautiloids of the Lhasa Terrane and those of the Himalaya, North China, and Sibumasu terranes. Our results support Middle Ordovician paleogeographic reconstructions that place North China rather than South China much closer to Australia. Nine species assigned to six genera of Meitanoceratidae, Wutinoceratidae, Armenoceratidae, Ormoceratidae, and Discoactinoceratidae are described in detail: *Pomphoceras nyalamense* (Chen, 1975), *Pomphoceras yaliense* (Chen, 1975), *Wutinoceras* cf. *W. foerstei* (Endo, 1930), *Mesowutinoceras giganteum* Chen in Chen and Zou, 1984, *Armenoceras tani* (Grabau, 1922), *Armenoceras teicherti* Endo, 1932, *Armenoceras xizangense* new species, *Deiroceras globosom* Zou and Shen in Chen and Zou, 1984, and *Discoactinoceras* cf. *D. multiplexum* Kobayashi, 1927.

UUID: http://zoobank.org/ba851fea-e107-4754-a0f4-a70744e325ab

### Introduction

Ordovician cephalopods of the Xainza region, North Tibet, were first reported by the Tibet Geological Bureau General Survey Team (1980) during mapping of the Shigatse geological map sheet. Subsequently, many Ordovician cephalopods from this region were described by Lai (1982a, b), Chen (1986, 1987), Li and Cheng (1988), and in a series of works by Cheng et al. (2005a, b, c, 2006). However, most of the recorded taxa were from the Upper Ordovician Keerduo and Gangmusang formations, which are both suggested as of Sandbian–Katian age by Xia (1983; Fig. 1.1), based on the outcrops mainly in the Xainza region. There is no conclusive evidence about the Middle Ordovician strata and the corresponding fossils in the Xainza area, northern Tibet (Cheng et al., 2004; Zhang et al., 2004).

We have recovered nine species of actinocerid nautiloids, including one new species, from the Lhasai Formation, Middle Ordovician in Lhasai, Xainza County, northern Tibet. This is the first detailed taxonomic description of Middle Ordovician nautiloids from Xainza, which allows for more detailed stratigraphic correlation and better paleogeographic assessments.

## **Geological setting**

The Xainza region is located in the northern part of the Lhasa Terrane, which is separated from the Himalaya Terrane by the Yarlung-Zangbo suture to the south and from the Qiangtang Terrane by the Bangon-Nujiang suture to the north (Fig. 1.2; Zhang et al., 2010). The Middle Ordovician Lhasai Formation was first introduced during the geological investigations by the Jilin Institute of Geological Survey (Zhang et al., 2003) in the Lhasai section, eastern Xiongmei town, in the sparsely populated northern part of Xainza County. The Ordovician in this section is represented, in ascending order, by the Middle Ordovician Lhasai Formation, the Middle to Upper Ordovician Keerduo and Gangmusang formations, and the overlying Silurian strata.

Among them, in the Lhasai Formation, abundant cephalopods, brachiopods, sponges, bryozoans, and conodonts are recorded (Qu et al., 2002, 2004; Zhang et al., 2003; Zheng, 2005), indicating a Middle Ordovician age. The unit is lithostratigraphically divided into three parts: (1) the lower part, consisting of limestone intercalated with some purple thinbedded, silty, micritic limestone, with abundant cephalopods; (2) the middle part, consisting of limestone intercalated with

<sup>\*</sup> Corresponding author



Figure 1. (1) Location of the studied area in North Tibet, western China, with the tectonic sutures bounding the Lhasa Terrane (base map after Qu et al., 2002; Xu et al., 2011). (2) Lithostratigraphic and biostratigraphic subdivisions of the Ordovician in the Xainza Region in Tibet, western China; lithostratigraphic and biostratigraphic data from Xia (1983) and National Commission of Stratigraphy of China (2014). (3) Locality of the Lhasai section in Xainza County.

yellow thin-bedded calcareous siltstone; and (3) the upper part, mainly consisting of bioclastic limestone, micritic limestone, and conglomeratic limestone.

#### Materials and methods

Most of the actinocerid specimens described herein were collected by some of the authors from the Lhasai section, which is located near Lhasai village, about 26 km east of Xiongmei town (31.2605°N, 89.1722°E to 31.2748°N, 89.1645°E), during the 2002 and 2012 investigations, which focused on the Middle Ordovician succession of the Xainza Region (Fig. 1.3).

All nautiloid shells are recrystallized and shell structures are poorly preserved. Due to poor preservation, only one specimen was found for each species. Most shells are slightly fragmented. All specimens were cut in median section, polished, and photographed with a Nikon D600 digital camera, Leica M125 microscope, and Leica DSC450C camera enhanced by Leica's LAS software. Our identifications are based mainly on the position and shape of the siphuncle, the types of the septa and septal neck, the details of the connecting rings, the shape of the segment, and the endosiphuncular canal system, following Teichert et al. (1964), Chao et al. (1965), Flower (1968), Frey (1995), Zhu and Li (1996), and Niko and Sone (2014). The siphuncle segment compression ratio (SCR) is an important term introduced by Frey (1995) and is defined as the ratio of the maximum diameter of the connecting rings to the length of camerae.

To investigate quantitatively the paleogeographic affinity of the actinocerid nautiloids, the occurrence (presence or absence) data of 24 nautiloid genera from nine terranes or regions (Fig. 2; Table 1) are compiled into a binary data set. Cluster analysis (CA) methods in the PAST version 3.15 software (Hammer et al., 2001) were adopted, using the Jaccard similarity coefficient (Jaccard, 1901a, b), which is commonly used in paleobiogeographic studies (e.g., Shi, 1993; Rong et al., 1995; Shen and Shi, 2000, 2004).

*Repository and institutional abbreviation.*—All specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP).

### Age of the actinocerid nautiloids of Lhasai Formation

The actinocerid nautiloids of Lhasai Formation are comparable to those from other Asian terranes (e.g., Qiangtang Terrane, Sibumasu Terrane, South and North China). According to the latest detailed restudy of the Ordovician Huaiyuan Epeirogeny in North China and adjacent regions, two distinct phases of the tectonic event are distinguished. The early phase was initiated from the Floian to early Darriwilian and is manifested by an extensive diachronous hiatus in the platform facies across North China (Zhen et al., 2016). According to a recent restudy of the conodonts from the Ordovician of North China, several stratigraphic units that were regarded as mainly of early Ordovician and Dapingian age, including the Zhuozishan, the Sandaokan, and the Majiagou formations, are revised as Darriwilian (late Middle Ordovician) (Wang et al., 2014a, b, 2016; Zhen et al., 2016).

Actinocerid nautiloids of the Lhasai Formation comprise nine species in six genera, including *Pomphoceras nyalamense* (Chen, 1975), *P. yaliense* (Chen, 1975), *Wutinoceras* cf.



**Figure 2.** Global paleogeographic distribution of actinocerid nautiloids in the Middle Ordovician: 1. Xainza region, North Tibet; 2. Nyalam, South Tibet; 3. Inner Mongolia, North China; 4. Liaoning, North China; 5. Guizhou, South China; 6. Shan Plateau, Myanmar; 7. Southern Thailand; 8. Langkawi Islands, Malaysia; 9. Queensland, North Australia; 10. Tasmania (Tas. for short in the figure), Australia. Base map of paleogeographic reconstruction is modified from Burrett et al. (2014). Light blue = relatively shallow platform and shelf seas; dark blue = relatively deep shelf seas; yellow = land or submarine highs.

**Table 1.** Occurrences (presence or absence) of actinocerid nautiloids in the Middle Ordovician. MYS = Malaysia (Kobayashi, 1958, 1959; Stait and Burrett, 1982); MMR = Myanmar (Niko and Sone, 2014); THA = Thailand (Brown et al., 1951; Kobayashi, 1958, 1959; Kobayashi and Hamada, 1964; Burton, 1974; Ingavat et al., 1975; Stait and Burrett, 1984); HIM = Himalaya (Chen, 1975; Chen, 1983, 1984); LHA = Lhasa (this paper); TAS = Tasmania (Teichert and Glenister, 1953; Stait, 1984); N AUS = North Australia (Teichert and Glenister, 1952; Wade, 1977); NC = North China (Chao et al., 1965; Chen and Zou, 1984; Zhu and Li, 1996); SC = South China (Yang, 1978, 1980).

Genus	MYS	MMR	THA	Himalaya	Lhasa	TAS	N AUS	NC	SC
Actinoceras	1	0	1	0	0	0	1	1	0
Adamsoceras	0	0	0	0	0	1	0	0	0
Armenoceras	1	1	1	1	1	0	1	1	0
Cyclonybyoceras	0	0	0	1	0	0	0	0	0
Discoactinoceras	0	0	0	0	1	0	0	1	0
Georgina	0	0	1	1	0	0	1	0	0
Hoeloceras	0	0	0	0	0	0	0	1	0
Hunjiangoceras	0	0	0	0	0	0	0	1	0
Meitanoceras	0	0	0	1	0	0	0	1	1
Mesaktoceras	0	0	0	0	0	0	1	0	0
Mesowutinoceras	0	0	0	0	1	0	0	1	0
Nybyoceras	0	0	0	0	0	1	0	1	0
Órdosoceras	0	1	0	1	0	0	0	1	0
Ormoceras	1	0	1	1	1	1	1	1	1
Orthonybyoceras	0	0	0	0	0	1	0	0	0
Pararmenoceras	0	0	0	0	0	0	0	1	0
Paratunkuskoceras	0	1	0	0	0	0	0	1	0
Parormoceras	0	0	0	1	1	0	0	1	0
Polydesmia	0	0	0	0	0	0	0	1	0
Pomphoceras	0	0	0	1	0	0	0	1	0
Sactoceras	0	0	0	0	0	0	0	1	0
Selkirkoceras	0	0	1	0	0	0	0	1	0
Tunkuskoceras	0	0	0	0	0	0	0	1	0
Wutinoceras	1	1	1	1	1	1	0	0	0

W. foerstei (Endo, 1930), Mesowutinoceras cf. M. giganteum Chen in Chen and Zou, 1984, Armenoceras tani (Grabau, 1922), A. teicherti Endo, 1932, A. xizangense new species, Deiroceras globosom Zou and Shen in Chen and Zou, 1984, and Discoactinoceras cf. D. multiplexum Kobayashi, 1927. They all

Discoactinoceras cf. D. multiplexum Kobayashi, 1927. They all belong to the order Actinocerida. A majority of the species from Xainza are diagnostic of the Darriwilian (Middle Ordovician) according to a comparison with those from North China. For example, *Pomphoceras* is found in the Zhuozishan Formation of the Ordos Region (Chen and Zou, 1984), the Majiagou Formation of southern Jilin, North China (Zhu and Li, 1996), and the Chiatsun Formation of Nyalam, Himalaya Terrane (Chen, 1975), which are all restricted to the Darriwilian. Wutinoceras was originally described from the Majiagou Formation (Wuting Formation; Darriwilian) in Benxi (Penhis-hu) and Nanpiao, Liaoning, North China (Endo, 1930, 1932; Kobayashi and Matumoto, 1942), and has also been recorded in the Kakit Bukit Formation (partly Darriwilian) in the Langkawi Islands, Malaysia (Stait and Burrett, 1982; Stait et al., 1987), and in the Whiterock (Darrwilian) of North America (Flower, 1968). Armenoceras is very common in the Middle Ordovician of North China (Endo, 1932; Chao et al., 1965; Zhu and Li, 1996) and was discovered in the Thung Song Group and the Tha Manao Formation of Thailand (Kobayashi, 1958, 1959; Stait and Burrett, 1984), the Whiterock part of the Kakit Bukit Formation of Malaysia (Kobayashi, 1958, 1959; Stait and Burrett, 1984; Stait et al., 1987), the Wunbye Formation of Myanmar (Niko and Sone, 2014), the Middle Ordovician in Queensland and Tasmania, Australia (Whitehouse, 1936; Teichert and Glenister, 1952), and in North America, Greenland, and Siberia, Russia (Balashov, 1962). Therefore, the age of the actinocerid nautiloids from the Lhasai Formation of Xainza is Middle Ordovician, and most probably Darriwilian.

### **Paleobiogeographic implications**

The Xainza region is tectonically located close to the northern margin of the Lhasa Terrane, which was part of the northeastern peri-Gondwana region during the Early–Middle Ordovician (Metcalfe, 2001; Burrett et al., 2014). The Middle Ordovician nautiloid faunas of the Lhasa Terrane and some other Chinese terranes (e.g., the Himalaya and North China terranes) are characteristically dominated by actinocerids (e.g., Chen, 1975; Chen and Zou, 1984) and indicate that the nautiloids of these regions have a strong affinity. Several global Darriwilian cephalopod biogeographic regions were identified, including Laurentian, Rheic, East Asian (i.e., southern Tibet, Tarim, South and North China), and Siberia regions (Kröger, 2013). Drawing on specimens from the Xainza region, the detailed paleogeographic reconstruction of northeastern peri-Gondwana during the Middle Ordovician may now be firmly established.

Pomphoceras is a key element of the Zhuozishan Formation in Inner Mongolia (North China) and in the Chiatsun Formation in Nyalam (Himalaya Terrane). In addition, Pomphoceras nyalamense is present in both the Lhasa and Himalaya terranes (Chen, 1975), and Pomphoceras valiense is found in the North China, Lhasa, and Himalaya terranes (Chen, 1975; Chen and Zou, 1984). Pomphoceras resembles Ordosoceras in external form, inner construction, and systematic phylogeny; the latter is the Middle Ordovician index fossil of North China (Chang, 1959; Chen and Zou, 1984). Ordosoceras is also recorded from Myanmar (Sibumasu Terrane; Niko and Sone, 2014), which indicates that the actinocerids from Sibumasu have close affinities with those of North China. Discoactinoceras is recorded in Inner Mongolia (Zou, 1981) and Liaoning (Kobayashi, 1978), both from North China, so its occurrence in the Xainza Region of Tibet also supports a close relationship of the two terranes. Wutinoceras and Armenoceras are widespread genera and are





Figure 3. Cluster analysis of the Middle Ordovician actinocerid nautiloids of peri-Gondwana using PAST (Hammer et al., 2001) based on the Jaccard similarity coefficient.

common in the Himalaya Terrane (Chen, 1975), Sibumasu (Stait and Burrett, 1982; Niko and Sone, 2014), Australia (Stait, 1984), and North America (Flower, 1968). Some common elements of the actinocerids from Xainza are shared with North Australia (Teichert and Glenister, 1952; Wade, 1977), but few with Tasmania (Stait, 1984). Nevertheless, there are few forms shared with Lhasa and South China during the Middle Ordovician (Chen and Liu, 1976; Yang, 1978, 1980). Among them, the dominant form *Meitanoceras* is an endemic genus, which is only reported in the Middle Ordovician Meitan Formation from Chongqing, Guizhou, and Yunnan, South China. *Ormoceras* is a widespread genus, distributed in most parts of the world during this period. However, in general, there are few resemblances between the nautiloids of South and North China (Yang, 1980).

The Middle Ordovician actinocerids of the Lhasa Terrane show close affinity with those of the Himalaya Terrane, North China, and the Sibumasu Terrane (Fig. 3). The similarities of the Middle Ordovician actinocerid nautiloids can be interpreted as reflecting similar paleogeographic situations in low paleolatitude; all these terranes are located in a northern tropical region. This also supports the Middle Ordovician reconstructions that place North China close to Australia and place South China close to the Middle East (e.g., Burrett and Stait, 1987; Burrett et al., 1990, 2014; Metcalfe, 2011) rather than the reconstructions that have these positions reversed (e.g., PaleoGIS 4.0 for ArcGIS, 2011). The affinities of nautiloids from these regions have a similar paleobiogeographic relationship to those of other marine organisms. For example, brachiopod affinities between Tibet and Sibumasu have been recognized from 230 genera of rhynchonelliform brachiopods from 65 localities during the Dapingian and Darriwilian (Harper et al., 2013).

### Systematic paleontology

Class Cephalopoda Cuvier, 1797 Subclass Nautiloidea Agassiz, 1847

### Order Actinocerida Teichert, 1933 Family Meitanoceratidae Kobayashi, 1977

Genus Pomphoceras Zou and Shen in Chen and Zou, 1984

*Type species.—Pomphoceras wuhaiense* Zou and Shen in Chen and Zou, 1984

Pomphoceras nyalamense (Chen, 1975) Figures 4.3, 5.4–5.6

1975 Ordosoceras nyalamense Chen, p. 272, text fig. 1, pl. 1, figs. 14, 15.

*Occurrence.*—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

Description.—The orthocone is composed of nine camerae. It is about 47 mm in length and 38 mm in width, with a large expansion angle of 28.6°; conch cross section is dorsoventrally slightly depressed; external shell wall is not preserved. Septal curvature and cameral length are moderate; there are seven to eight camerae within the length of the corresponding lateral conch diameter; siphuncle is large, probably central in position. Siphuncular wall consists of cyrtochoanitic septal necks and thin connecting rings. Diameter of septal foramina is probably 4.2 mm. Septal necks are long and straight and brims are recumbent. Lengths of necks and brims are 1.8 mm and 0.8 mm, respectively. Maximum diameter of connecting rings is 11.6 mm, while the corresponding conch diameter is 37.8 mm. The anteriors of the connecting rings are curved and one-third part of the posterior is inflated and then progresses straight down obliquely; adnation area is narrow. SCR is 2.2. Cameral deposits well developed as episeptal-mural and hyposeptal deposits. The endosiphuncular canal system consists of a large central canal, radial canals, and perispatium. Central canal is probably 3.4 mm in diameter and distal ends of the radial canals are nearly horizontal.

*Material.*—An incomplete orthocone cut and polished in median section. NIGP166262.

*Remarks.*—According to Chen and Zou (1984), the conch of the genus *Pomphoceras* is slightly curved adapically, circular in cross section; siphuncle is small, central or subcentral. The segment shape of *Pomphoceras* is similar to that of *Meitanoceras* and *Ordosoceras*, but differs from *Meitanoceras* in having small septal foramina and from *Ordosoceras* in that its radial canals seem to be straight and directly transverse.

*Pomphoceras nyalamense* is similar to the type species of *Pomphoceras, P. wuhaiense* Zou and Shen in Chen and Zou (1984, p. 73, text fig. 23, pl. 15, figs. 3, 4) from Inner Mongolia, in its general siphuncular shape and central position of the siphuncle, but differs in that the former has a larger expansion rate.

Pomphoceras yaliense (Chen, 1975) Figures 4.1, 5.7–5.9

- 1975 Ordosoceras yaliense Chen, p. 274, pl. 1, figs. 5, 6.
- 1984 *Pomphoceras yaliense*; Chen and Zou, p. 74, pl. 15, fig. 5, pl. 19, fig. 8.



Figure 4. Illustration of siphuncular segments of actinocerid nautiloids from Lhasai Formation in Xainza, Tibet, showing the characteristics of different species: (1) *Pomphoceras yaliense* (Chen, 1975), NIGP166263 (P25Hs-10-13-1); (2) *Wutinoceras* cf. W. foerstei (Endo, 1930), NIGP166261 (qD2226-b1); (3) *Pomphoceras nyalamense* (Chen, 1975), NIGP166262 (PM4-9-DH6); (4) *Armenoceras tani* (Grabau, 1922), NIGP166268 (qD0274-b1); (5) *Armenoceras xizangense* n. sp., NIGP166267 (PM4-9-DH3); (6) *Armenoceras teicherti* Endo, 1932, NIGP166269 (PM4-9-DH4); (7) *Deiroceras globosom* Zou and Shen in Chen and Zou, 1984, NIGP166264 (P25Hs-9-1); (8) *Mesowutinoceras giganteum* Chen in Chen and Zou, 1984, NIGP166266 (6283-11); (9) *Discoactinoceras cic. D. multiplexum* Kobayashi, 1927, NIGP166265 (P25Hs-16-4). (1-3, 6, 8) Scale bars = 5 mm; (4, 5) scale bars = 1 mm.

*Occurrence*.—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

*Description.*—An orthocone with 16 camerae is approximately 48.5 mm in length and 40.5 mm in width, with a high expansion rate and a dorsoventrally circular cross section. External shell wall is not available. Septa are curved and cameral length is moderate. There are 14 camerae in length of corresponding lateral conch diameter. Siphuncle is relatively large, central in position. Siphuncular wall consists of cyrtochoanitic septal necks and thin

connecting rings. Diameters of septal foramina range from 3.2 to 3.8 mm. Septal necks are long and straight and brims are recumbent. The neck and brim length are 0.9–1.1 mm and 0.5–0.7 mm, respectively. The maximum diameters of connecting rings are 8.3–9.5 mm, which is approximately one-third of the corresponding conch diameters; the anterior of connecting rings are curved and one-third part of the posterior is inflated and then straight down obliquely. SCR is large and ranges from 3.1 to 3.5. Cameral deposits are well developed as episeptal-mural and hyposeptal deposits. The endosiphuncular canal system consists of a large central canal, radial canals, and perispatium. Central canal



Figure 5. Photographs of *Wutinoceras* and *Pomphoceras* species from the Lhasai Formation in Xainza, Tibet. (1–3) *Wutinoceras* cf. *W. foerstei* (Endo, 1930), NIGP166261 (qD2226-b1); (1) longitudinal polished section, side view; (2) general siphuncle shape and endosiphuncular deposits; (3) details of septal necks, connecting rings, and cameral deposits. (4–6) *Pomphoceras nyalamense* (Chen, 1975), NIGP166262 (PM4-9-DH6); (4) longitudinal polished section, side view; (5) general siphuncle shape, vascular system, and endosiphuncular deposits; (6) details of septal necks, connecting rings, and radial canals. (7–9) *Pomphoceras yaliense* (Chen, 1975), NIGP166262 (PM4-9-DH6); (4) longitudinal polished section, side view; (5) general siphuncle shape, vascular system, and endosiphuncular deposits; (6) details of septal necks, connecting rings; (8) general siphuncle shape, vascular system, and endosiphuncular deposits; (7–9) *Pomphoceras yaliense* (Chen, 1975), NIGP166262 (PM4-9-DH6); (4) longitudinal polished section, side view; (7–9) *Pomphoceras yaliense* (Chen, 1975), NIGP166263 (P25Hs-10-13-1); (7) details of septal necks and connecting rings; (8) general siphuncle shape, vascular system, and endosiphuncular deposits; (9) longitudinal polished section, side view; (1, 4, 9) Scale bars = 1 cm; (2, 3, 5–8) scale bars = 1 mm.

diameters are probably 0.7–2.5 mm; they are located centrally in the siphuncle. Distal ends of radial canals are nearly horizontal.

*Material.*—An incomplete orthocone cut and polished in median section. NIGP166263. *Remarks.*—Chen (1975) erected *Ordosoceras yaliense* on the basis of an incomplete specimen from the Chiatsun Formation of Nyalam, southern Tibet. Its small septal foramina and straight and directly transverse radial canals indicate this species should be placed in the genus *Pomphoceras* (Chen and Zou, 1984).

*P. yaliense* has shorter septal necks and denser camerae than other species of *Pomphoceras*.

Family Wutinoceratidae Shimizu and Obata, 1936 emend Flower, 1968 Genus *Wutinoceras* Shimizu and Obata, 1936

Type species.—Nybyoceras foerstei Endo, 1930

Wutinoceras cf. W. foerstei (Endo, 1930) Figures 4.2, 5.1–5.3

- 1930 Nybyoceras foerstei Endo, p. 298, pl. 60, figs. 1a-c.
- 1932 *Nybyoceras foerstei*; Endo, p. 79, pl. 25, figs. 3–5, pl. 26, figs. 9, 10.
- 1933 Nybyoceras foerstei; Teichert, p. 145, pl. 10, figs. 9, 10.
- 1936 Wutinoceras foerstei; Shimizu and Obata, p. 263.
- 1957 *Nybyoceras foerstei*; Yü and Chao, p. 233, pl. 128, figs. 9, 10.
- 1965 Wutinoceras foerstei; Chao et al., p. 62, pl. 15, figs. 1, 2.

*Occurrence.*—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

Description.—Specimen NIGP166261 is a 101 mm long fragment of an incomplete straight chamber, 65 mm in diameter, with conch cross section nearly circular. External shell wall is not preserved. There are 4.8 camerae in the length of the corresponding conch. The siphuncle is ventral in position. The siphuncle wall consists of long recumbent cyrtochoanitic septal necks and thick connecting rings. The ratios of maximum diameter of connecting ring per corresponding conch diameter are about 0.36. SCR ranges from 2.2 to 2.9. The diameter of the septal foramina is 4.6 mm. The brims are short, 0.4 mm in length, and septal necks are 0.8 mm in length. The segments connect with the bottom of the septa on the dorsal side and connect with the top of the septa on the ventral side. Cameral deposits are better developed at the episeptal-mural and hyposeptal positions in the anterior. Siphuncular deposits developed in the central canal. The central canal is probably 2.0 mm in diameter. Distal ends of radial canals are nearly horizontal with perispatial deposits.

*Material.*—An incomplete orthocone cut and polished in median section. NIGP166261.

*Remarks.*—The external construction, conch shape, and siphuncular characteristics of this specimen are the same as those of the type material of *Wutinoceras foerstei* (Endo, 1930), but this specimen has the longer septal necks and narrower brim, which may be the result of bad cutting and polishing. Consequently, this specimen has been identified as *Wutinoceras* cf. *W. foerstei* (Endo, 1930). The species is most similar to *Wutinoceras lui* Chang, 1959 with regard to the position and construction of the siphuncle, except that the segments of *W. lui* are not in contact with the top of the septa on the ventral side. *W. remotum* Chen, 1975 has sparser camerae with 3–3.5 camerae in the length of the corresponding conch and

segments are not in contact with the bottom of the septa on the dorsal side. *W. moeseini* (Thein, 1968) has a subventral siphuncle and longer brims, which differs from *W. foerstei*. *W. robustum* (Kobayashi and Matumoto, 1942) from the Darriwllian of Malaysia (Stait and Burrett,1982) was assigned to *W. moeseini* (see Niko and Sone, 2014) because the SCR of this specimen is approximately 2.0, which is smaller than that of *W. foerstei*.

Genus Mesowutinoceras Chen, 1976

Type species.—Mesowutinoceras discoides Chen, 1976

Mesowutinoceras giganteum Chen in Chen and Zou, 1984 Figures 4.8, 6.6

1984 *Mesowutinoceras giganteum* Chen in Chen and Zou, p. 75, text-fig. 24, pl. 5, fig. 3, pl. 6, figs. 13, 14.

*Occurrence.*—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

*Description.*—A large orthoconic fragment is available that is 29 mm in length and 20 mm in width, with only its dorsal side preserved. Siphuncle is subcentral in position. Siphuncular wall consists of long recumbent cyrtochoanitic septal necks and thick connecting rings. Brims are relatively long and adnation area is broad. Ratios of maximum diameter of connecting ring per corresponding conch diameter are about 0.48; segment is ellipsoid. Cameral deposits weakly developed at episeptal and hyposeptal positions. Siphuncular deposits are filling siphuncle. Central canal is unknown and perpendicular to radial canal. Distal ends of radial canals are anastomosing with perispatium near the most inflated portions of connecting rings.

*Material.*—A large orthocone cut and polished in median section. NIGP166266.

*Remarks.*—This specimen is very similar to *M. giganteum* described by Chen in Chen and Zou (1984) from the Ordos area because of its large size, subcentral siphuncle position, ellipsoidal segment, and recumbent septal necks, except that only the dorsal side of the specimen studied herein is preserved. This species differs from the type species *M. discoides* (Chen, 1976) from the Shandong area in being larger and having a wider body size and wider segments.

Family Armenoceratidae Troedsson, 1926 Genus Armenoceras Foerste, 1924

Type species.—Actinoceras hearsti Parks, 1913.

Armenoceras tani (Grabau, 1922) Figures 4.4, 7.5, 7.7, 7.8

- 1922 Actinoceras tani Grabau, p. 80, pl. 7, figs. 4–7.
- 1932 Armenoceras hatai Endo, p. 86, pl. 18, figs. 1–3.
- 1932 Armenoceras tani; Endo, p. 99, pl. 21, fig. 7, pl. 14, fig. 2, pl. 40, fig. 3.



Figure 6. Photographs of *Deiroceras*, *Discoactinoceras*, and *Mesowutinoceras* from the Lhasai Formation in Xainza, Tibet. (1–3) *Deiroceras globosom* Zou and Shen in Chen and Zou, 1984, NIGP166264 (P25Hs-9-1); (1) longitudinal polished section, side view; (2) general siphuncle shape, central canals, cameral deposits, and endosiphuncular deposits; (3) details of septal necks and connecting rings. (4, 5) *Discoactinoceras* cf. *D. multiplexum* Kobayashi, 1927, NIGP166265 (P25Hs-16-4); (4) longitudinal polished section, side view; (5) details of septal necks and connecting rings. (6) *Mesowutinoceras giganteum* Chen in Chen and Zou, 1984, NIGP166266 (6283-11), longitudinal polished section, side view. (1, 4, 6) Scale bars = 1 cm; (2, 3, 5) scale bars = 1 mm.

- 1957 Armenoceras tani; Yü and Chao, p. 232, pl. 127, figs. 8, 9.
- 1959 Armenoceras cf. A. tani; Chang, p. 265, pl. 1, fig. 4, pl. 3, figs. 2, 3.
- 1965 *Armenoceras tani*; Chao et al., p. 66, pl. 15, figs. 13, 14, pl. 18, figs. 5, 6.

*Occurrence.*—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

*Description.*—Longiconic orthocone with gradual shell expansion and dorsoventrally depressed cross section. It is a phragmocone 98.1 mm in length and 48 mm in lateral diameter. External wall and body chamber are not preserved. There are nearly 8–9 camerae per corresponding lateral conch diameter. Siphuncle is large and subcentral in position. The diameters of

foramina range from 5.6 to 7.1 mm at lateral conch diameter 38.2 to 4.79 mm. Septal necks are recumbent cyrtochoanitic and connecting rings are thick. SCR is approximately 2.4–2.6. The ratios of diameters of connecting rings to corresponding conch diameters are about 0.3. Brims are relatively long at 1.6 mm with 1.3 mm septal necks. Connecting rings show strong inflation with a very broad adnation area. Cameral deposits not well developed; siphuncle is filled with siphuncular deposits except for the vascular system, which is differentiated into central canals, radial canals, and perispatium.

*Material.*—A longiconic orthocone cut and polished in median section. NIGP166268.

*Remarks.*—*Armenoceras tani* (Endo, 1932) appears similar to *A. myanmarense* Niko and Sone (2014) from the Shan Plateau, Myanmar, but the former differs in having more depressed segments

Figure 7. Photographs of Armenoceras from the Lhasai Formation in Xainza, Tibet. (1–4) Armenoceras xizangense n. sp., holotype NIGP166267 (PM4-9-DH3); (1) longitudinal polished section, side view; (2, 3) details of septal necks; (4) general siphuncle shape, vascular system, and endosiphuncular deposits. (5, 7, 8) Armenoceras tani (Grabau, 1922), NIGP166268 (qD0274-b1); (5) longitudinally cut and polished section, side view; (7) general siphuncle shape, vascular system, and endosiphuncular deposits. (6, 9, 10) Armenoceras teicherti Endo, 1932, NIGP166269 (PM4-9-DH4); (6) longitudinal polished section, side view; (9) details of septal necks. (6, 9, 10) Armenoceras teicherti Endo, 1932, NIGP166269 (PM4-9-DH4); (6) longitudinal polished section, side view; (9) details of septal necks and connecting rings; (10) general siphuncle shape, vascular system, and endosiphuncular deposits. (1, 5, 6) Scale bars = 1 cm; (2–4, 7–9) scale bars = 1 mm.



and a narrower siphuncle, which is one-third of the corresponding conch diameter. *A. manchurense* Kobayashi (1927) from Liaoning area is similar to *A. tani* except for the large siphuncle size and complex cameral deposits. *A. tani* shares several characteristics with *A. coulingi* (Grabau, 1922) from Shandong area (e.g., siphuncle diameter, cameral density, and septal concavity), but *A. tani* has a subcentral siphuncle and more-depressed siphuncular segments.

### Armenoceras teicherti Endo, 1932 Figures 4.6, 7.6, 7.9, 7.10

- 1932 Armenoceras teicherti Endo, p. 89, pl. 19, fig. 1, pl. 40, fig. 6.
- 1965 Armenoceras teicherti; Chao et al., p. 67, pl. 16, fig. 8.

*Occurrence.*—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

Description.-Specimen NIGP166269 is an almost complete orthoconic phragmocone with circular cross section; it is 67 mm in length and 24 mm at maximum lateral diameter within 29 camerae. It has a moderate expansion rate, with 11° in apical part. External features and body chamber are not preserved. There are 6, 8, and 10 camerae of corresponding conch diameter in the apical, middle, and adoral parts, respectively. The siphuncle is central in position. The siphuncular wall consists of recumbent cyrtochoanitic septal necks and thin connecting rings. Ratios of maximum diameter of connecting ring to corresponding lateral conch diameter are about 0.3. Siphuncular segment is discoidal and SCR is 1.8-2.2. Septal necks are 0.5 mm in length where brims are 0.8 mm and adnation area is broad. Cameral deposits are well developed in episeptal-mural and hyposeptal positions. Siphuncle is filled with endosiphuncular deposits. The vascular system is unknown.

*Material.*—A complete orthocone cut and polished in median section. NIGP166269.

*Remarks.*—*Armenoceras tani* (Grabau, 1922) is most similar to *A. teicherti*, but differs in having a depressed circular cross section and a subcentral siphuncle. *A. coulingi* (Grabau, 1922) has a larger body size than *A. teicherti*. *A. concavum* (Endo, 1932) is different from *A. teicherti* in having higher camerae and smaller SCR.

### Armenoceras xizangense new species Figures 4.5, 7.1–7.4

*Holotype*.—Holotype NIGP166267 (A complete orthocone cut and polished in median section).

*Diagnosis.*—Large siphuncle, occupying two-thirds of the corresponding later conch diameter, small SCR of approximately 4.

*Occurrence*.—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

Description.—A large, longiconic orthocone with gradual shell expansion and dorsoventrally depressed cross section is available for study. Phragmocone is 101 mm in length and 37.2 mm in lateral conch diameter. External wall and body chamber are not preserved. There are 3.6-4.5 camerae per corresponding lateral diameter. Siphuncle is large and subcentral in position. The ratio of lateral diameter to length is 3.5. The siphuncular wall consists of recumbent cyrtochoanitic septal necks and thin connecting rings. Diameters of septal foramina are 7.5 and 9.3 mm at lateral diameters of 28.7 and 32.3 mm, respectively, where maximum diameters of connecting rings are 16.8 and 21 mm. Ratios of maximum diameter of connecting rings to corresponding lateral conch diameter are about 0.67. SCR is 2.2-2.3. Brims are relatively long, 1.7 mm in length where septal neck is 0.9 mm and adnation area is broad. Cameral deposits well developed in episeptal-mural and hyposeptal positions. Siphuncle is filled with deposits except for the vascular system. Radial canals are perpendicular to central canal. Distal ends of radial canals anastomosing with perispatium.

*Etymology.*—The species name '*xizangense*' is in reference to the origin of the holotype, Tibet, also called 'Xizang' in Chinese.

*Remarks.*—This new species shares several characteristics with *A. teicherti* and *A. submarginale* (Grabau, 1922), for example, the moderate expansion and large siphuncle, but *A. teicherti* has a circular cross section and *A. submarginale* has a submarginal siphuncle, which distinguish them from *A. xizangense*. *A. xizangense* is most similar to *A. magnitubulatum* Endo (1932) with its large siphuncle size, but *A. xizangense* has a wider siphuncle occupying two-thirds of the lateral conch diameter rather than three-fifths as in *A. magnitubulatum*. *A. magnitubulatum* also has larger foramina and endocones. *A. xizangense* has 3.6–4.5 camerae per corresponding lateral diameter, less than the five camerae of *A. centrale* (Kobayashi and Matumoto, 1942), and *A. centrale* has a smaller siphuncle, which is less than one-half of the lateral conch.

Family Ormoceratidae Saemann, 1853 Genus *Deiroceras* Hyatt, 1884

Type species.—Orthoceras python Billings, 1857

Deiroceras globosom Zou and Shen in Chen and Zou, 1984 Figures 4.7, 6.1–6.3

1984 *Deiroceras globosum* Zou and Shen in Chen and Zou, p. 77, pl. 13, figs. 14, 15.

*Occurrence.*—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

*Description.*—Specimen NIGP166264 is a longiconic orthocone with subcircular cross section; it is 31 mm in length and 11 mm in lateral conch diameter. It has moderate expansion, with  $9^{\circ}$  angle in apical part. External shell wall and body chamber are not well preserved. There are 3–4 camerae per corresponding lateral conch diameter. The concavity is nearly equal to the length of one camera. Siphuncle is subcentral in position. Ratios of maximum diameters of connecting rings to corresponding lateral conch diameter are 0.26. Siphuncular wall consists of short, recumbent cyrtochoanitic septal necks and thick connecting rings. Septal foramina are 0.7-0.9 mm. Septal necks are comparatively short and brims are weakly recumbent. Connecting rings are weakly inflated in the anterior part of each siphuncle segment. Siphuncular segment is gently rounded, with SCR approximately 0.8. Cameral deposits well developed as episeptal-mural and hyposeptal deposits in ventral side and as episeptal deposits on dorsal side. Siphuncular deposits well developed. Central canal is straight and weakly subdorsal; notches developed in the endosiphuncular deposits toward the posterior of the upper of the siphuncular segments, indicating the radial canals are better developed adoral to the septal foramina rather than apically.

*Material.*—A longiconic orthocone cut and polished in median section. NIGP166264.

*Remarks.*—According to Teichert et al. (1964) and Dzik (1984), *Deiroceras* is most similar to *Ormoceras* except for the siphuncular segment shape, and *Deiroceras* has elongate connecting rings that are longer than wide.

This specimen has several similarities with the type specimen described by Zou and Shen (in Chen and Zou, 1984) from Inner Mongolia, such as 3–4 camerae per corresponding lateral conch diameter, the concavity equal to one camerae length, and moderate siphuncle size.

Family Discoactinoceratidae Kobayashi, 1978 Genus Discoactinoceras Kobayashi, 1927

Type species.—Discoactinoceras multiplexum Kobayashi, 1927

Discoactinoceras cf. D. multiplexum Kobayashi, 1927 Figures 4.9, 6.4, 6.5

- 1927 Discoactinoceras multiplexum Kobayashi, p. 202, pl. 22, figs. 7a, b.
- 1931 *Discoactinoceras multiplexum*; Kobayashi, p. 56, pl. 4, figs. 1a, b.
- 1965 *Discoactinoceras multiplexum*; Chao et al., p. 61, pl. 14, figs. 3–6.
- 1978 *Discoactinoceras multiplexum*; Kobayashi, p. 226, textfigs. 1, 2, pl. 31, figs. 1–5.
- 1981 *Discoactinoceras multiplexum* Kobayashi in Zou, p. 358, pl. 2, fig. 7.

*Occurrence.*—Lhasai Formation, Darriwilian (Middle Ordovician), near Lhasai village, about 26 km east of Xiongmei town, Xainza County, North Tibet.

*Description.*—The siphuncle is preserved and the orthoconic phragmocone with circular cross section is 21 mm in length. Siphuncle is large and central in position. Siphuncular foramina are broad. Siphuncle segments are about four times as wide as long. Septal necks are short and brims are short. Siphuncle is filled with deposits, and vascular systems are unknown.

*Material*.—An orthoconic fragment cut and polished in median section. NIGP166265.

*Remarks.*—Kobayashi (1978) proposed a new family Discoactinoceratidae because the genus *Discoactinoceras* developed intrasiphuncular stereoplasmic deposits and recumbent cyrtochoanitic septal necks. This specimen (NIGP166265) is most similar to the specimen described by Zou (1981) from the Inner Mongolia area in its body size and large siphuncle.

### Acknowledgments

We are indebted to C. Li (Jilin University) for providing several specimens and stratigraphic information. We are grateful to D. Evans and an anonymous reviewer for their constructive suggestions of the manuscript. Financial support from the Chinese Academy of Sciences (XDPB05, XDB10010100), the National Natural Science Foundation of China (grant No. 41290260, 41521061), and the Ministry of Science and Technology of China (2013FY111000) is acknowledged. This is a contribution to the IGCP 653 project ('The Onset of Great Ordovician Biodiversification Event').

#### References

- Agassiz, L., 1847, An Introduction to the Study of Natural History, in a Series of Lectures Delivered in the Hall of the College of Physicians and Surgeons: New York, Greeley & McElrath, 58 p.
- Balashov, Z.G., 1962, Ordovician nautiloids from the Siberian Platform: Leningrad, Leningrad University, 205 p. [in Russian]
- Billings, E., 1857, Report for the year 1856, of E. Billings Esq., palaeontologist, addressed to Sir William E. Logan, provincial geologist: Geological Survey of Canada, Report of Progress, for the years 1853–54–55–56, p. 247–345.
- Brown, G.F., Buravas, S., Charaljavanaphet, J., Jalichandra, N., Johnston, W.D. Jr., Sresthaputra, V., and Taylor, G.C., 1951, Geologic Reconnaissance of the Mineral Deposits of Thailand: U.S. Geological Survey Bulletin, v. 984, 183 p.
- Burrett, C., and Stait, B., 1987, China and Southeast Asia as part of the Tethyan margin of Cambro-Ordovician Gondwanaland, *in* McKenzie, K., ed., Shallow Tethys, 2: Rotterdam, Balkema, p. 65–77.
- Burrett, C., Long, J., and Stait, B., 1990, Early–middle Palaeozoic biogeography of Asian terranes derived from Gondwana, *in* McKerrow, W., and Scotese, C., eds., Palaeozoic Palaeogeography and Biogeography: Geological Society Memoir, v. 12, p. 163–174.Burrett, C., Khin, Z., Meffre, S., Lai, C.K., Khositanont, S., Chaodumrong, P.,
- Burrett, C., Khin, Z., Meffre, S., Lai, C.K., Khositanont, S., Chaodumrong, P., Udchachon, M., Ekins, S., and Halpin, J., 2014, The configuration of Greater Gondwana: Evidence from U–Pb geochronology of detrital zircons from the Palaeozoic and Mesozoic of Southeast Asia and China: Gondwana Research, v. 26, p. 31–51.
  Burton, C.K., 1974, The Satun Group (Nai Tak Formation and Thung Song
- Burton, C.K., 1974, The Satun Group (Nai Tak Formation and Thung Song Limestone) of Peninsular Thailand: Sains Malaysiana, v. 3, p. 15–34.
- Chang, J.T., 1959, Nautiloids of the Lower Ordovician from the district Zhuozishan, Ikechzhasmen, Inner Mongolia: Acta Palaeontologica Sinica, v. 7, p. 259–271. [in Chinese with Russian abstract]
- Chao, K.K., Liang, H.L., Tsou, S.P., Lai, C.G., and Chang, J.T., 1965, Cephalopod Fossils of China: Beijing, Science Press, 126 p. [in Chinese]
- Chen, J.Y., 1975, Nautiloid fauna from the Mount Everest area, *in* Nanjing Institute of Geology and Palaeontology, ed., Scientific Investigation Report of the Mount Everest Area, Palaeontology: Beijing, Science Press, p. 267–308. [in Chinese]
- Chen, J.Y., 1976, Advances in the Ordovician stratigraphy of North China with a brief description of nautiloid fossils: Acta Palaeontologica Sinica, v. 15, p. 55–74. [in Chinese with English abstract]
- Chen, J.Y., and Liu, G.W., 1976, Ordovician nautiloids, *in* Nanjing Institute of Geology and Palaeontology, ed Stratigraphy and Palaeontology of Southwest China Beijing, Science Press, p. 138–143. [in Chinese]

- Chen, J.Y., and Zou, X.P., 1984, Ordovician cephalopods from the Ordos area, China: Memoirs of Nanjing Institute of Geology and Palaeontology 20, p. 33–84. [in Chinese with English abstract]
- Chen, T.E., 1983, The discovery of *Georgina* Wade from southern Xizang (Tibet), and its significance: Bulletin of Nanjing Institute of Geology and Palaeontology, Academia Sinica, 6, p. 117–131. [in Chinese with English abstract]
- Chen, T.E., 1984, The Ordovician cephalopod fauna and the subdivision of Ordovician from southern Xizang (Tibet): Acta Palaeontologica Sinica, v. 23, p. 452–471. [in Chinese with English abstract]
- Chen, T.E., 1986, Paleozoic and Cretaceous strata from Xainza and Baingoin, Xizang-Ordovician system: Bulletin of Nanjing Institute of Geology and Palaeontology 10, p. 3–12. [in Chinese with English abstract]
- Chen, T.E., 1987, Ordovician nautiloids from Xainza: Bulletin of Nanjing Institute of Geology and Palaeontology, v. 11, p. 133–191. [in Chinese with English abstract]
- Cheng, L.R., Zhang, Y.J., and Zhang, Y.C., 2004, New progress in the study of Paleozoic strata in the Xainza area, Tibet: Geological Bulletin of China, v. 23, p. 1018–1022. [in Chinese with English abstract]
- Cheng, L.R., Zhang, Y.C., and Zhang, Y.J., 2005a, Discovery of the Early Ordovician strata in Xainza County, Tibet and its significance: Journal of Stratigraphy, v. 29, p. 38–41. [in Chinese with English abstract]
- Cheng, L.R., Zhang, Y.C., and Zhang, Y.J., 2005b, A new Ordovician nautiloid genus (*Variabioceras*) in the Xainza area, northern Tibet: Geological Bulletin of China, v. 24, p. 363–368. [in Chinese with English abstract]
- Cheng, L.R., Zhang, Y.J., and Zhang, Y.C., 2005c, Ordovician nautiloid fossils of Xainza Region, Tibet: Journal of Jilin University (Earth Science Edition), v. 35, p. 273–283. [in Chinese with English abstract]
- Cheng, L.R., Zhang, Y.C., and Zhang, Y.J., 2006, New materials of Ordovician nautiloids from Xainza, Tibet: Acta Palaeontologica Sinica, v. 45, p. 533–539. [in Chinese with English abstract]
- Cuvier, G., 1797, Note sur une nouvelle espèce de guêpe cartonnière: Magasin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts, v. 17, p. 146–148.
- Dzik, J., 1984, Phylogeny of the Nautiloidea: Palaeontologia Polonica, v. 45, p. 3–219.
- Endo, R., 1930, The presence of Nybyoceras in South Manchuria: Journal of the Scientific Laboratories, Denison University, v. 25, p. 297–300.
- Endo, R., 1932, The Canadian and Ordovician formations and fossils of South Manchuria: Washington, D.C, U.S. Government Printing Office, 152 p.
- Flower, R.H., 1968, Part 1 The first great expansion of the actinoceroids: State Bureau of Mines and Mineral Resources New Mexico, Memoirs 19, p. 1–16.
- Foerste, A.F., 1924, Silurian cephalopods of northern Michigan: Contributions from the Museum of Geology University of Michigan, v. 2, p. 19–120.
- Frey, R.C., 1995, Middle and Upper Ordovician Nautiloid Cephalopods of the Cincinnati Arch Region of Kentucky, Indiana, and Ohio: Washington, D.C, U.S. Government Printing Office, 126 p.
- Grabau, A.W., 1922, Ordovician Fossils of North China: Beijing, Geological Survey of China, 109 p.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001, PAST: Paleontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4, no. 1, p. 1–9, http://palaeoelectronica.org/2001\_1/past/ issue1\_01.htm.
- Harper, D.A.T., Rasmussen, C.M.Ø., Liljeroth, M., Blodgett, R.B., Candela, Y., Jin, J.S., Percival, I.G., Rong, J.Y., Villas, E., and Zhan, R.B., 2013, Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods: Geological Society, London, Memoirs, v. 38, p. 127–144.
- Hyait, A., 1883–1884, Genera of fossil cephalopods: Proceedings of the Boston Society of Natural History, v. 22, p. 253–338.
- Ingavat, R., Muenlek, S., and Udomratn, C., 1975, On the discoveries of some Permian fusulinids and Ordovician cephalopods of Banrai, West Thailand: Journal of the Geological Society of Thailand, v. 1, p. 81–89.
- Jaccard, P., 1901a, Distribution de la Flore Alpine dans le Bassin des Dranses et dans quelques régions voisines: Naturelles Bulletin De La Societe Vaudoise Des Sciences, v. 37, p. 241–272.
- Jaccard, P., 1901b, Étude comparative de la distribution florale dans une portion des Alpes et du Jura: Naturelles Bulletin De La Societe Vaudoise Des Sciences, v. 37, p. 547–579.
- Kobayashi, T., 1927, Ordovician fossils from Corea and South Manchuria: Japanese Journal of Geology and Geography, v. 5, p. 173–212.
- Kobayashi, T., 1931, Studies on the Ordovician stratigraphy and palaeontology of North Korea with notes on the Ordovician fossils of Shantung and Liaotung: Bulletin of Geological Survey of Chosen, v. 11, p. 1–60.
- Kobayashi, T., 1958, Some Ordovician fossils from the Thailand-Malayan borderland: Japanese: Journal of Geology and Geography, v. 29, p. 223–231.

- Kobayashi, T., 1959, On some Ordovician fossils from northern Malaya and her adjacence: Journal of the Faculty of Science, University of Tokyo, Section 2, v. 11, p. 387–407.
- Kobayashi, T., 1977, An occurrence of Ordosoceras in Jehol, Northeast China, and a note on the Polydesmiidae: Transactions and Proceedings of the Paleontological Society of Japan, New Series, v. 107, p. 125–134.
- Kobayashi, T., 1978, *Discoactinoceras* and the Discoactinoceratidae Fam. nov: Transactions and Proceedings of the Paleontological Society of Japan, New Series, 109, p. 223–234.
- Kobayashi, T., and Hamada, T., 1964, On the Middle Ordovician fossils from Satun, the Malaysian frontier of Thailand: Geology and Palaeontology of Southeast Asia, v. 1, p. 269–278.
- Kobayashi, T., and Matumoto, T., 1942, Three new Toufangian nautiloids from Eastern Jehol: Japanese Journal of Geology and Geography, v. 18, p. 313–317.
- Kröger, B, 2013, Cambrian–Ordovician cephalopod palaeogeography and diversity: Geological Society, London, Memoirs, v. 38, p. 429–448.
- Lai, C.G., 1982a, New materials of Palaeozoic cephalopods from Xizang (Tibet) of China: Selective Papers on the Geology of Qinghai-Tibet Plateau, v. 7, p. 1–28. [in Chinese with English abstract]
- Lai, C.G., 1982b, Ordovician cephalopods from Xainza, Xizang (Tibet): Acta Palaeontologica Sinica, v. 21, 553–560. [in Chinese with English abstract]
- Li, X.S., and Cheng, L.R., 1988, Some Ordovician and Silurian cephalopods from Shenzha and Bange districts, northern Xizang: Journal of Changchun University of Earth Science, v. 18, p. 241–248. [in Chinese with English abstract]
- Metcalfe, I., 2011, Tectonic framework and Phanerozoic evolution of Sundaland: Gondwana Research, v. 19, p. 3–21.
- National Commission of Stratigraphy of China 2014, The stratigraphic chart of China: Acta Geoscientica Sinica, 35. [in Chinese]
- Niko, S., and Sone, M., 2014, Actinocerid cephalopods from the Ordovician of Myanmar, and their paleobiogeographic implications for northern Gondwana: Paleontological Research, v. 18, p. 94–103.
- PaleoGIS 4.0 for ArcGIS 2011, The Rothwell Group, L.P. www.paleogis.com (accessed August 2011).
- Parks, W.A., 1913, Notes on fossils, *in* Tyrrell, J.B., ed., Hudson Bay Exploring Expedition, *in* Ontario Bureau of Mines, ed., Twenty-Second Annual Report of the Bureau of Mines: Toronto, Cameron, p. 161–209.
- Qu, Y.G., Zhang, S.Q., Zheng, C.Z., and Wang, Z.H., 2002, The discovery of Armenoceras of Early Ordovician from Xiongmei, Xainza County, Tibet: Geological Bulletin of China, v. 21, p. 355–356. [in Chinese]
- Qu, Y.G., Wang, Y.S., Zhang, S.Q., Wang, Z.H., Lü, P., and Duan, J.X., 2004, New results and major progress in regional geological survey of the Toiba District Sheet: Geological Bulletin of China, v. 23, 492–497. [in Chinese with English abstract]
- Rong, J.Y., Li, R.Y., and Kul'Kov, N.P., 1995, Biogeographic analysis of Llandovery brachiopods from Asia with a recommendation of use of affinity indices: Acta Palaeontologica Sinica, v. 34, p. 428–453.
- Saemann, L., 1853, Ueber die Nautiliden: Palaeontographica, v. 3, p. 121-163.
- Shen, S.Z., and Shi, G.R., 2000, Wuchiapingian (early Lopingian, Permian) global brachiopod palaeobiogeography: A quantitative approach: Palaeogeography. Palaeoclimatology: Palaeoecology, v. 162, p. 299–318.
- Shen, S.Z., and Shi, G.R., 2004, Capitanian (late Guadalupian, Permian) global brachiopod palaeobiogeography and latitudinal diversity pattern: Palaeogeography. Palaeoclimatology: Palaeoecology, v. 208, p. 235–262.
- Shi, G.R., 1993, Multivariate data analysis in palaeoecology and palaeobiogeography—A review: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 105, p. 199–234.
- Shimizu, S., and Obata, T., 1936, Three new genera of Ordovician nautiloids belonging to the Wutinoceratidae (Nov.) from east Asia: Journal of Shanghai Science Institute, v. 2, p. 27–35.
- Stait, B., 1984, Re-examination and redescription of the Tasmanian species of *Wutinoceras* and *Adamsoceras* (Nautiloidea, Ordovician): Geologica et Palaeontologica, v. 18, p. 53–57.
- Stait, B., and Burrett, C., 1982, *Wutinoceras* (Nautiloidea) from the Setul Limestone (Ordovician) of Malaysia: Alcheringa, v. 6, 193–196.
- Stait, B., and Burrett, C., 1984, Ordovician nautiloid faunas of central and southern Thailand: Geological Magazine, v. 121, p. 115–124.
- Stait, B., Wyatt, D., and Burrett, C., 1987, Ordovician nautiloid faunas of Langkawi Islands, Malaysia and Tarutao Island, Thailand: Neues Jahrbuch fur Palaeontologie Abh, v. 174, p. 373–391.
- Teichert, C., 1933, Der Bau der actinoceroiden Cephalopoden: Palaeontographica, Abt. A, v. 78, p. 111–230.
- Teichert, C., and Glenister, B.F., 1952, Fossil nautiloid faunas from Australia: Journal of Paleontology, v. 26, p. 730–752.
- Teichert, C., and Glenister, B.F., 1953, Ordovician and Silurian cephalopods from Tasmania, Australia: Bulletin of American Paleontology, v. 34, 187–248.

- Teichert, C., Kummel, B., Sweet, W.C., Stenzel, H.B., Furnish, W.M., Glenister, B.F., Erten, H.K., Moore, R.C., and Zeller, D.E., 1964, Treatise on Invertebrate Paleontology, Part K, Mollusca, v. 3: Lawrence, The University of Kansas Press, 466 p.
- Thein, M.L., 1968, On some nautiloid cephalopods from the area east of Kyaukse, Burma: Union of Burma Journal of Science and Technology, v. 1, p. 67–76.
- Tibet Geological Bureau General Survey Team 1980, New discovery of Paleozoic strata from Xainza regions, Tibet: Geological Review, v. 26, p. 150–151. [in Chinese]
- Troedsson, G.T., 1926, On the Middle and Upper Ordovician Faunas of Northern Greenland, I. Cephalopods: Grønland, Meddel, v. 71, 157 p.
- Wade, M., 1977, Georginidae, New family of actinoceratoid cephalopods, Middle Ordovician: Australia, Memoirs of Queensland Museum, v. 18, p. 1–15.
- Wang, Z.H., Bergström, S.M., Zhen, Y.Y., Zhang, Y.D., and Wu, R.C., 2014a, New conodont data from the Lower Ordovician of Tangshan, Hebei Province, North China: Acta Micropalaeontologica Sinica, v. 31, p. 1–14. [in Chinese with English abstract]
- Wang, Z.H., Bergström, S.M., Zhen, Y.Y., Zhang, Y.D., and Wu, R.C., 2014b, A review of the Darriwilian biostratigraphic conodont zonation in Tangshan, Hebei Province based on the new conodont collections: Acta Palaeontologica Sinica, v. 53, p. 1–15. [in Chinese with English abstract]
- Wang, Z.H., Zhen, Y.Y., Zhang, Y.D., and Wu, R.C., 2016, Review of the Ordovician conodont biostratigraphy in the different facies of North China: Journal of Stratigraphy, v. 40, p. 1–16. [in Chinese with English abstract]
   Whitehouse, F.W., 1936, The Cambrian faunas of north-eastern Australia,
- Parts 1 and 2: Memoirs of Queensland Museum, v. 11, p. 59–112.
- Xia, D.X., 1983, The Palaeozoic stratigraphy of Xainza area, Northern Tibet. *in* Editorial Board of Contribution to the Geology of the Qinghai-Xizang Plateau, ed Contribution to the Geology of the Qinghai-Xizang Plateau, v. 2, p 106–120. [in Chinese]
- Xu, Z.Q., Yang, J.S., Li, H.B., Ji, S.C., Zhang, Z.M., and Liu, Y., 2011, On the tectonics of the India-Asia collision: Acta Geologica Sinica, v. 85, p. 1–33. [in Chinese with English abstract]
- Yang, S.W., 1978, Nautiloidea. in Working Group on Stratigraphy and Palaeontology of Guizhou, ed., Atlas of Palaeontology of Southwest China,

Guizhou Province (1): Beijing, Geological Publishing House, p. 358–379. [in Chinese]

- Yang, S.W., 1980, Some new materials of Ordovician actinoceroids from southwest China: Acta Palaeontologica Sinica, v. 19, p 170–173. [in Chinese with English abstract]
- Yü, C.C., and Chao, K.K., 1957, Cephalopoda. *in.*, Nanjing Institute of Geology and Palaeontology, ed., Chinese Index Fossils, Invertebrate Palaeontology: Beijing, Geological Publishing House, p. 223–248. [in Chinese]
- Zhang, S.Q., Qu, Y.G., and Zheng, C.Z., 2003, The discovery and significance of the Lower Ordovician Lhasai Formation in the Xainza region, northern Xizang: Sedimentary Geology and Tethyan Geology, v. 23, p. 44–48. [in Chinese with English abstract]
- Zhang, Y.C., Cheng, L.R., and Zhang, Y.J., 2004, The Ordovician system in the Xainza region, North Tibet: Journal of Jilin University (Earth Science Edition), v. 24, p. 502–508. [in Chinese with English abstract]
- Zhang, Y.C., Cheng, L.R., and Shen, S.Z., 2010, Late Guadalupian (middle Permian) fusuline fauna from the Xiala Formation in Xainza County, central Tibet: Implication of the rifting time of the Lhasa Block: Journal of Paleontology, v. 84, 955–973.
- Zhen, Y.Y., Zhang, Y.D., Wang, Z.H., and Percival, I.G., 2016, Huaiyuan Epeirogeny—Shaping Ordovician stratigraphy and sedimentation on the North China Platform: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 448, p. 363–370.
- Zheng, C.Z., 2005, The Ordovician–Silurian stratigraphy study of the Yungzhug area, North Tibet: Journal of Stratigraphy, v. 29, p. 16–21. [in Chinese with English abstract]
- Zhu, M.Y., and Li, X.S., 1996, Early Ordovician actinoceroids from southern Jilin: Acta Palaeontologica Sinica, v. 35, p. 349–365. [in Chinese with English abstract]
- Zou, X.P., 1981, Early Ordovician nautiloids from Qingshuihe, Nei Monggol (Inner Mongolia) and Pianguan, Shanxi Province: Acta Palaeontologica Sinica, v. 20, p. 353–362. [in Chinese with English abstract]

Accepted 4 December 2017