



Distribution of the Silurian brachiopod genus *Atrypoides*, and its first report in the Chejiaba Formation (upper Ludlow), Guangyuan, South China

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Abstract.—*Atrypoides* is a Silurian smooth atrypide with a worldwide distribution and high species-level diversity especially during Ludlow to Prídolí. In this study, the occurrences of 67 species, 14 subspecies, and 23 forma, cf., aff., or var. species are summarized. Among them, *Atrypoides recta* from Aeronian of Siberia is the earliest known occurrence of this genus, while *Atrypoides elatior* or *Atrypoides polaris modica* from upper Prídolí strata of the Czech Republic and China, respectively, should be the youngest species. No valid Devonian occurrence of *Atrypoides* has been recorded due to absence of convincing identification or poor stratigraphic information. The rapid evolution and cosmopolitan nature of *Atrypoides* allow some species to be used as index fossils for strata of Ludlow and Prídolí in South China. The age of the Chejiaba Formation in Guangyuan, Sichuan Province, South China, has been clarified based on the occurrence of *Atrypoides*. Specimens from this locality, which are preserved *in situ*, are described herein and illustrated with reconstruction of life style for the first time.

Introduction

The Silurian Period was a complex interval characterized by elevated tectonic activity and rapid sea level fluctuations. Consequently, Silurian lithologic sequences in South China are commonly discontinuous (Rong and Chen, 2003; Chen et al., 2014; Rong et al., 2019). Llandovery strata are relatively well developed (Chen and Rong, 1996), while Wenlock successions are found only sporadically in a few areas (Rong et al., 2019; Wang et al., 2021). Although the Ludlow and Prídolí strata are widely distributed in South China, little information is available due to severe weathering or insufficient research (Tang et al., 2010; Wang et al., 2010, 2011, 2017, 2018; Rong et al., 2019). Thus, limited information is available for stratigraphic correlation of the upper Silurian across the region.

Silurian strata in Guangyuan, Sichuan Province are well developed and have been studied extensively (Chen et al., 1991; Wan et al., 1991; Jin et al., 1992; Tang et al., 2010; Wang et al., 2017). The Chejiaba Formation is unconformably sandwiched between the Llandovery Ningqiang Formation and the Devonian Yuntaiguan Formation, making dating the unit difficult. Conodonts (e.g., *Ozarkodina snajdri* [Walliser, 1964]) and chitinozoans (*Angochitina* sp. and *Sphaerochitina* sp.) in the Chejiaba Formation suggest a Ludlow age, but more work is needed to confirm this (Tang et al., 2010; Wang, 2013).

Discovery of the brachiopod *Atrypoides* in the Chejiaba Formation may further clarify the age of this unit. This atrypide genus has a wide distribution in the Silurian Period (with suspect

reports of occurrences in the Devonian), but is particularly abundant in Ludlow and Prídolí strata (Copper, 1977, 2004; Jones and Rong, 1982). With 67 species listed, the rapid evolution of the genus, in conjunction with its wide distribution, makes it a useful fossil for biostratigraphic correlation and constraining stratigraphic age.

This paper is the first report of *Atrypoides foxi* (Jones, 1974) (*in situ* preservation) from the Chejiaba Formation. Globally, *Atrypoides foxi* has been found only in Ludlow and Prídolí strata, confirming the Ludlow age suggested by microfossils, but perhaps indicating a broader time of deposition. This has important implications for correlation of Ludlow and Prídolí strata in South China that are bound by unconformities, which makes dating difficult, especially in areas where the stratigraphic sequences are sporadically distributed.

Materials and methods

The research area is located near Gujiashan Tunnel, Chaotian Town, Guangyuan City, Sichuan Province (32°40'6.46"N, 105°56'56.30"E) (Fig. 1). The reconstruction of National Highway G108 and Expressway G5 exposed many new outcrops in this area that have not been previously studied for fossils. Fossils were collected by Prof. Yi Wang of the Nanjing Institute of Geology and Palaeontology (NIGP) from calcareous mudstones in the Chejiaba Formation. Serial sections were made using acetate film with acetone.

All specimens are conjoined and most of them were found *in situ*, clustered together, with beaks down (Fig. 2.1). We reconstructed its original life orientation exactly according to its preservation status based on a bulk of specimens (Fig. 2.2).

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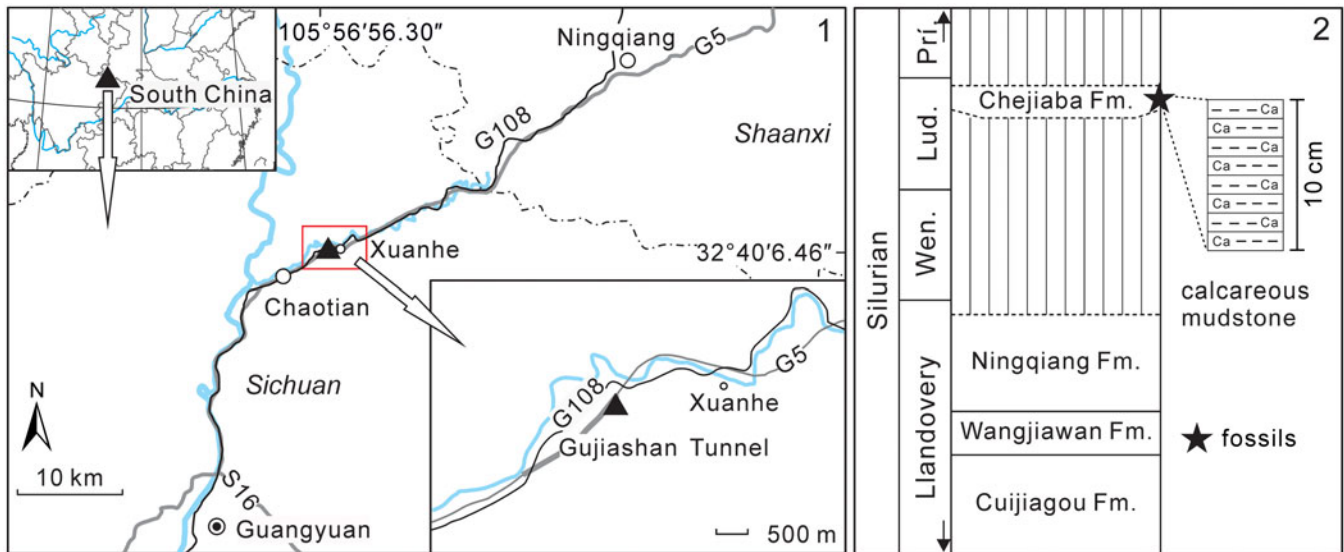


Figure 1. Simplified geographic map and Silurian stratigraphy of northern Sichuan, South China. (1) Map showing the location where brachiopod fossils were discovered. (2) Stratigraphic distribution of *Atrypodea foxi* (Jones, 1974) in the Chejiaba Formation at Chaotian, Guanyuan City, Sichuan, South China. The unit producing fossils is nearly 10 cm thick.

Although there are many records of the genus, few *in situ* occurrences of *Atrypodea* are known, and this is the first *in situ* occurrence of these shells documented from South China.

Repositories and institutional abbreviations.—All figured specimens are housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences and State Key Laboratory of Palaeobiology and Stratigraphy sample collection, Nanjing Institute of Geology and Palaeontology (BHR).

Systematic paleontology

Subphylum Rhynchonelliformea Williams et al., 1996
 Class Rhynchonellata Williams et al., 1996
 Order Atrypida Rzhonsnitskaya, 1960
 Suborder Lissatrypidina Copper, 1996
 Family Lissatrypidae Twenhofel, 1914
 Genus *Atrypodea* Mitchell and Dun, 1920

Type species.—*Meristina* (?) *australis* Dun, 1904; Molong Limestone (Ludlow), Silurian, New South Wales, Australia.

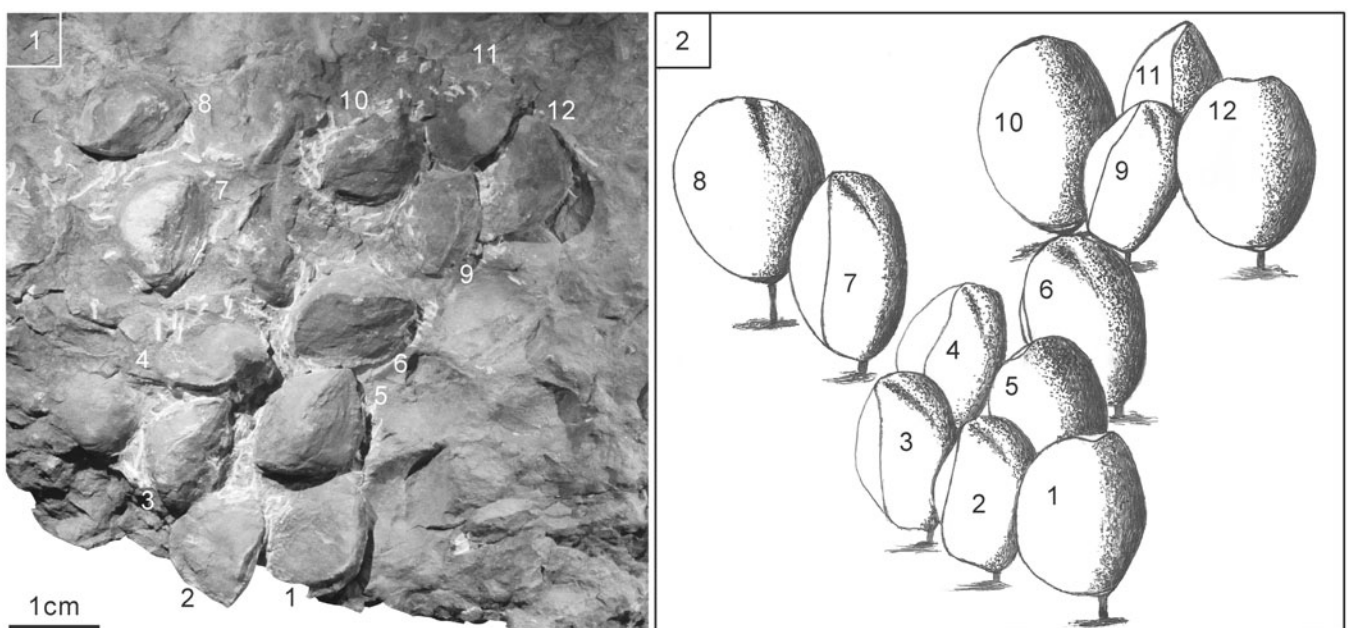


Figure 2. *Atrypodea foxi* (Jones, 1974) from the Chejiaba Formation at Chaotian, Sichuan Province, preserved *in situ* with the beak down and anterior commissure upright (BHR2001–2012) (1), and their ecological reconstruction (2).

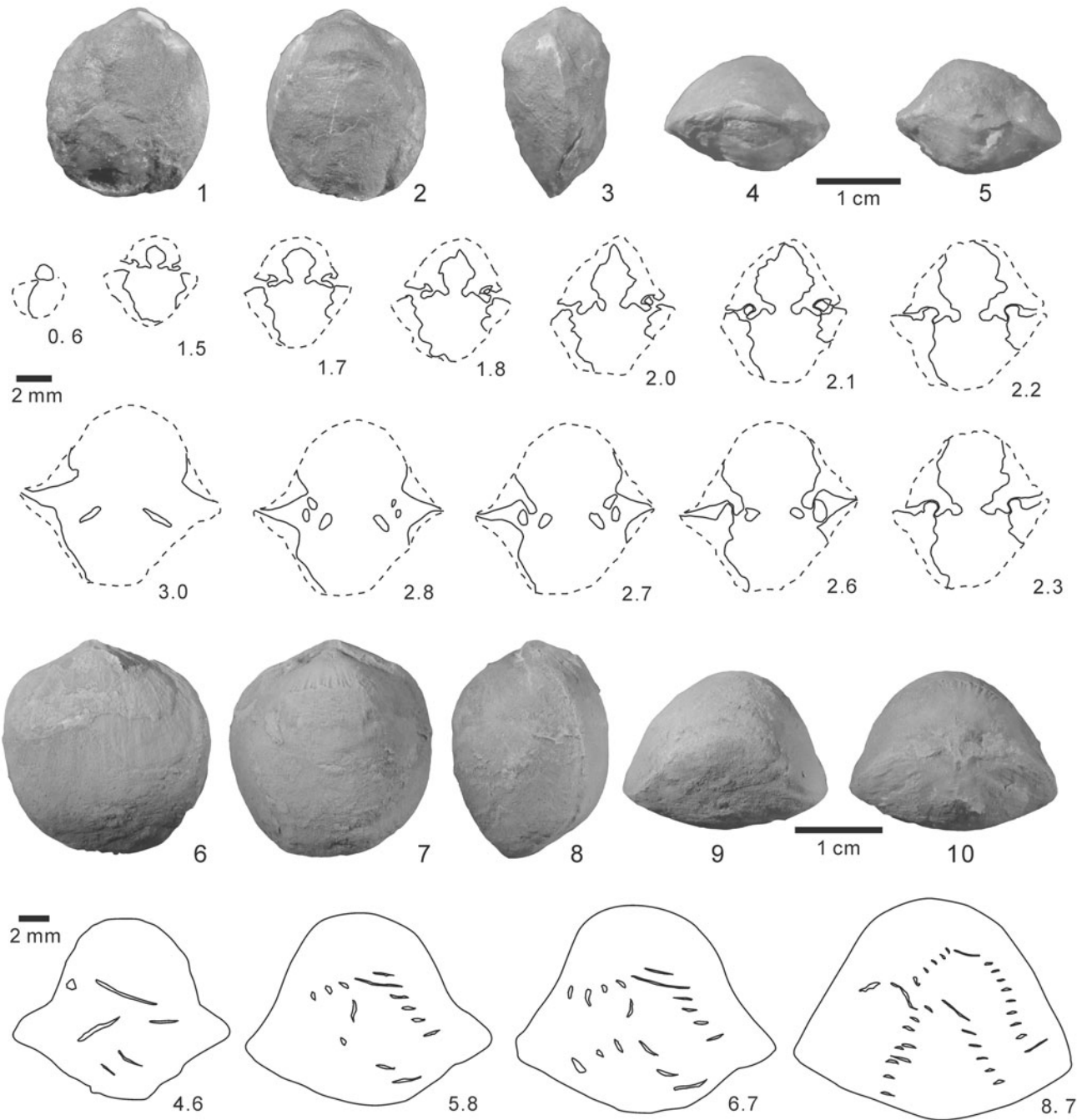


Figure 3. *Atrypa foxi* (Jones, 1974), Chejiaba Formation, Ludlow, Chaotian, Guangyuan City, Sichuan, South China. (1–5) NIGP 179419, ventral, dorsal, lateral, anterior, and posterior views of articulated shell with its serial sections. (6–10) NIGP 179420, ventral, dorsal, lateral, anterior, and posterior views of articulated shell with its serial sections. Numbers on serial sections are mm from poster end of shell.

Diagnosis.—Medium to large, wide to elongate, biconvex to dorsibiconvex, usually prominently uniplicate; shell smooth, with small apical to transapical foramen and obscured deltidial region; both ventral and dorsal valves thickened posteriorly, with muscle scars weakly incised; solid teeth, dental plates absent; relatively slender hinge, socket plates, small crural bases; ventrally positioned jugal processes with bulky jugal plates; dorsal-dorsolateral spiralia with 5–13 whorls; dorsal septum absent.

Occurrence.—*Atrypa* is known from the Llandovery (China, Russia, and Canada), Wenlock (China, Czech Republic, Australia, Altai, Urals, and Canada), Ludlow–Prídolí (worldwide), and ?Lower Devonian (Czech Republic, South Tienshan, and North Urals).

Remarks.—Three genera (*Atrypella* Kozłowski, 1929; *Globaltrypa* Mizens and Sapelnikov in Mizens, 1985; and *Lingatrypa* Mizens, 1985) were listed as synonyms of

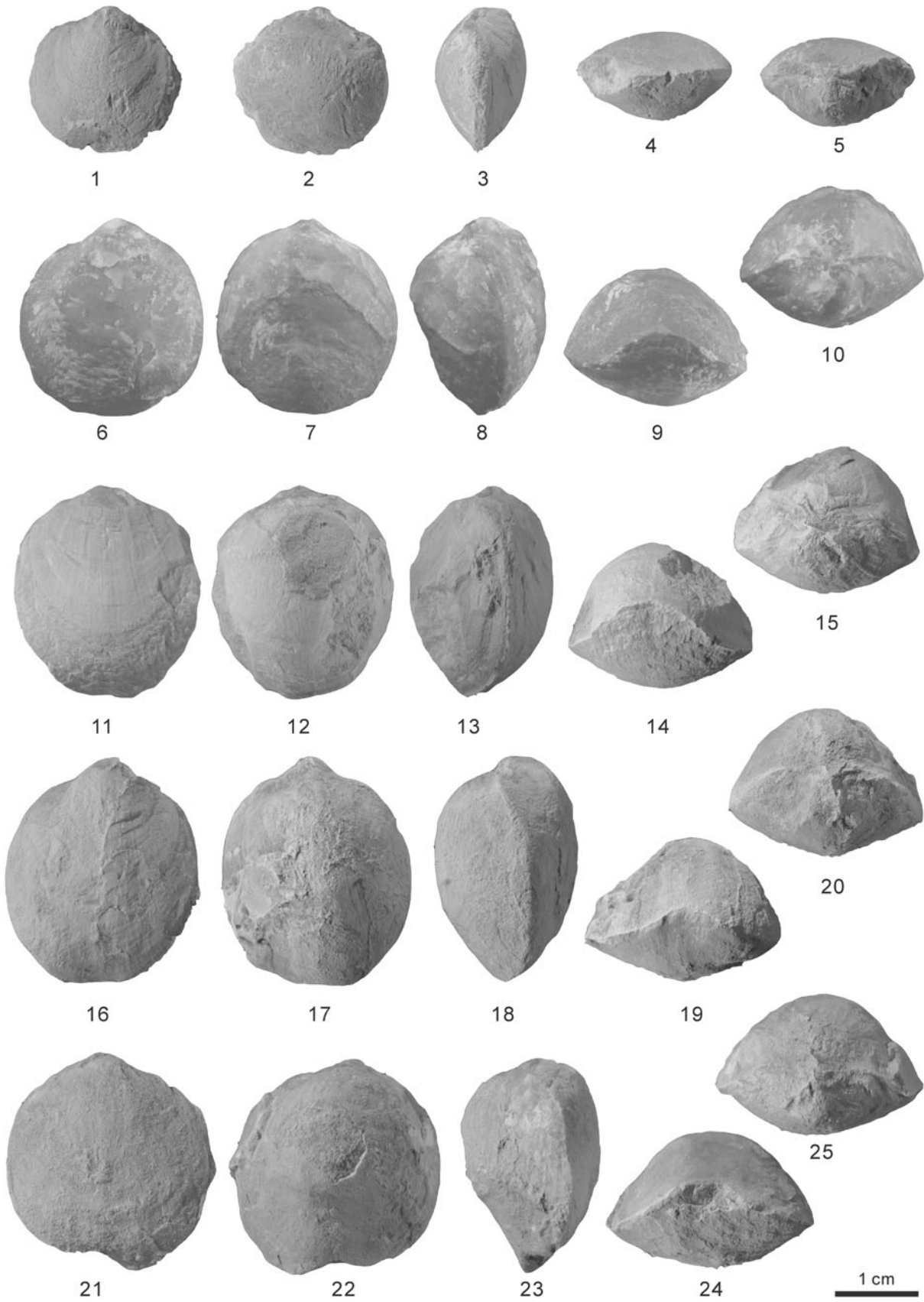


Figure 4. *Atrypoidea foxi* (Jones, 1974), Chejiaba Formation, Ludlow, Chaotian, Guangyuan City, Sichuan, South China. (1–5) NIGP 179421, ventral, dorsal, lateral, anterior, and posterior views of articulated shell. (6–10) NIGP 179422, ventral, dorsal, lateral, anterior, and posterior views of articulated shell. (11–15) NIGP 179423, ventral, dorsal, lateral, anterior, and posterior views of articulated shell. (16–20) NIGP 179424, ventral, dorsal, lateral, anterior, and posterior views of articulated shell. (21–25) NIGP 179425, ventral, dorsal, lateral, anterior, and posterior views of articulated shell.

Atrypoidea in Copper (2002). Although *Lissatrypella* Sapelnikov and Mizens, 1982, was treated as subgenus in Copper (2002), little difference can be detected between *Atrypoidea* (*Atrypoidea*) and *Atrypoidea* (*Lissatrypella*). Here, we consider that *Lissatrypella* could be a synonym of *Atrypoidea* rather than its subgenus.

A better understanding of the geographical and chronological distribution of genus *Atrypoidea* will clarify its stratigraphic significance. The validity of some species is questionable, and the genus is in need of careful review to determine whether many of the species are synonymous. Some of the synonyms have already been identified, such as *A. phoca* (Salter, 1852) and *A. scheii* (Holtedahl, 1914) (Jones, 1974, 1981; Rong et al., 1987); *A. qujingensis* Wang, Rong, and Yang, 1980, *A. dorsoconvexa* Wang, Rong, and Yang, 1980, and *A. foxi* (Jones, 1974) (Jones and Rong, 1982; Rong et al., 1987).

In this study, 67 species, 14 subspecies, and 23 forma, cf., aff., or var. species in total are listed (see details in Appendices 1, 2), partly based on summary work by Copper (1977, 2004), supplemented with much new information, such as the horizon or distribution of 15 species. In addition, 12 species, together with 8 subspecies and 10 forma, cf., or aff. species, are newly added (see below for major contribution of this study).

Atrypoidea bailongjiangensis Fu, 1982, from Prídolí rocks of Gansu, China, still was recognized as a valid species by Copper (2004), instead of being considered the same as *A. polaris* (Jones and Packard, 1980, from the Prídolí, Arctic Canada (Rong et al., 1987), which supported by this study. *Atrypoidea camelina pavdensis* (Mizens, 1977) was regarded as subspecies of *A. camelina* (von Buch, 1840) by Copper (2004), but was treated as valid species *A. pavdensis* (Mizens, 1977) by Breivel and Breivel (1988). It is listed as a valid species in this study.

Atrypoidea lentiformis (Wang, 1956) came from the Xiushan Formation of South China. The Xiushan Formation previously was thought to have been deposited over the Wenlock–?Ludlow (Wang, et al., 1980; Copper, 2004), but has been revised as Telychian in age with updated information (Rong et al., 2019). *Glassia obovata* var. *magna* Grabau, 1925, from the Lojoping Formation, South China, was re-assigned to *Lissatrypa* by Rong and Yang (1981).

Copper (1977, 2004) listed some forma species as subspecies without additional information, for example, listing *A. scheii* forma *concinna* (Oradovskaya, 1975) as *A. scheii concinna* (Oradovskaya, 1975), similar to *A. scheii* forma *gibbera* (Nikiforova, 1970), *A. elongata* forma *lata* Sapelnikov and Mizens, 1982, *A. phoca* forma *paracamelina* (Nikiforova, 1970), *A. phoca* forma *subscheii* (Nikiforova, 1970), *A. phoca* forma *typica* (Nikiforova, 1970) and *A. scheii* forma *typica* (Nikiforova, 1970). In addition, *A. insigne* forma *grebensis* (Nikiforova, 1970) was revised into *A. insigne* var. *grebensis* (Nikiforova, 1970) by Copper (2004), and *A. insigne*

(Nikiforova, 1970) together with *A. modesta* (Nikiforova, 1970) were listed as subspecies *A. insigne insigne* (Nikiforova, 1970) and *A. modesta modesta* (Nikiforova, 1970), respectively, by Copper (1977) without explanation. Here, we reinstate them with data from the original article.

Atrypoidea foxi (Jones, 1974)

Figures 3, 4

- 1952 *Atrypella scheii* (Holtedahl, 1914); Kirk and Amsden, p. 58, pl. 7, figs. 12–22.
- 1974 *Atrypella lentiformis* (Wang, 1956); Rong et al., p. 205, pl. 96, figs. 18, 23.
- 1974 *Atrypella foxi* Jones, p. 968, pls. 1, 2.
- 1979b *Atrypoidea foxi*; Jones, p. 2208, pl. 1, figs. 22–48.
- 1980 *Atrypoidea qujingensis* Wang, Rong, and Yang, p. 112, pl. 1, figs. 1–16; pl. 2, figs. 12, 13; pl. 3, figs. 6–9, 11, 12, 14, 16, 17; pl. 4, figs. 1, 5.
- 1980 *Atrypoidea dorsoconvexa* Wang, Rong, and Yang, p. 112, pl. 2, figs. 1–11, 14–17; pl. 3, figs. 10, 13; pl. 4, figs. 1, 6, 8, 9.
- 1982 *Atrypella foxi*; Jones and Rong, p. 924, pl. 1, figs. 1–36.
- 1985 *Atrypoidea foxi*; Rong et al., p. 40, pl. 3, figs. 1–4.
- 1985 *Atrypoidea qujingensis*; Fang, p. 57, pl. 5, fig. 4.
- 1985 *Atrypoidea dorsoconvexa*; Fang, p. 57, pl. 5, fig. 5.
- 1995 *Atrypella foxi*; Wang, p. 744.
- 2018 *Atrypoidea foxi*; Zhou and Huang, p. 59, text figs. 11–14.

Type specimen.—Holotype: solid articulate shell, G.S.C. 34636 (Geological Survey of Canada), from Read Bay Formation, Ludlow, Somerset Island, Arctic Canada (Jones, 1974, p. 968, pl. 1, fig. 1a–c).

Occurrence.—The fossils in this manuscript were collected from the Chejiaba Formation (Ludlow), Guangyuan City, Sichuan Province, South China, and form the basis for the description below.

Description.—Shell smooth with a few faint growth lines; medium-sized, subcircular to slightly elongate, biconvex to dorsibiconvex; width 17.3–27.9 mm (average 25 mm), length 17.1–23.2 mm (average 22.3 mm), thickness 11.1–18.6 mm (average 16.4 mm); average length/width ratio 1.1. Teeth strong, dental plates absent. Hinge plates developed, extending ventrally. Spiralia dorsally directed (sometimes broken and misplaced), with ~10 whorls. Anterior commissure of the small individual is nearly straight, while fully grown shells are uniplicate.

Materials.—Twenty-three articulated shells. NIGP 179419–179425; BHR 2001–2016.

Remarks.—*Lissatrypa scheii* Holtedahl, 1914, was established based on the fossils from Ludlow strata of Ellesmere Island,

Occurrences of <i>Atrypa</i> species												
plate/area	Species	Llan.	Wen.	Lud.	Pri.	plate/area	Species	Llan.	Wen.	Lud.	Pri.	
South China	<i>A. foxi</i>					↑ Baltica (Urals, and Russian Arctic islands)	<i>A. columbella</i>					
	<i>A. inflata</i>						<i>A. cuboidiformis</i>					
	<i>A. jjudingshanensis</i>						<i>A. elongata</i>					
	<i>A. lentiformis</i>						<i>A. gigas</i>					
	<i>A. obesa</i>						<i>A. insigne</i>					
	<i>A. prunum</i>						<i>A. kuschvensis</i>					
	<i>A. ventriplana</i>						<i>A. ladgeica</i>					
West Qinling	<i>A. polaris</i>						<i>A. linguata</i>					
	<i>A. quadrata</i>						<i>A. linguifera</i>					
	<i>A. trapezoida</i>						<i>A. linguliformis</i>					
North China	<i>A. foxi</i>						<i>A. modesta</i>					
	<i>A. gashaomiaensis</i>						<i>A. operosa</i>					
	<i>A. linguata</i>						<i>A. ovata</i>					
	<i>A. neimongolica</i>						<i>A. pavdensis</i>					
Tarim	<i>A. alexandrina</i>						<i>A. penitus</i>					
	<i>A. columbella</i>						<i>A. pentagonalis</i>					
	<i>A. minuta</i>						<i>A. petropadovski</i>					
	<i>A. muschketovi</i>						<i>A. phoca</i>					
	<i>A. nasa</i>						<i>A. prunum</i>					
	<i>A. operosa</i>						<i>A. renitens</i>					
	<i>A. prunum</i>						<i>A. sosvaensis</i>					
	<i>A. tectiformis</i>						<i>A. subcamelina</i>					
	<i>A. tianshanensis</i>						<i>A. subrecta</i>					
Bohemia	<i>A. columbella</i>						<i>A. turjensis</i>					
	<i>A. elatior</i>						<i>A. uralica</i>					
	<i>A. linguata</i>						<i>A. vagranica</i>					
	<i>A. modesta</i>						<i>A. vangyrica</i>					
	<i>A. renitens</i>											
Gondwana	<i>A. angusta</i>						Laurentia (except Arctic Canada and Alaska)	<i>A. carinata</i>				
	<i>A. australis</i>							<i>A. latilingulata</i>				
Kolyma Okhotsk	<i>A. phoca</i>					<i>A. lentiformis</i>						
Siberia	<i>A. recta</i>					<i>A. linguata</i>						
	<i>A. columbella</i>					<i>A. planata</i>						
Altai	<i>A. linguata</i>					<i>A. praelingulata</i>						
	<i>A. minuta</i>					<i>A. shrocki</i>						
	<i>A. minzhini</i>					Laurentia (Arctic Canada)	<i>A. bioherma</i>					
	<i>A. operosa</i>						<i>A. erebus</i>					
	<i>A. sphaerica</i>						<i>A. foxi</i>					
	<i>A. tectiformis</i>						<i>A. gigantus</i>					
	<i>A. hemsea</i>						<i>A. netserki</i>					
Baltica (main area)	<i>A. phoca</i>					<i>A. phoca</i>						
	<i>A. prunum</i>					<i>A. polaris</i>						
	<i>A. saaremaaensis</i>					<i>A. prunum</i>						
	<i>A. sulcata</i>					Laurentia (Alaska)	<i>A. borealis</i>					
	<i>A. alata</i>						<i>A. foxi</i>					
	<i>A. camelina</i>					<i>A. tenuis</i>						

Figure 5. Global and stratigraphic (Llandovery–Prídolí) occurrences of species of *Atrypa* (based on data in Appendix 1). Dark blue means present.

Arctic Canada. Holtedahl (1924) later claimed that *Lissatrypa scheii* Holtedahl, 1914, was a variety of *Lissatrypa phoca* (Salter, 1852). Kirk and Amsden (1952) thought fossils from the upper Silurian in southeastern Alaska were *L. scheii* Holtedahl, 1914, and placed it into the genus *Atrypella* as

A. scheii (Holtedahl, 1914). However, the characters designated *A. scheii* (Holtedahl, 1914) by Kirk and Amsden (1952) are different from those identified by Holtedahl (1914) in the originally named *L. scheii*. Jones (1974) concluded that *A. scheii* is a subjective junior synonym of *A. phoca*.

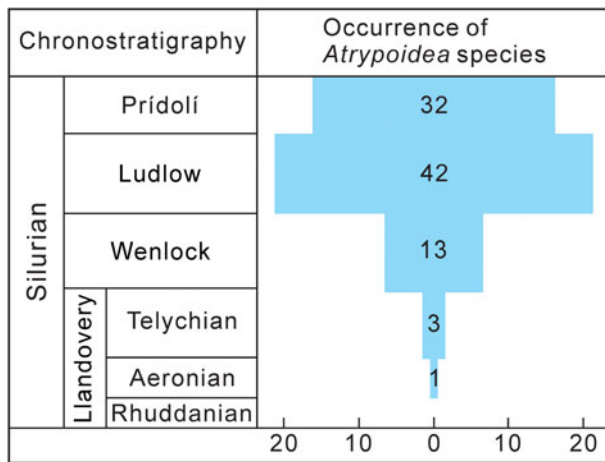


Figure 6. Spindle diagram of *Atrypoides* species distribution from Llandovery–Prídolí (based on data in Appendix 1).

Consequently, a new species, *A. foxi*, was established and *A. scheii* (Holtedahl, 1914) of Kirk and Amsden (1952) was considered as a synonym of the former by Jones (1974). In his study of *Atrypoides* from New South Wales, Australia, Copper (1977) compared the similarities in internal and external morphological characteristics of *Atrypoides* and *Atrypella* and treated the two genera as synonyms, discarding *Atrypella*.

Protathyris lentiformis Wang, 1956, was erected based on fossils from Telychian rocks in Dagan, NE Yunnan, South China. Rong et al. (1974) thought the specimens from the Miaokao Formation in the Qujing and Dagan areas of Yunnan and the fossils of Wang (1956) were the same species (but they actually are not) and synonymized *Protathyris lentiformis* Wang, 1956, with *Atrypella lentiformis* (Wang, 1956). Two new species of *Atrypoides*, *A. qujingensis* Wang, Rong, and Yang, 1980, and *A. dorsoconvexa* Wang, Rong, and Yang, 1980, were established. *Atrypella lentiformis* (Wang, 1956) of Rong et al. (1974) is different from *Protathyris lentiformis* in Wang (1956), and was redefined as *A. qujingensis* by Wang et al. (1980). *Atrypoides lentiformis* (Wang, 1956) is preserved and refers to Telychian *Atrypoides* of South China. Jones and Rong (1982) compared the *Atrypoides* fauna of Canada and South China using a quantitative approach and determined both *A. qujingensis* Wang, Rong, and Yang, 1980, and *A. dorsoconvexa* Wang, Rong, and Yang, 1980, should be synonymized under *Atrypoides foxi* (Jones, 1974).

Discussion

Range and distribution worldwide.—The origin of *Atrypoides* is still unclear. Llandovery species include *Atrypoides lentiformis* (Wang, 1956), *Atrypoides praelingulata* Jin, Caldwell, and Norford, 1993, *Atrypoides recta* (Nikiforova in Nikiforova and Andreeva, 1961), and *Atrypoides subrecta* (Mizens, 1977) (see Fig. 5). *Atrypoides lentiformis* (Wang, 1956) has been found in Telychian strata in South China (Wang, 1956; Sheng, 1975; Wang et al., 1980) and Canada (Jin et al., 1993). *Atrypoides praelingulata* Jin, Caldwell, and Norford, 1993, was described from the Attawapiskat Formation (Telychian) of Hudson Bay Lowlands, Canada.

Atrypoides subrecta (Mizens, 1977) came from Telychian strata in the Urals. *Atrypoides recta* (Nikiforova in Nikiforova and Andreeva, 1961) was reported from Aeronian strata of Siberia, making it the earliest recorded species of the genus worldwide. This may indicate that *Atrypoides* may have originated in Siberia before dispersing to other plates later in the Silurian.

Globally, there are few species in the Llandovery and Wenlock, but by the Ludlow and Prídolí, the genus had diversified considerably (Figs. 6, 7). Thirteen species occur only in China, the Czech Republic, Australia, Altai, the Urals, and Canada in the Wenlock, and the genus became cosmopolitan subsequently with as many as 42 species in the Ludlow and 32 species in the Prídolí.

Atrypoides has been reported from the Devonian of the Czech Republic (Barrande, 1879; Walmsley et al., 1974), North Urals (Khodalevich and Bogoyavlenskaya, 1977), and South Tianshan (Biske et al., 1977; Wang, 1988). Walmsley et al. (1974) noted *Lissatrypa linguata* (von Buch, 1834) from the Devonian of Bohemia, but this has been revised to *Cryptatrypa* and *Dubaria* by Smith and Johnson (1977). *Atrypa cephe* Barrande, 1879, *Atrypa fugitiva* Barrande, 1879, and *Atrypa linguata* var. *columbella* Barrande, 1879, from the Devonian of the Prague Basin may not be *Atrypoides* either (Copper, 2004).

Atrypoides aff. *A. scheii* (Holtedahl, 1914) is listed in a faunal list (without description and figures) by Biske et al. (1977) from the base of the Kunjak Formation, ?Lower Devonian, Isfara River Basin, South Tianshan. The other fossils from this assemblage do not definitively indicate a Devonian age. Both *Atrypoides* cf. *A. columbella* (Barrande, 1847) and *Atrypoides minuta* (Kulkov, 1967) from the Albishmebrak Formation (Early Devonian), South Tianshan, were mentioned by Wang (1988) and *Atrypoides* fossils from North Urals were referred to by Rong et al. (1987) with no description or figures.

As noted above, although there are reports of Devonian species of the genus, most are only known from records lacking detailed stratigraphic information, or the identification is questionable. To date, we know of no definitive occurrence of *Atrypoides* in the Devonian (Smith and Johnson, 1977; Rong et al., 1987; Copper, 2004). The youngest species may be *Atrypoides elatior* Havlíček and Štorch, 1990, from the upper Prídolí of the Prague Basin, Czech Republic, or *Atrypoides polaris modica* Rong, Zhang, and Chen, 1987, from the top of the Yanglugou Formation (upper Prídolí) in Tawo, Gansu and Zoige, Sichuan, China.

The geographical distribution of *Atrypoides* species (Fig. 7) was mainly confined to epeiric seas in low latitudes, indicating that they preferred relatively warmer tropical environments typical of most atrypides (e.g., Copper, 1977; Huang et al., 2018).

Range and distribution in China.—*Atrypoides* have been found in Telychian, Wenlock, Ludlow, and Prídolí rocks in China, although the distribution of each species varies (Fig. 8). *Atrypoides lentiformis* (Wang, 1956) is distributed throughout the Xiushan Formation (Telychian) and its contemporaneous strata, including small collections from Shiqian (NE Guizhou, Wang et al., 1980), Xiushan and Wuxi (Chongqing, field work), Butuo (South Sichuan, field work), and Ningqiang (South Shaanxi, Chen et al., 1991), and larger collections from

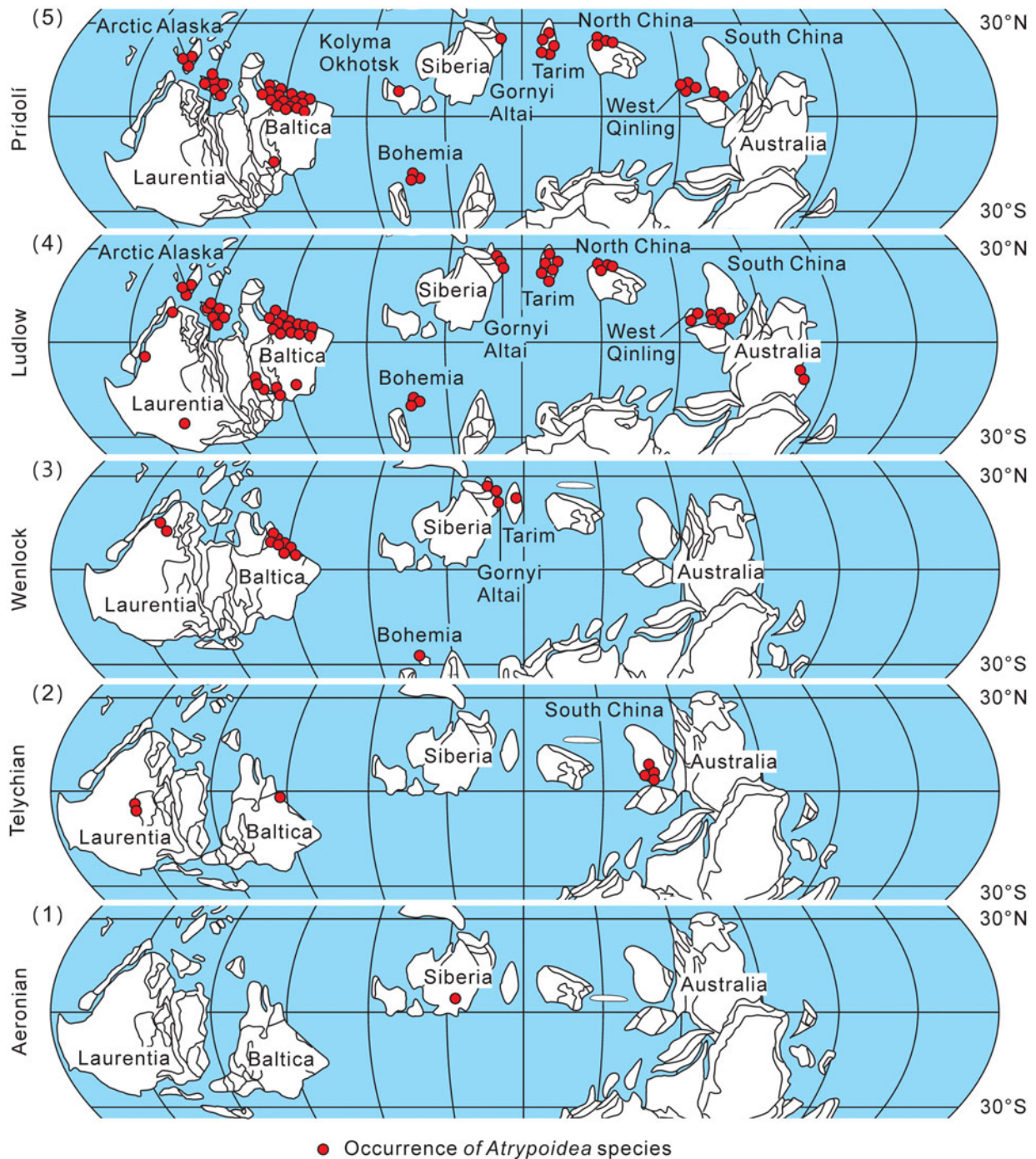


Figure 7. Distribution of *Atrypoidea* on Silurian geographical reconstructions at (1) Aeronian, (2) Telychian, (3) Wenlock, (4) Ludlow, and (5) Prídolí (Torsvik and Cocks, 2017; Rong et al., 2019). Based on the data in Appendix 1.

Changning and Gongxian (South Sichuan, Wang et al., 1980), Guangyuan (North Sichuan, Sheng, 1975; three species therein were revised as *A. lentiformis* by Wang et al., 1980), Dagan and Yanjin (NE Yunnan, Wang et al., 1980). *Atrypoidea lentiformis* from the bottom of the Xiushan Formation in Wuxi, Chongqing, is the earliest one in China (Fig. 8).

Due to the influence of the Kwangsian Orogeny, Wenlock strata are largely absent in South China (Chen et al., 2014; Rong et al., 2019), so the fossil record for this interval is sparse.

However, in contrast to South China, the Wenlock is developed in other blocks of China, and there is only one Wenlock species in China, *Atrypoidea tianshanensis* Rong and Zhang in Wang et al., 2001, on the Tarim block (Fig. 8).

In South China, earlier records of *Atrypoidea* from the Ludlow and Prídolí were limited to eastern Yunnan (Wang et al., 1980; Wang, 1995; Zhou and Huang, 2018) and Maowen, Sichuan, including *A. foxi* (Jones, 1974), *A. inflata* (Fang, 1974), *A. obesa* Fang, 1985, *A. ventriplana* Wang, Rong, and Yang,

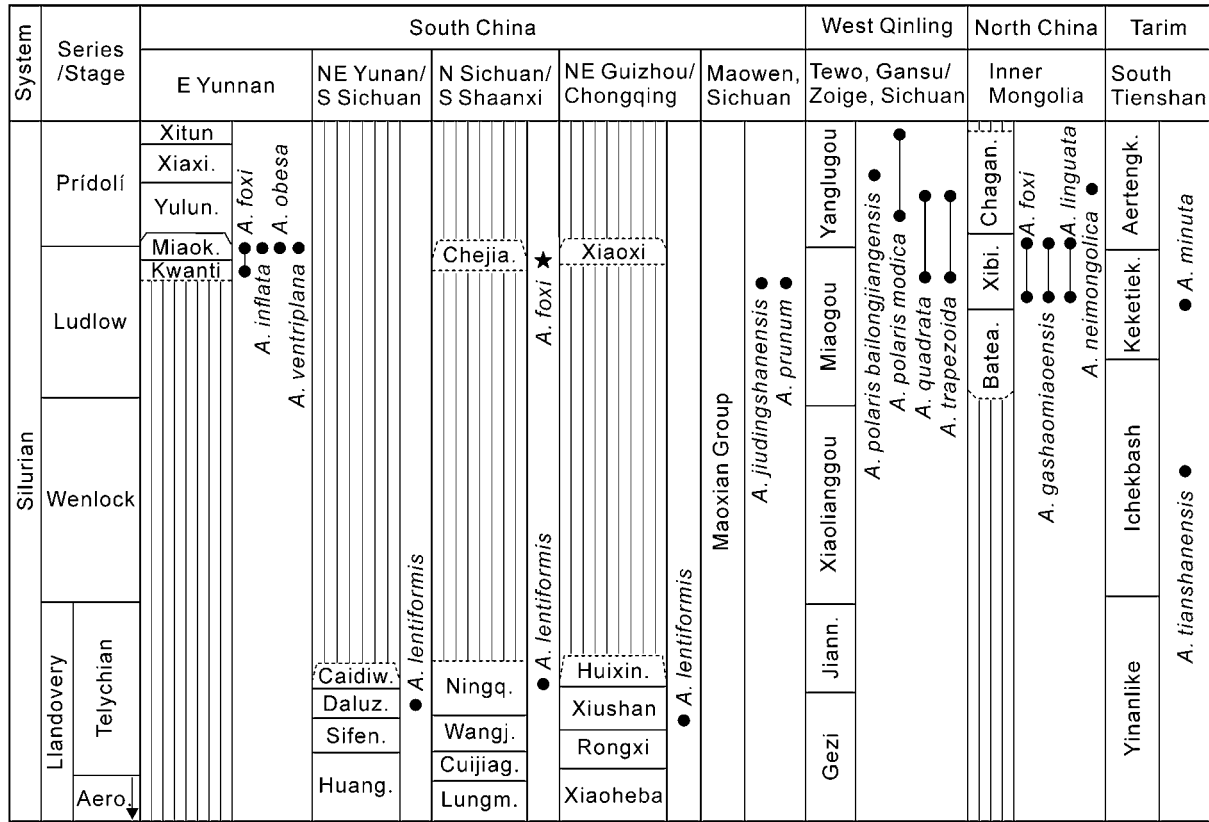


Figure 8. Occurrence of *Atrypoida* in Silurian sequence of China. Aero. = Aeronian; Xiaxi. = Xiaixishancun; Yulun. = Yulongssu; Miaok. = Miaokao; Caidiw. = Caidiwan; Daluz. = Daluzhai; Sifen. = Sifengya; Huang. = Huanggexi; Chejia. = Chejiaba; Ningq. = Ningqiang; Wangj. = Wangjiawan; Cuijiag. = Cuijiagou; Lungm. = Lungmachi; Huixin. = Huixingshao; Jiann. = Jiannigou; Chagan. = Chaganhebu; Xibi. = Xibiehe; Batea. = Bateaobao; Aertengk. = Aertengkesi; Keketiek. = Keketiekedaban.

1980, *A. jiujiangshanensis* Tong, 1984, and *A. prunum* (Dalman, 1828). *Atrypoida foxi* (Jones, 1974) is especially abundant, often forming an enrichment layer. The discovery of *A. foxi* (Jones, 1974) in the Chejiaba Formation is not only the first discovery in northern Sichuan, but also the first outside Yunnan in South China.

In other blocks, eight species were collected from Ludlow–Prídolí strata. *Atrypoida polaris modica* Rong, Zhang, and Chen, 1987, from the top of the Yanglugou Formation of the Tewo and Zoige region, is the last occurrence of *Atrypoida* in China.

Conclusions

In this paper, the global occurrences of 67 species of the *Atrypoida* together with its earliest species, *A. recta* from the Aeronian of Siberia, are summarized. In Llandovery and Wenlock times, the distribution of *Atrypoida* is limited, and only a few species are known. Through the rest of the Silurian, the genus rapidly diversified and became nearly cosmopolitan in distribution. Although there are some reports of Devonian *Atrypoida*, there is no convincing record at present of the genus after the end of the Silurian. *Atrypoida elatior* or *A. polaris modica* from the upper Prídolí should be the youngest species. *Atrypoida* lived in circum-tropical areas throughout their geologic life, indicating their preference for warm water.

This great diversity and wide distribution make *Atrypoida* a useful biostratigraphic tool. *Atrypoida foxi* only appears in

Ludlow–Prídolí globally, supporting the Ludlow age of the Chejiaba Formation. *Atrypoida foxi* is of practical significance for the rapid recognition of Ludlow and Prídolí strata during field survey in South China.

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Declaration of competing interests

The authors declare no competing interests.

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Appendix 1: 67 species and 14 sub-specific taxa of *Atrypoidea* based on summary work by Copper (1977, 2004) and the present study.

+species whose horizon or distribution is supplemented;
** newly added species; * newly added subspecies.

1⁺ *Atrypoidea australis* (Dun, 1904); Wenlock–Ludlow: New South Wales, Australia (Strusz, 1984, 2007, 2013, 2017; Strusz and Percival, 2018).

2 *Atrypoidea alata* (Nikiforova, 1970); upper Prídolí: Vaigach, Russia.

3** *Atrypoidea alexandrina* Nikiforova in Menakova, 1991; Prídolí: Tajikistan.

4 *Atrypoidea angusta* Mitchell and Dun, 1920; Ludlow: New South Wales, Australia.

5 *Atrypoidea bioherma* Jones and Narbonne, 1984; middle Ludlow: Somerset Island, Arctic Canada.

6 *Atrypoidea borealis* (Kirk and Amsden, 1952); Ludlow–Prídolí: Southeast Alaska (Copper, 1977).

7 *Atrypoidea camelina* (von Buch, 1840); Prídolí: eastern slopes of central Urals (Breivel and Breivel, 1988).

7.1* *Atrypoidea camelina camelina* (von Buch, 1840); Prídolí: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).

7.2 *Atrypoidea camelina karpovensis* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

7.3 *Atrypoidea camelina penitus* (Khodalevich, 1939); Ludlow: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).

7.4* *Atrypoidea camelina scheii* (Holtedahl, 1914); Prídolí: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).

8 *Atrypoidea carinata* (Johnson in Johnson and Reso, 1964); Ludlow: Nevada.

9** *Atrypoidea columbella* (Barrande, 1847); Wenlock: Altai (Kulkov, 1967); Ludlow: eastern slopes of Urals (Breivel and Breivel, 1988); Prídolí: Prague Basin and Urals (Havlíček and Štorch, 1990); Ludlow–Prídolí: South Tianshan, border area between Tajikistan and Kirgizstan (Wang, 1988).

10⁺ *Atrypoidea cuboidiformis* (Khodalevich, 1939); Prídolí: Urals (Breivel and Breivel, 1988).

11 *Atrypoidea elatior* Havlíček and Štorch, 1990; Prídolí: Prague Basin.

12** *Atrypoidea elongata elongata* (Khodalevich, 1939); Wenlock–Ludlow: eastern slopes of northern and central Urals.

13⁺ *Atrypoidea erebus* Jones, 1979a; Ludlow–Prídolí: Arctic Canada (Jones, 1979b).

14⁺ *Atrypoidea foxi* (Jones, 1974); Ludlow–Prídolí: Arctic Canada (Jones, 1979b), Southeast Alaska (Kirk and Amsden, 1952), Yunnan, South China (Rong et al., 1974; Wang et al., 1980; Jones and Rong, 1982; Fang, 1985; Wang, 1995; Zhou and Huang, 2018), Inner Mongolia, North China (Rong et al., 1985).

15 *Atrypoidea gashaomiaensis* Rong, Su, and Li, 1985; Ludlow–Prídolí: Inner Mongolia, North China.

16 *Atrypoidea gigantus* Jones, 1981; Prídolí: Arctic Canada.

17 *Atrypoidea gigas* (Khodalevich, 1939); Prídolí: North Urals.

18 *Atrypoidea globa* (Tschernyschew, 1885); unknown: western slopes of Urals.

19 *Atrypoidea hemsea* Copper, 2004; Ludlow: Gotland.

20 *Atrypoidea inflata* (Fang, 1974); Ludlow–Prídolí: Qujing, Yunnan, South China (Rong and Yang, 1980; Wang et al., 1980; Fang, 1985).

21 *Atrypoidea insigne* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

22 *Atrypoidea juidingshanensis* Tong, 1984; Ludlow: Maowen, Sichuan, South China.

23⁺ *Atrypoidea kuschvensis* (Tschernyschew, 1893); Wenlock–Prídolí: eastern slopes of Urals (Sapelnikov and Mizens, 1982).

24 *Atrypoidea ladzeica* Beznosova, 1977; Prídolí: North Urals.

25** *Atrypoidea latilingulata* Jin and Chatterton, 1997; Wenlock: Avalanche Lake area, southwestern District of Mackenzie, Canada.

26 *Atrypoidea lentiformis* (Wang, 1956); Telychian: Yunnan, Sichuan, Shaanxi and Guizhou, South China (Wang et al., 1980), Hudson Bay Lowlands, Canada (Jin et al., 1993).

27⁺ *Atrypoidea linguata* (von Buch, 1834); Wenlock: Avalanche Lake area, southwestern District of Mackenzie, Canada (Jin and Chatterton, 1997), eastern slopes of Urals (Breivel and Breivel, 1988), Altai (Kulkov, 1967); Ludlow: Prague Basin (Havlíček and Štorch, 1990); Ludlow–Prídolí: Bohemia (Walmsley et al., 1974), Inner Mongolia, North China (Su, 1976).

27.1* *Atrypoidea linguata linguata* (von Buch, 1834); Wenlock–Ludlow: Barrandien, Czech Republic (Sapelnikov and Mizens, 1982).

27.2* *Atrypoidea linguata operosa* (Kulkov, 1967); Ludlow–Prídolí: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).

27.3* *Atrypoidea linguata turjensis* (Khodalevich, 1939); Wenlock: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).

28 *Atrypoidea linguifera* (Khodalevich, 1939); Ludlow: North Urals.

29** *Atrypoidea linguliformis* Breivel and Breivel, 1988; Ludlow: eastern slopes of Urals.

30** *Atrypoidea minuta* (Kulkov, 1967); Wenlock: Altai; Ludlow: South Tianshan in Xinjiang, China (Wang, 1988).

31 *Atrypoidea minzhini* Rozman, 1988; Ludlow: Gobi Altai, Mongolia.

32 *Atrypoidea modesta* (Nikiforova, 1970); Ludlow: Vaigach, Russia; Ludlow: Prague Basin (Havlíček and Štorch, 1990).

32.1 *Atrypoidea modesta postmodesta* (Nikiforova, 1970). Ludlow: Vaigach, Russia.

33** *Atrypoidea muschketovi* (Nikiforova, 1937); Prídolí: Central Asia.

34 *Atrypoidea nasa* (Nikiforova, 1949); Ludlow: Kirgizstan.

- 35 *Atrypoidea neimongolica* Hou and Zhao in Su, 1976; Prídolí: Inner Mongolia, North China (Rong et al., 1985).
- 36⁺ *Atrypoidea netserki* Jones, 1981; Ludlow–Prídolí: Arctic Canada (Smith and Johnson, 1977).
- 37 *Atrypoidea obesa* Fang, 1985; Ludlow: Qujing, Yunnan, South China.
- 38⁺ *Atrypoidea operosa* (Kulkov, 1967); Wenlock: eastern slopes of Urals (Breivel and Breivel, 1988); Ludlow: central Altai (Kulkov, 1967), South Tianshan in Xinjiang, China (Wang et al., 2001).
- 39** *Atrypoidea ovata* Breivel and Breivel, 1988; Ludlow: eastern slopes of Urals.
- 40 *Atrypoidea pavdensis* (Mizens, 1977); Wenlock: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982; Breivel and Breivel, 1988).
- 41 *Atrypoidea penitus* (Khodalevich, 1939); Ludlow: Urals.
- 41.1 *Atrypoidea penitus elongata* (Khodalevich, 1939); Ludlow: Isov region, Urals.
- 42 *Atrypoidea pentagonalis* Beznosova and Mizens, 1980; Prídolí: Urals.
- 43** *Atrypoidea petropadovski* Breivel and Breivel, 1988; Prídolí: eastern slopes of Urals.
- 44⁺ *Atrypoidea phoca* (Salter, 1852); Ludlow–Prídolí: Arctic Canada (Holtedahl, 1914; Jones, 1974, 1979b, 1981; Rong et al., 1987); Prídolí: Latvia (Paškevičius, 1973), Northeast Eurasia (Baranov, 2015).
- 44.1* *Atrypoidea scheii fossula* (Nikiforova, 1970); Prídolí: Vaigach, Russia.
- 44.2* *Atrypoidea scheii gibbera* (Nikiforova, 1970); Prídolí: Vaigach, Russia.
- 45 *Atrypoidea planata* Perry, 1984; Ludlow: Yukon, Canada.
- 46⁺ *Atrypoidea polaris* Jones and Packard, 1980; Prídolí: Arctic Canada.
- 46.1 *Atrypoidea polaris bailongjiangensis* (Fu, 1982); Prídolí: Tewo, Gansu, China (Rong et al., 1987).
- 46.2 *Atrypoidea polaris modica* Rong, Zhang, and Chen, 1987; Prídolí: Tewo, Gansu and Zoige, Sichuan, China (Fu, 1982).
- 47 *Atrypoidea praelingulata* Jin, Caldwell, and Norford, 1993; Telychian: Hudson Bay Lowlands, Canada.
- 48⁺ *Atrypoidea prunum* (Dalman, 1828); Ludlow: Gotland (Dalman, 1828; Hisinger, 1828; Gagel, 1890; Copper, 1977, 2004), Estonia (Copper, 1977, 2004; Kaljo and Rubel, 1982), Podolia (Nikiforova et al., 1985), Arctic Canada (Copper, 1977), Maowen, Sichuan, China (Tong, 1984); Ludlow–Prídolí: Tajikistan (Menakova, 1991).
- 48.1* *Atrypoidea prunum gigas* (Khodalevich, 1939); Ludlow–Prídolí: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).
- 49 *Atrypoidea quadrata* Fu, 1982; Ludlow–Prídolí: Tewo, Gansu, China.
- 50** *Atrypoidea recta* (Nikiforova in Nikiforova and Andreeva, 1961); Aeronian: Moyero River Basin, Northwest Siberia (Havlíček and Štorch, 1990).
- 51⁺ *Atrypoidea renitens* (Barrande, 1879); Wenlock: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982); Ludlow: Prague Basin (Havlíček and Štorch, 1990).
- 52 *Atrypoidea saaremaaensis* Copper and Rubel in Copper, 1977; Ludlow: Estonia.
- 53 *Atrypoidea shrocki* (Cooper, 1942); Ludlow: Indiana, USA.
- 54 *Atrypoidea sphaerica* (Sapelnikov, 1956); Ludlow: Altai.
- 55** *Atrypoidea sosvaensis* Breivel and Breivel, 1988; Ludlow: eastern slopes of Urals.
- 56⁺ *Atrypoidea subcamelina* (de Verneuil, 1845); Prídolí: eastern slopes of Urals (Breivel and Breivel, 1988).
- 57⁺ *Atrypoidea subrecta* (Mizens, 1977); Telychian–Wenlock: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982; Breivel and Breivel, 1988).
- 58 *Atrypoidea sulcata* (Lindström, 1861); Ludlow: Gotland (Gagel, 1890; Bassett and Cocks, 1974; Copper, 2004).
- 59** *Atrypoidea tectiformis* (Tschernyschew, 1893); Prídolí: Central Asia (Nikiforova, 1937), Urala, Altai (Nikiforova, 1937).
- 60 *Atrypoidea tenuis* (Kirk and Amsden, 1952); Ludlow–Prídolí: Southeast Alaska.
- 61 *Atrypoidea tianshanensis* Rong and Zhang in Wang et al., 2001; Wenlock: South Tianshan in Xinjiang, China.
- 62 *Atrypoidea trapezoida* Fu, 1982; Ludlow–Prídolí: Tewo, Gansu, China.
- 63 *Atrypoidea turjensis* (Khodalevich, 1939); Wenlock: eastern slopes of northern and central Urals.
- 64⁺ *Atrypoidea uralica* (Khodalevich, 1939); Ludlow–Prídolí: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982; Breivel and Breivel, 1988).
- 65 *Atrypoidea vagranica* (Khodalevich, 1939); Ludlow: Urals.
- 66 *Atrypoidea vangyricea* Beznosova and Mizens, 1980; Prídolí: Urals.
- 67 *Atrypoidea ventriplana* Wang, Rong, and Yang, 1980; Ludlow: Qujing, Yunnan, South China.

Appendix 2: 23 sub-specific taxa of *Atrypoidea* based on summary work by Copper (1977, 2004)

* newly added forma, cf., or aff. species.

1* *Atrypoidea* cf. *A. columbella* (Barrande, 1847); Ludlow–Prídolí: South Tianshan in Xinjiang, China (Wang, 1988; Wang et al., 2001).

2* *Atrypoidea linguata* forma *columbella* (Barrande, 1847); Wenlock–Prídolí: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).

3 *Atrypoidea linguata* var. *columbella* (Barrande, 1847); Prídolí: Prague Basin.

4 *Atrypoidea scheii* forma *concinna* (Oradovskaya, 1975); Ludlow–Prídolí: Kolyma River Basin, NE Russia.

5 *Atrypoidea scheii* forma *crassa* (Modzalevskaya, 1981); Prídolí: Chernyshev Range, Prepolar Urals.

6 *Atrypoidea scheii* forma *fossula* (Beznosova and Mizens, 1980); Prídolí: Foma-Yu River, Urals.

7 *Atrypoidea scheii* forma *gibbera* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

8 *Atrypoidea insigne* forma *grebensis* (Nikiforova, 1970); upper Prídolí: Vaigach, Russia.

9* *Atrypoidea* cf. *A. karpovensis* (Nikiforova, 1970); Prídolí: Zoige, Sichuan, China (Rong et al., 1987).

10* *Atrypoidea* cf. *A. kuschvensis* (Tschernyschew, 1893); Prídolí: Vaigach, Russia (Nikiforova, 1970).

11 *Atrypoidea elongata* forma *lata* Sapelnikov and Mizens, 1982; Prídolí: eastern slopes of northern and central Urals.

12* *Atrypoidea* aff. *A. linguifera* (Khodalevich, 1939); Ludlow: eastern slopes of Urals (Breivel and Breivel, 1988).

13* *Atrypoidea elongata* forma *linguifera* (Khodalevich, 1939); Ludlow: eastern slopes of northern and central Urals (Sapelnikov and Mizens, 1982).

14 *Atrypoidea phoca* forma *longa* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

15* *Atrypoidea phoca* forma *media* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

16 *Atrypoidea phoca* forma *paracamelina* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

17* *Atrypoidea* cf. *A. phoca* (Salter, 1852); Ludlow: South Tienshan in Xinjiang, China (Wang et al., 2001); Ludlow–Prídolí: Inner Mongolia, North China (Rong et al., 1985).

18* *Atrypoidea* ex gr. *phoca* (Salter, 1852); Ludlow–Prídolí: Lithuania (Musteikis and Modzalevskaya, 2002), Russian Arctic islands (Musteikis and Modzalevskaya, 2002), northern and central Urals (Musteikis and Modzalevskaya, 2002); Prídolí: Podolia (Ukraine) (Musteikis and Modzalevskaya, 2002), Byelorussia (Musteikis and Modzalevskaya, 2002).

19* *Atrypoidea modesta* forma *postmodesta* (Nikiforova, 1970); Ludlow: Vaigach, Russia.

20 *Atrypoidea phoca* forma *subscheii* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

21 *Atrypoidea scheii* forma *superma* (Modzalevskaya, 1981); Prídolí: Chernyshev Range, Prepolar Urals.

22 *Atrypoidea phoca* forma *typica* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

23 *Atrypoidea scheii* forma *typica* (Nikiforova, 1970); Prídolí: Vaigach, Russia.

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