

LOWER DEVONIAN (PRAGIAN) BRACHIOPODS FROM THE DASHATIAN SECTION, GUANGXI, SOUTH CHINA

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Abstract. Lower Devonian brachiopods in South China are very rare since most areas lack deposits owing to an uplift movement of the Guangxi (Caledonian) Orogeny. In this paper, we describe a brachiopod fauna consisting of 13 species in 12 genera from the Nagaoling Formation at the Dashatian section in the suburb area of the Nanning City, Guangxi, South China. This fauna is dominated by small rhynchonellide and spiriferide species, along with chonetidines, strophomenides, atrypides, athyridides and others. The early Pragian age for the brachiopod-bearing horizons in the Nagaoling Formation is constrained by the associated early Pragian conodonts *Eognathodus sulcatus* Zone. About 33% genera of the brachiopod fauna are endemic to South China, therefore they do not provide any clear evidence for its paleobiogeographical link to the faunas of Europe, Australia, or North America. This fauna is paleoecologically interpreted as being deposited in a shallow, oxygen-rich, low to moderate energy, subtidal palaeoenvironment in the early Pragian and it corresponds to the benthic assemblage BA2 to upper BA3.

INTRODUCTION

The Lower Devonian marine deposits in South China have a limited distribution due to the regional uplift by the Guangxi (Caledonian) Orogeny. A Lower Devonian brachiopod fauna was first documented from the Nagaoling Formation of the Nagaoling Hill, Liuqing Village of Guangxi, represented by the *Orientospirifer nagaolingensis* Assemblage (Hou 1959; Hou & Xian 1975). An equivalent of the Nagaoling Formation containing diverse fossils has been found in northeast Vietnam that is adja-

cent to Guangxi, but with a totally different brachiopod fauna represented by the *Euryspirifer tonkiensis* Assemblage (Thanh et al. 2013). The Nagaoling brachiopod fauna is therefore potentially very important in studying the Lower Devonian and its worldwide correlations. However, this fauna is so far poorly known, with only nine genera of Brachiopoda being documented due to the limited outcrops and fossils. Moreover, due to the absence of high resolution biostratigraphic tools (e.g., conodont and others), the Nagaoling brachiopod fauna has been roughly assigned to the Gedinnian-Siegenian interval, which is approximately correlative to the Lochkovian-Pragian interval of the present international

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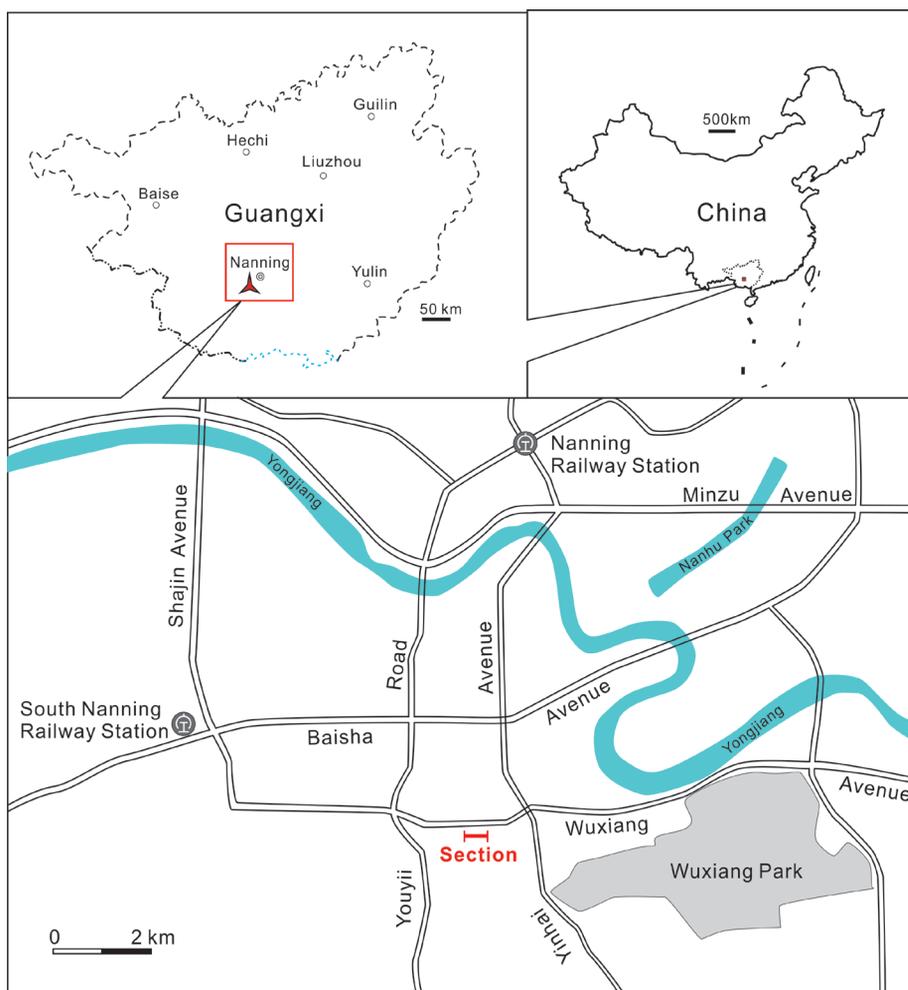


Fig. 1 - Location map showing the Dashatian section in the suburb of Nanning City, Guangxi, South China.

timescale (Becker et al. 2012). In addition, so far the biostratigraphical successions of both stages have not been well established in South China.

Recently, an upper Lochkovian to Pragian succession (and probably part of Emsian) has been found in a roadcut at the Dashatian section near Nanning City of Guangxi, South China (Wang et al. 2016), where it is mainly composed of siltstones and mudstones alternated with carbonates. Abundant brachiopods in association with conodonts, tentaculitides, bivalves and other biota have been found in the lower and middle parts of the section (Wang et al. 2016; Wei et al. 2019). In this paper, we report the brachiopods from the Dashatian section with detailed descriptions and discussions on their age and palaeoecological implications.

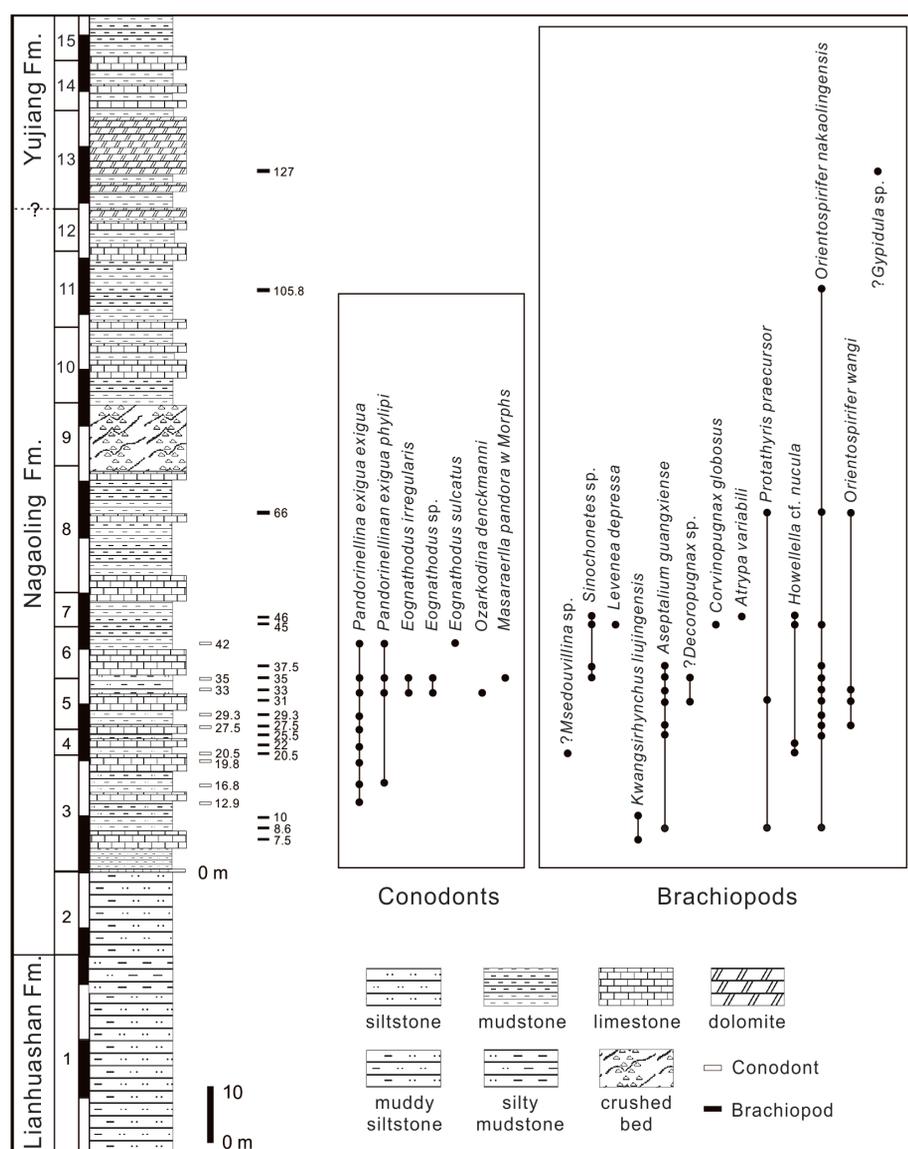
GEOLOGICAL SETTING

The studied section is located in the suburb of Nanning City of Guangxi, about 1 km west of

intercross of Wuxiang Avenue and Yinghai Avenue ($22^{\circ}45'40''\text{N}$; $108^{\circ}18'06''\text{E}$) (Fig. 1). This region was uplifted during the late Silurian as the consequence of the Kwangxian (=Guangxi) (Caledonian) Orogeny (Chen et al. 2014). Marine environments re-occurred in this areas from the beginning of Devonian, and seawater transgressed northward from the southern Qinfang Trough (Wu et al. 1987; Liu et al. 1993; Chen et al. 2001). This transgression is recorded by marine deposits in the Guangxi area, where the Lochkovian terrigenous siliciclastic-dominated rocks are replaced by siliciclastic rocks interbedded with carbonates in the Pragian and Emsian, and followed mainly by carbonates in the Middle to Late Devonian.

The Dashatian section, with 208 m strata exposed along the southern roadcut of the Wuxiang Avenue, contains a part of the Lianhuashan Formation, the Nagaoling Formation and probably a part of the Yujiang Formation (Fig. 2). The base of the section, exposed in the anticline crest, is composed of yellowish-brown or grey silty mudstone

Fig. 2 - Stratigraphic successions of the Dashatian section in Guangxi of South China, with occurrences of brachiopods (black bars) and conodonts (white bars). Both brachiopods and conodonts are sampled by meters from the base of bed 3 in the Nagaoling Formation. Conodonts data from Wang et al. (2016).



or muddy siltstone, which is named Lianhuashan Formation with about 35 m in thickness. The main part of the section is represented by the Nagaoling Formation, which consists of greyish-green or yellow - gray siltstones and mudstones alternated with carbonates in the lower part. At about 85 m above the base of the Nagaoling Formation, a fault crushed zone (about 10 m thick) is present, which is composed of broken yellow mudstone. In the upper part of the section, greyish-black mudstones and carbonates dominate, with argillaceous limestone and dolostone interbedding. This part could be tentatively placed into the base of the Yujiang Formation, but a more precise assignment requires further work.

Brachiopods have been collected by the author (S. Shen) and others in the framework of conodont sampling figured by Wang et al. (2016), with

meters (from the base of bed 3 in which limestone is firstly developed) are adopted as sampling numbers as shown in Fig. 2.

BRACHIOPOD FAUNAL COMPOSITION AND AGE DETERMINATION

At the Dashatian section, brachiopods are richer in the lower parts (beds 3 to 8) of the Nagaoling Formation, whilst a few species occur in the middle and upper parts of the section (beds 11 and 13). A majority of the brachiopods have been collected from several horizons in the lower part, and from which conodonts have been described by Wang et al. (2016). Besides, tentaculitides from the lower part of the Nagaoling Formation of this section have been described by Wei et al. (2019). In this

paper, a total of 13 species in 12 genera of eight orders are identified from the Dashatian section (see Fig. 2 for name and range).

In the fauna, small-sized rhynchonellides and spiriferides are predominant in the Nagaoling Formation. Four species of rhynchonellides (*Aseptalum guangxiense* (Wang, 1964), *Kwangsirhynchus liujingensis* Hou & Xian, 1975, *Corvinopugnax globosus* Hou & Xian, 1975, ?*Decoropugnax* sp.) were found in several horizons with very high abundance. Spiriferides from this formation are characteristic, represented by a large number of disarticulated valves and some conjoined shells of *Orientospirifer nakaolingensis* (Hou, 1959), *O. wangi* (Hou, 1959), along with some small *Howellella* cf. *nucula* (Barrande, 1879) accumulating in the lower part of the Nagaoling Formation. Other groups of brachiopods from this section are sparse, commonly with few numbers for each species and genus (see systematics for details).

Five species of the studied fauna are all cosmopolitan in the Lower Devonian (mainly Pragian-Emsian), including ?*Mesodowillina* sp., *Levenea depressa* Wang, 1955, *Atrypa variabilis* Wang & Rong, 1986, *Protathyris praecursor* Kozłowski, 1929 and *Howellella* cf. *nucula*. However, the other five species, *Aseptalum guangxiense*, *Kwangsirhynchus liujingensis*, *Orientospirifer nakaolingensis*, *O. wangi* and *Sinochonetes* sp., are endemic to South China. They have only been found until now from the Pragian of Guangxi, in the Liujing section which is about 60 km east of the Dashatian section (Hou 1959; Hou & Xian 1975; Yang et al. 1977; Wang et al. 1981; Zhang & Pojeta 1986). It indicates that this brachiopod fauna is most likely Pragian in age. A questionable species of *Gypidula*, which is a common species in the Emsian, is recovered from the upper part of the Dashatian section. It suggests a possible Emsian age for the upper part of the section.

The age determination of the brachiopod fauna is supported by conodonts studied by Wang et al. (2016). Conodonts from the brachiopod-bearing horizons at the Dashatian section are assigned to the *Eognathodus irregularis-Gondwania profunda* Zone in North America, or *Eognathodus sulcatus* Zone in Europe, suggesting an early Pragian age. However, Wei et al. (2019) reported tentaculitides from the lower part of Nagaoling Formation at the Dashatian section, suggesting a slightly older age at the Lochkovian/Pragian boundary. Nevertheless, judging from the brachiopod fauna, apart from a single

conjoined shell from the upper part of the section (sample 127) which could be probably related to the Emsian, most the species found in the lower and middle parts of the Nagaoling Formation at the Dashatian section favor a Pragian age (probably early Pragian), rather than the Lochkovian/Pragian boundary interval.

COMPARISON WITH COEVAL FAUNAS AND IMPLICATION TO PALAEOECOLOGY

In South China, Lochkovian and Pragian brachiopods are rarely found owing to the hiatus as a consequence of the regional uplift caused by the Kwangsi Orogeny. The only reported brachiopod fauna from the lower part of the Lower Devonian was from the Nagaoling Formation at the Liujing section (Hou & Xian 1975), which is located 60 km east of the Dashatian section. The Nagaoling brachiopod fauna therefore represents the first record of the Devonian shallow benthic fauna in South China. Generally, the Pragian brachiopod fauna from the Dashatian section shows a great similarity to that from the Liujing section, with eight genera and species in common. In addition, there are other four species, including *Mesodowillina* sp., *Levenea depressa*, ?*Decoropugnax* sp. and *Atrypa variabilis*, which were found for the first time in the Nagaoling Formation from the Dashatian section.

It has been observed on a global scale that there is a fundamental difference between the brachiopod faunas associated with the deep-water calcareous facies of Bohemia (Boucot et al. 1969) and those from shallow water terrigenous facies of the Rhineland. Brachiopods from the lower Pragian in Bohemia are characterized by atrypides (*Reticulatrypa fairhillensis* Savage, 1970, *Ogilviella prolifica* Savage, 1970, *Atrypina talenti* Savage, 1970, *Atrypa reticularis inversa* Savage, 1970, *Spirigerina subpramarginalis* Khalifin, 1948) and smooth spiriferides (*Quadrithyris robusta molongensis* Savage, 1969, *Proreticularia* (= *Alaskospira*) *beddiei* Savage, 1969, *Ambocoelia praecox dorsiplicata* Savage, 1969) as well as *Cyrtina praecedens* Kozłowski, 1929, and have close similarities to those from eastern Australia (Savage 1968, 1969, 1970, 1971; Lenz et al. 1985; Havlíček 1994). In contrast, the brachiopod fauna from terrigenous facies of lower Siegenian in the Rhineland, which is regarded as intertidal to upper subtidal settings, is

composed of sole *Crassirensseleeria crassicosta* (Koch, 1881) (Schemm-Gregory & Jansen 2007; Jansen, 2019).

The coeval *Davidsoniatrypa johnsoni* Lenz, 1968 fauna from the conodont *sulcatus* Zone (early Pragian) from Yukon of Canada is characterized by high diversity of atrypides (e.g., *Davidsoniatrypa johnsoni*, and a number of species of *Atrypa*, *Desquamatia* and *Spinatrypa*) and *Gypidula*, or spiriferides (*Ambocoelia praecox*, *Plicocyrtina sinuplicata*) (Lenz 1977). This fauna is evident to be of Bohemian-Uralian affinity, suggesting a deeper water carbonate palaeoenvironment.

By comparison, the brachiopod fauna from the Nagaoling Formation at the Dashatian section exhibits a unique characteristic in light of faunal composition and sedimentary palaeoenvironment. At the generic level, only some long range or cosmopolitan taxa are common to other regions, such as *Mesodouwillina*, *Gypidula*, *Protathyris* and *Howellella*. However, species composition is varied in different areas. It is obvious that the brachiopod fauna from the Dashatian section, with 33% of endemic species, is quite distinct from those in Europe, Australia, or North America.

As for the environment, the brachiopod-bearing horizons in the Dashatian section consist of thin-bedded argillaceous limestones and mudstones, representing a shallow subtidal, low-moderate energy settings. Brachiopods in the Nagaoling Formation are of moderate diversity, with small-sized spiriferides and rhynchonellides being particularly abundant (make up about 47% and 34% of the specimens respectively). *Orientospirifer* from the Dashatian section is largely derived from the mudstones or argillaceous limestone, accompanied usually with some other small species such as *Sinochonetes* sp., *Aseptalum guangxiense* and *Howellella* cf. *nucula*. The species of *Orientospirifer* are commonly preserved as disarticulated valves, but a few conjoined shells are observed occasionally. It readily suggests a shallow, moderate to weak water energy palaeoenvironment above the wave base, which is compatible to the benthic assemblage BA2 to upper BA3 (Boucot 1975).

At the type section of the Nagaoling Formation in Liujing, Guangxi, where the *Orientospirifer* fauna was first illustrated, the diverse fossils including brachiopods, bivalves, gastropods, tentaculitides and others are transported and poorly preserved

in the basal part of the section, suggesting littoral to neritic conditions (Kuang et al. 1989). In an equivalent of the Nagaoling Formation of Nandan, brachiopod fragments assigned to *Orientospirifer wangi* have been found from the top of the Danling Formation at Luofu section (Zhang & Pojeta 1986), accompanied by sparse bivalves and fishes. The deposits are argillaceous sandstones, siltstones and sandy mudstones, which are thought to be tidal flat facies with alternating hydrodynamic conditions in the early Pragian (Li 1989).

Wang & Yang (1998) illustrated the *Orientospirifer wangi* fauna (including six species in five genera) from the top of the Zhangmu Formation at the Zhangmu section, Yulin, which was located on the margin of the Qinfang trough (Fig. 3). This fauna is correlated with the upper Pragian based on graptolites, and occurs chiefly in the mudstones and cross-bedded sandstones, which suggest a high energy littoral facies (Yang et al. 1999). However, the *Orientospirifer* fauna in the Zhangmu section is very different from those in the shallow water facies in the early Pragian (i.e., Liujing and Dashatian sections), in light of the very low diversity and composition. In addition, a deeper water habitat (BA3) of the Zhangmu fauna is suggested by Yang et al. (1999), in association with occurrences of unidentified small-sized rhynchonellide brachiopods and accompanied fossils of trilobites, gastropods and bivalves.

The *Orientospirifer* fauna has also been reported from the silty mudstones or shales in the lower Emsian, with extraordinary accumulation of *O. wangi* in the Miaohuan and Dale sections as shown in Fig. 3, although the occurrences are still in doubt due to the lack of any description or illustration. The later "*Orientospirifer*" communities were reported to be associated with *Lingula* in many localities, suggesting shallow, restricted habitats in BA2 (Xian et al. 1992). They are different from those in the early Pragian from the Nagaoling Formation in view of very low diversity and almost exclusive occurrence of *Orientospirifer* (occasionally with rare *Howellella*).

In summary, the brachiopods represented by the *Orientospirifer-Aseptalum* fauna attained dominance in the early Pragian in South China, readily dwelling in the clastic facies of the littoral zones in Guangxi. The seafloor settings (with moderate water hydrodynamic conditions and water depth in BA2 to upper BA3) in the Dashatian and Liujing

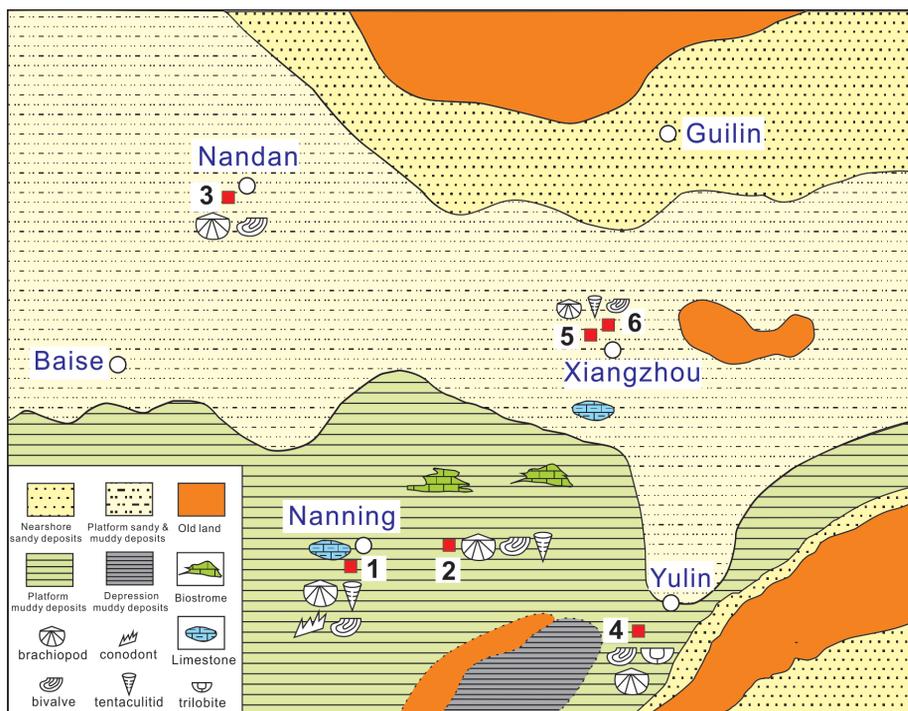


Fig. 3 - Sedimentary reconstruction of the Pragian in Guangxi of South China. *Orientalospirifer* community reported from section 1-6 are indicated. 1) Dashatian section (this paper); 2) Liujiing section; 3) Luofu section; 4) Zhangmu section; 5) Miaohuan section (Shanglun Mb., Nayi Mb.); 6) Dale section (Tonggen Fm.). Base map compiled from Wang (1985), Wu et al. (1987) and Yu et al. (2018).

sections seem favorable for faunal diversification, which is quite different from the stressed setting of the tidal flat represented by Luofu section in the early Pragian. However, the fauna declined in diversity and abundance in the late Pragian and Emsian based on data from both shallow environments (Miaohuan and Dale sections) and deep water facies (Zhangmu section) in South China. The restricted shallow water condition in the Miaohuan and Dale sections, as well as alternating deposits of shallow and deep water facies in Zhangmu, seems to have negative effects on the faunal diversification.

Apart from brachiopods, diverse marine fossils from the Dashatian section, including conodonts, tentaculitides, gastropods, ostracods and bryozoans, also support a shallow benthic setting interpretation. The thick-shelled tentaculitides found from the mudstones and argillaceous limestones in the Dashatian section also suggest a favorable habitat with rich oxygen and weak hydrodynamic condition for benthic faunas (Wei et al. 2019).

SYSTEMATIC PALAEOLOGY

All specimens are housed in the Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGP).

Order **Strophomenida** Öpik, 1934
 Superfamily Strophomenoidea King, 1846
 Family Amphistrophiidae Harper, 1973
 Subfamily Mesodouvillininae Harper & Boucot, 1978

Genus *Mesodouvillina* Williams, 1950

Type species: *Stropheodonta subinterstitialis seretensis* Kozłowski, 1929

? *Mesodouvillina* sp.

Pl. 1, figs 1, 2

Material: One single ventral valve (NIGP170328).

Remarks. The single valve differs from *Leptostrophia* in having transversely semicircular, gently convex outline and unequally parvicostellate ornament. Externally, the specimen somewhat resembles *Megastrophia semispherioidea* (Hou & Xian, 1975) and *Mesodouvillina birmanica* (Reed) in Wang et al. (1974, pl. 4, figs 24-27), which were assumed as conspecifics according to Wang & Rong (1986, p. 89), but the latter two species have subcircular outlines, much larger sizes, and strong convexities of ventral valves. However, further identification is not permitted due to unknown internal characters.

Occurrences. Bed 4 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Order **Orthida** Schuchert & Cooper, 1932
 Suborder **Dalmanellidina** Moore, 1952
 Superfamily Dalmanelloidea Schuchert, 1913
 Family Dalmanellidae Schuchert, 1913
 Subfamily Isorthinae Schuchert & Cooper, 1931
 Genus *Levenea* Schuchert & Cooper, 1931

Type species: *Orthis subcarinata* Hall, 1857

Levenea depressa Wang, 1955

Pl. 1, figs 3, 4

- 1955 *Levenea depressa* Wang, p. 161, pl. 93, figs 3-8.
 1956 *Levenea depressa* Wang, pp. 158-160, pl. 3, figs 1-6.
 1964 *Levenea depressa* Wang; Wang et al., p. 122, pl. 14, figs 11-15.
 1975 *Levenea depressa* Wang; Hou & Xian, p. 19, pl. 4, figs 6-8.
 1986 *Levenea depressa* Wang; Wang & Rong, p. 77, pl. 3, figs 1-4; pl. 4, figs 1-27.

Material: Two dorsal valves (NIGP170329, 170330).

Remarks. Our two dorsal valves have subcircular outline, bifurcating costae, with weak concentric lamellae and narrow sulcus beginning from the beak. This species has been recorded largely from the Yujiang Formation (Emsian) in Guangxi as is shown in the above list. The Emsian form shows slight differences in having developed fascicostellate costae, and variably developed concentric lamellae. The ornamentation, however, is not sufficient for differentiation of species.

Occurrences. Bed 7 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Order **Productida** Sarytcheva & Sokolskaya, 1959
 Suborder **Chonetidina** Muir-Wood, 1955
 Superfamily Chonetoidea Bronn, 1862
 Family Chonetidae Bronn, 1862
 Subfamily Dagnachonetinae Racheboeuf, 1981
 Genus *Sinochonetes* Wang, Boucot and Rong, 1981
 Type species: *Chonetes minutisulcatus* Hou & Xian, 1975

***Sinochonetes* sp.**

Pl. 1, figs 5-9

Material: Four complete ventral valves (NIGP170331-170334) and numerous fragmentary valves.

Remarks. Specimens of medium size, transverse, moderately convex with a weak median sulcus in some specimens, flat ears, rounded cardinal extremities, and long and straight hinge-line equal

to the maximum width of the valve; costae low and rounded, originating from umbo, commonly bifurcating, superimposed by undulating concentric fila; two or three tubular spines along either side of the hingeline, developing at high angle or nearly perpendicular to the hinge margin; interior unobserved.

This species is characterized by transverse semicircular outline, flat ears, varying development of sulcus and bifurcating costae superimposed by undulating concentric fila. It differs from the species of *Parachonetes*, which has a similar outline but without sulcus and fold (see Johnson 1966, p. 367 for description).

Our specimens differ from the type species *Sinochonetes minutisulcatus* (Hou & Xian 1975, p. 25, pl. 1, figs 3, 4) that is recorded from the Nagaoling Formation, as the latter has subcircular outline, shorter and smaller ears and slightly coarser costae. *Chonetes ellipticus* Hou & Xian, 1975 (p. 26, pl. 1, figs 1, 2), and the specimens attributed to *Chonetes sarcinulatus* (Schlotheim) by Wang et al. (1974, pl. 1, figs 1-4) from the Nagaoling Formation are very close as well. They are both considered synonyms of the type species, as no more differences but the varied development of sulcus and fold are observed based on 199 specimens by Wang et al. (1981, p. 290).

Occurrences. Beds 6, 7 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Order **Pentamerida** Schuchert & Cooper, 1931
 Suborder **Pentameridina** Schuchert & Cooper, 1931
 Superfamily Gypiduloidea Schuchert & LeVene, 1929
 Family Gypidulidae Schuchert & LeVene, 1929
 Subfamily Gypidulinae Schuchert & LeVene, 1929
 Genus *Gypidula* Hall, 1867

Type species: *Gypidula typicalis* Amsden, 1953

?*Gypidula* sp.

Pl. 1, figs 21-24

Material: One conjoined shell (NIGP170335).

Remarks. The specimen is characterized by small shell with elongate triangular outline; posterior portion very narrow with weak and small ventral beak; weakly developed ventral fold and anteriorly

distinct dorsal sulcus, commonly with three simple, angular costae on flanks originating near umbo.

The single specimen is comparable to genera of the subfamily Gypidulina, as having simple costae without bifurcating and lacking micro-ornamentation. It is somewhat similar to *Siberella* by coarse and angular costae arising from umbo, as well as small and narrow ventral beak. But *Siberella* has larger size, transverse outline and weak and less costae on flanks. Our specimen somewhat resembles *Gypidula loczyi* Grabau, 1931 (Grabau 1931, p. 75, text-fig. 4; Hou & Xian 1975, p. 28, pl. 4, figs 11-14) by size and outline, but with more and stronger costae on flanks. Here we retain it as a questionable taxon as further assignment is not permitted by the limited material.

Occurrences. Bed 13 at Dashatian section, southern Guangxi, South China.

Order **Rhynchonellida** Kuhn, 1949

Superfamily Uncinuloidea Rzhonsnitskaia, 1956

Family Innaechiidae Baranov, 1980

Subfamily Corvinopugnacinae Savage, 1996

Genus *Corvinopugnax* Havlíček, 1961

Type species: *Rhynchonella corvina* Barrande, 1847

Corvinopugnax globosus Hou & Xian, 1975

Pl. 1, figs 10, 11

1975 *Corvinopugnax globosus* Hou & Xian, pp. 36-37, pl. 2, figs 6, 7.

Material: One ventral valve and one dorsal valve (NIGP170336, 170337).

Remarks. Our specimens resemble those from the Nagaoling Formation at the Liujing section in Guangxi, by having medium size, slightly transverse subcircular outline; distinct ventral sulcus and dorsal fold occurring from mid-length; smooth umbo; simple costae, weak at midlength and becoming rounded anteriorly; flanks weakly inclined, with five-six costae on each side; sulcus with three simple round costae, fold with five costae.

This species differs from the type species *C. corvina* (Barrande 1847) illustrated by Havlíček (1961, p. 36, pl. 13, figs 2, 3), as the latter has much more transverse subpentagonal outline, wide tongue with more costae and coarse plicae restricted to anterior.

Occurrences. Bed 7 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Genus *Aseptaliium* Hou & Xian, 1975

Type species: *Uncinulus guangxiensis* Wang, 1964

Aseptaliium guangxiense (Wang, 1964)

Pl. 1, figs 12-20, Fig. 4

1964 *Uncinulus guangxiensis* Wang, p. 62, pl. 21, figs 1-4.

1975 *Aseptaliium guangxiense*; Hou & Xian, p. 37, pl. 2, figs 1-5.

1977 *Aseptaliium guangxiense*; Yang et al., p. 382, pl. 151, fig. 10.

1982 *Aseptaliium guangxiense*; Bai et al., p. 101, pl. 19, fig. 2.

Material: Nineteen conjoined shells and several disarticulated valve fragments. (NIGP170338, 170339).

Remarks. Shell medium-sized, with transversely subpentagonal outline and subcuboidal profile, with flanks and tongue steeply sloping; shallow and broad sulcus and fold well defined; tongue prominent, rectangular, abruptly bent toward dorsal valve; costae numerous, flattened, beginning from beak, five-six on sulcus, and 8-10 on flanks. Dorsal interior with parallel, thin and short crural plates, connected to the floor posteriorly, becoming impending anteriorly; (sub)horizontal outer hinge plates divided; cardinal process, septalium, and median septum not observed (Fig. 4).

Hou et al. (2017) noted that *Aseptaliium* is closely similar to *Corvinopugnax* Havlíček, 1961, but differs in having relatively fine costae beginning from the beak and internally a deeply impressed

PLATE 1

Figs 1, 2 -? *Mesodouwillina* sp. ventral valve (NIGP170328) and enlargement showing surface ornamentations.

Figs 3, 4 - *Levenea depressa* Wang, 1955. Two dorsal valves, NIGP170329, 170330.

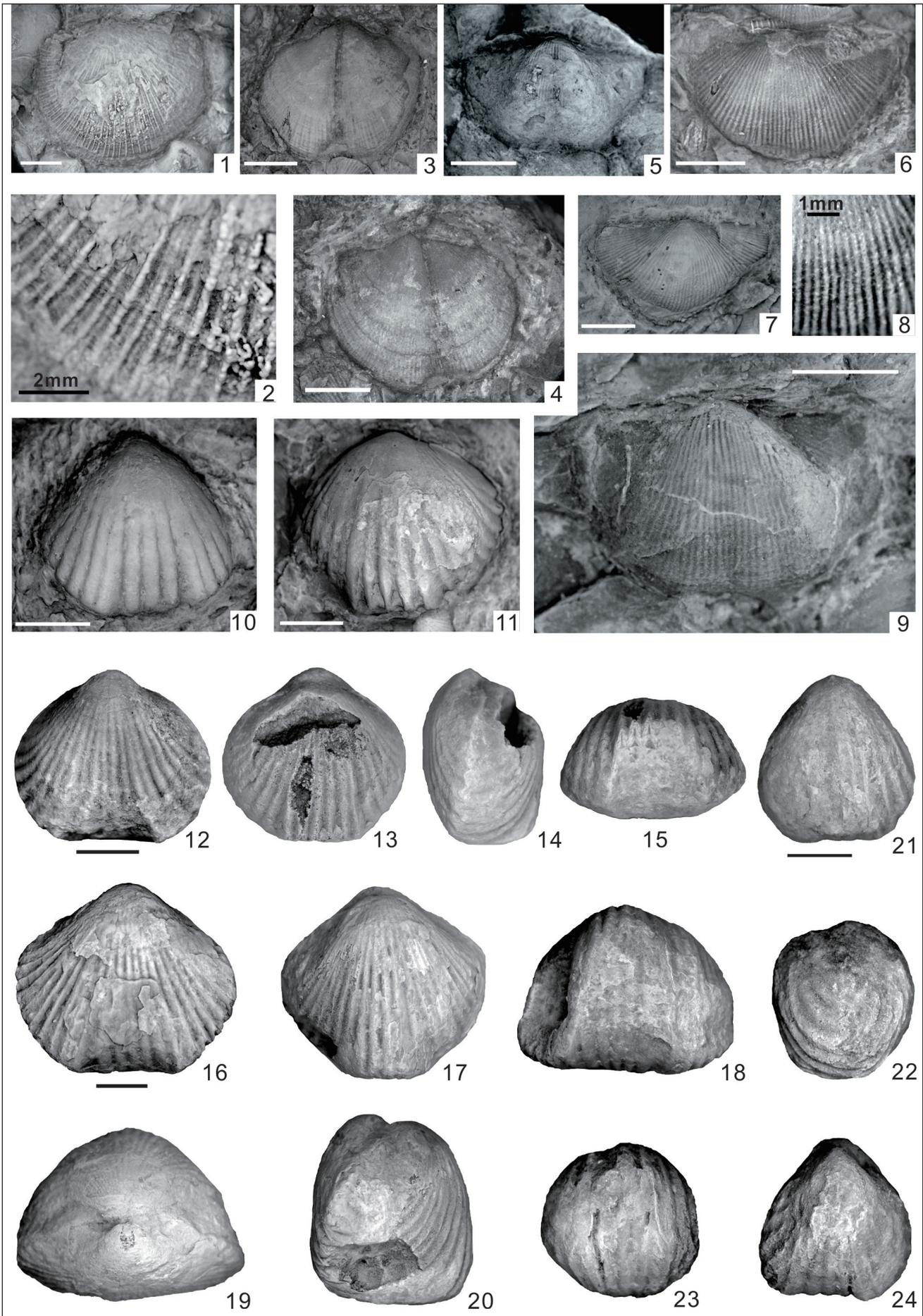
Figs 5-9 - *Sinochonetes* sp. 5, 6, 9, three ventral valves, NIGP170331-33; 7, 8, ventral valve and enlargement showing plications, NIGP170334.

Figs 10, 11 - *Corvinopugnax globosus* Hou et Xian, 1975. Ventral and dorsal valves, NIGP170336, 170337.

Figs 12-20 - *Aseptaliium guangxiense* (Wang, 1965). 12-15, a conjoined shell in ventral, dorsal, lateral and anterior views, NIGP170338; 16-20, a conjoined shell in ventral, dorsal, anterior, posterior and lateral views, NIGP170339.

Figs 21-24 - ?*Gypidula* sp. A conjoined shell in ventral, lateral, anterior and dorsal views, NIGP170335.

Scale bars are 5 mm except for those indicated.



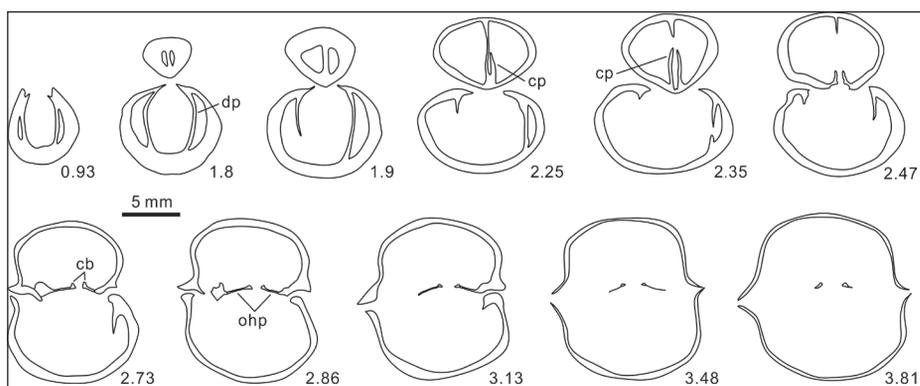


Fig. 4 - Serial sections of conjoined shell of *Aseptulum guangxiense* (Wang) showing internal structures; Nagaoling Formation (Pragian), Dashatian section, Nanning, southern Guangxi, China. cb, crural bases; cp, crural plates; dp, dental plates; ohp, outer hinge plates. Numbers at bottom of each section indicate distance (mm) from ventral beak.

ventral muscle field. Our specimens are confidently assigned to *Aseptulum* by both external and internal characters, and can be readily distinguished from *Corvinopugnax globosus*, even though *Aseptulum guangxiense* shows variable shell thickness, convexity and development of tongue.

Occurrences. Beds 3, 4, 5, 6 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Genus *Decoropugnax* Havlíček, 1960

Type species: *Terebratulula berenice* Barrande, 1847

?*Decoropugnax* sp.

Pl. 2, figs 1, 2

Material: Two ventral valves (NIGP170340, 170341).

Remarks. The specimens are comparable to the type species of *Decoropugnax* in terms of transversely trigonal outline, erected beak and smooth umbo; weak, broad fold and sulcus; wide and low tongue. However, our specimens have more developed costae originating near the umbo and becoming strongly rounded anteriorly; our specimens are tentatively assigned to this genus due to limited material and unknown internal characters.

Occurrences. Bed 5 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Superfamily Wellerelloidea Licharew, 1956

Family Mongolirhynchiidae Fu, 1983

Genus *Kwangsirhynchus* Hou & Xian, 1975

Type species: *Kwangsirhynchus liujingensis* Hou & Xian, 1975

Kwangsirhynchus liujingensis Hou & Xian, 1975

Pl. 2, figs 3-5

Material: Three incomplete dorsal valves (NIGP170342-170344).

Remarks. Small shell with subtriangular outline and strongly inflated anterior; simple costae subangular, covering the entire valve; three costae on fold beginning from the beak, abruptly thickening and protruding at anterior part to form a high acuminate fold.

Kwangsirhynchus luwuensis Xu & Yao (1984, p. 559, pl. 1, figs 1-3, 10) from the Yujiang Formation (lower Emsian) of southern Guangxi has sub-circular outline, densely arranged costae on flanks with narrow interspace; lower fold and sulcus, with

PLATE 2

Figs 1, 2 - ?*Decoropugnax* sp. Two ventral valves, NIGP170340, 170341.

Figs 3-5 - *Kwangsirhynchus liujingensis* Hou et Xian, 1975. 3, internal mold of dorsal valve, NIGP170342; 4, 5, dorsal valves, NIGP170343, 170344.

Fig 6 - *Atrypa variabilis* Wang et Rong, 1986. One ventral valve, NIGP170345.

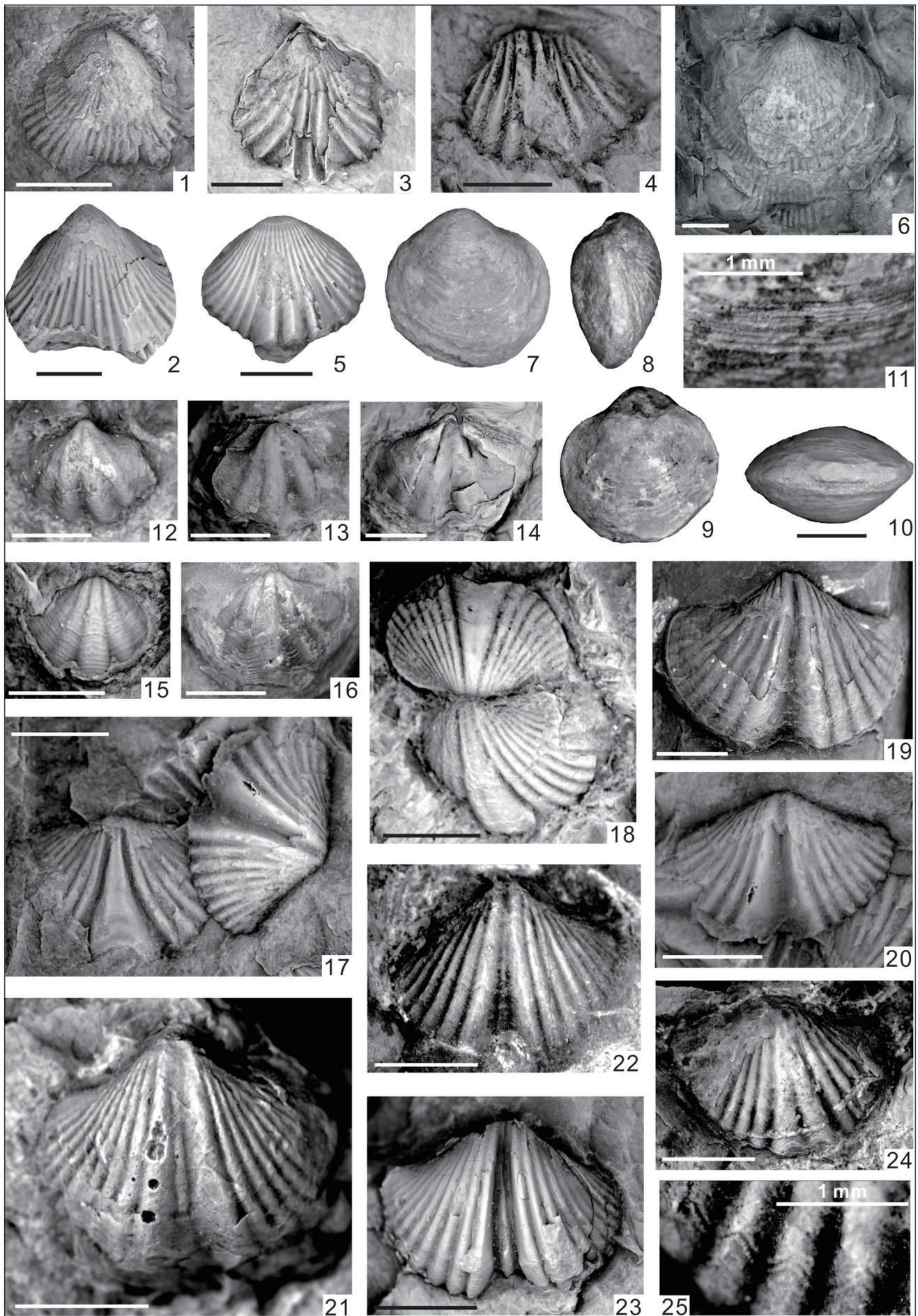
Figs 7-11 - *Protathyris praecursor* Kozłowski, 1929. One conjoined shell in ventral, lateral, dorsal, anterior views, and enlargement showing concentric lamellae, NIGP170346.

Figs 12-16 - *Howellella* cf. *nucula* (Barrande, 1879). 12, 13, ventral valves, NIGP170347, 48; 14, internal mold of ventral valve, NIGP170349; 15, 16, two dorsal valves, NIGP170350, 170351.

Figs 17-20 - *Orientospirifer nakaolingensis* (Hou, 1959). 17, one ventral valve and one dorsal valve, NIGP170352; 18, two dorsal valves, NIGP170353; 19, 20, two ventral valves, NIGP170354, 170355.

Figs 21-25 - *Orientospirifer wangi* (Hou, 1959). 21-23, three ventral valves, NIGP170356-58; 24, 25, one dorsal valve and enlargement showing micro-ornamentation, NIGP170359.

Scale bars are 5 mm except for those indicated.



4-5 rounded costae. *K. planosulcatus* Yang in Yang et al. (1977, p. 382, pl. 151, fig. 5) from the Yingtang Formation (Eifelian) of Xiangzhou, central Guangxi, differs in having a wide and weak sulcus and a fold with more costae.

Occurrences. Bed 3 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Order **Atrypida** Rzhonsnitskaia, 1960
 Superfamily Atrypoidea Gill, 1871
 Family Atrypidae Gill, 1871
 Subfamily Atrypinae Gill, 1871
 Genus *Atrypa* Dalman, 1828
 Type species: *Anomia reticularis* Linnaeus, 1758

Atrypa variabilis Wang & Rong, 1986
 Pl. 2, fig. 6

1938 *Atrypa reticularis* Linnaeus; Yin, pp. 49-50, pl. 2, fig. 13; pl. 3, fig. 1; pl. 5, fig. 1.
 1975 *Atrypa* sp.; Hou & Xian, p. 40, pl. 8, fig. 8.
 1986 *Atrypa variabilis* Wang & Rong, pp. 139-142; pl. 36, figs 7-11; pl. 37, figs 9-12; pl. 38, figs 1-11.

Material: One ventral valve (NIGP170345).

Remarks. The single ventral valve has strong similarity to those described by Hou & Xian (1975) and Wang & Rong (1986), both from the Yujiang Formation (Emisan) of Guangxi. It is characterized by faint convexity, coarse ribs interrupted by few concentric growth lamellae and inflated at crossing points and weak frills restricted to the anterior margins.

Occurrences. Bed 7 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Order **Athyridida** Boucot, Johnson, & Staton, 1964
 Superfamily Athyridoidea Davidson, 1881
 Family Athyrididae Davidson, 1881
 Subfamily Athyridinae Davidson, 1881
 Genus *Protathyris* Kozłowski, 1929
 Type species: *Protathyris praecursor* Kozłowski, 1929

Protathyris praecursor Kozłowski, 1929
 Pl. 2, figs 7-11

1929 *Protathyris praecursor* Kozłowski, p. 223.
 1932 *Protathyris praecursor*, Grabau, p. 90.

1975 *Protathyris praecursor*; Hou & Xian, p. 45, pl. 1, figs 7-13.
 1982 *Protathyris praecursor*; Tong, p. 335, pl. 2, figs 20-35.
 1985 *Protathyris praecursor*; Nikiforova et al., p. 55, pl. 15, figs 1-4.
 1986 *Protathyris praecursor*; Xu & Yao, p. 172, pl. 1, figs 2, 3.

Material: Four conjoined shells, two ventral valves, and three dorsal valves. (NIGP170346)

Remarks. Our specimens strongly resemble those described by Nikiforova (1985), having small size, transversely subcircular outline, very faint sulcus and fold confined to the anterior part, together with regular and slightly lamellose growth lines. The species described by Hou & Xian (1975) from the Nagaoling Formation has similar size, ornamentation, and development of sulcus and fold, but it has a slightly oval outline. This species has also been reported from the Lochkovian in China, the lower part of the Putonggou Formation in northwest Sichuan (Tong, 1982), and marls of the Qingzhou Formation of Luwu section in Linshan, southern Guangxi (Xu & Yao, 1986). The Lochkovian specimens show great similarities to those of the Nagaoling Formation in the Dashatian section, except for the developed uniplicate anterior commissure.

Protathyris ovalis Tong, 1982 from the Putonggou Formation in northwest Sichuan (Tong 1982, p. 335, pl. 2, figs 36-49) and Linshan of Guangxi (Xu & Yao 1986, p. 172, pl. 1, figs 1, 7, 8) differs in having distinct oval outline, larger convexity, and internally with longer dental plates.

Occurrences. Beds 3, 5, 8 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Order **Spiriferida** Waagen, 1883
 Suborder **Delthyridina** Ivanova, 1972
 Superfamily Delthyridoidea Phillips, 1841
 Family Delthyrididae Phillips, 1841
 Subfamily Howellellinae Johnson & Hou, 1994 in Carter & others, 1994
 Genus *Howellella* Kozłowski, 1946
 Type species: *Terebratula crispus* Von Hisinger, 1826

Howellella cf. *nucula* (Barrande, 1879)
 Pl. 2, figs 12-16

cf. 1879 *Spirifer nucula* Barrande, p. 100, pl. 2, figs 1a-f; 2a, b.
 cf. 1959 *Howellella nucula*; Havlíček, p. 95, pl. 18, figs 8, 9.
 1975 *Howellella* cf. *nucula*; Hou & Xian, p. 46, pl. 9, figs 7, 8.

Material: Seven ventral valves, and three dorsal valves (NIGP170347-170351).

Remarks. Small-sized, transversely oval in outline; sulcus wide and distinct, beginning from the beak; sulcus well defined by two strong plications; dorsal valve with corresponding fold; flanks commonly with two rounded plications that are separated by shallow troughs, the lateral plications are faint; surface covered by closely spaced growth lamellae.

Hou & Xian (1975) described *H. cf. nucula* (Barrande), and an indeterminate species from the Nagaoling Formation (Pragian) of the Liujing Section in Guangxi. The latter is closer to those from the young strata in the Yujiang Formation (Emasian), with much larger size, stronger and more plications on either flank (see Wang & Rong, 1986 for illustrations).

Howellella nucula australis Savage, 1969 (p. 480, pl. 91, figs 1-35) from the Mandagery Park Formation (early Pragian) in eastern Australia has similar external characters, but with a short median septum at the very apex of umbonal cavity in the ventral interior.

Howellella angustiplicata Kozłowski and *H. laeviplicatus* Kozłowski recorded from the Putonggou Formation in Sichuan (Tong, 1982) have similar sizes, but with more numerous and weaker plications on either flanks, as well as faint concentric lamellae. *H. globosa* (Tong, 1982, p. 336, pl. 2, figs 65-69) slightly resembles our specimens in size and ornamentation, but it has a typically globose profile.

Occurrences. Beds 4, 7 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Order **Spiriferida** Waagen, 1883

Suborder **Spiriferidina** Waagen, 1883

Superfamily Adolfoidea Sartenaer, 1966

Family Adolfindae Sartenaer, 1966

Subfamily Adolfinae Sartenaer, 1966

Genus *Orientospirifer* Hou and Xian, 1975

Type species: *Eospiriferina nakaolingensis* Hou, 1959

Orientospirifer nakaolingensis (Hou, 1959)

Pl. 2, figs 17-20

1959 *Eospiriferina nakaolingensis* Hou, p. 452, pl. 1, figs 1, 2.

1975 *Orientospirifer nakaolingensis* (Hou); Hou & Xian, p. 50, pl. 3,

figs 1-7.

1977 *Orientospirifer nakaolingensis* (Hou); Yang D.L. et al., p. 424, pl. 168, fig 7.

Material: More than ten conjoined shells and several disarticulated valves (NIGP170352-170355).

Remarks. This species is characterized by small size, transverse outline, distinctive fold and sulcus beginning from beak, eight-nine simple plications on flank, and weak concentric growth lamellae at the anterior part, occasionally preserved with fine, irregular capillae along the margin of growth lamellae. Ventral interior without median septum.

Occurrences. Beds 3, 4, 5, 6, 7, 8, 11 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

Orientospirifer wangi (Hou, 1959)

Pl. 2, figs 21-25

1959 *Eospiriferina wangi* Hou, p. 453, pl. 1, figs 3-5.

1975 *Orientospirifer wangi* (Hou); p. 50, pl. 3, figs 8-10.

1977 *Orientospirifer wangi* (Hou); Yang et al., p. 424, pl. 168, figs 9-19.

Material: Nine ventral valves, and one dorsal valve (NIGP170356-170359).

Remarks. This species shows a single plication on the sulcus and a furrow on the fold; otherwise, it is very similar to *O. nakaolingensis* from the same horizon. Based on the paratype by Hou (1959), a distinct median ridge beginning from the beak rapidly widens and strengthens anteriorly, with a corresponding furrow that divides the fold. However, here we find a few “intermediate forms” from the Dashatian section, with a narrow and weak ridge restricted at the posterior in the sulcus, and a faint furrow on the fold starting from the beak to the anterior (Pl. 2, fig. 18, 19). Nevertheless, no more features can be observed, and no internal structures are available due to the poor preservation of valves.

Occurrences. Beds 5, 8 of the Nagaoling Formation at Dashatian section, southern Guangxi, South China.

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