Journal of Paleontology, 97(2), 2023, p. 421–433

Published by Cambridge University Press
on behalf of The Paleontological Society
0022-3360/23/1937-2337
doi: 10.1017/jpa.2023.2

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

The first discovery of Lochkovian (Lower Devonian) conodonts in central Guangxi, South China and its geological implications

Jian-Feng Lu,* Wen Guo, Yi Wang, and Hong-He Xu

Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, East Beijing Road 39, Nanjing 210008, China <jflu@nigpas.ac.cn>, <wenguo@nigpas.ac.cn>, <yiwang@nigpas.ac.cn>, <hhxu@nigpas.ac.cn>

Abstract.—The Lochkovian, Pragian, and basal part of the Emsian, which represent the post-Kwangsian Orogeny strata in the South China Block, are mainly composed of siliciclastic rocks. This lithological composition impedes investigation of Pragian and Lochkovian conodont biostratigraphy in the South China Block, which results in a persistent controversy on the age of relevant lithological units. The present study provides new evidence by reporting for the first time Lochkovian conodonts obtained from the South China Block, specifically the Gaoling Member of the Nahkaoling Formation at the Lingli section, central Guangxi. The conodont fauna, consisting of *Pandorinellina exigua lingliensis* Lu n. subsp., *Pandorinellina exigua exigua*, *Zieglerodina*? *tuojiangensis* Lu n. sp., *Amydrotaxis praejohnsoni*, and *Eognathodus* cf. *E. irregularis*, places the studied interval of the Gaoling Member in the lower or middle Lochkovian (contingent upon varying definitions for the base of the middle Lochkovian) to lower Pragian. Moreover, *Amydrotaxis praejohnsoni*, which was reported previously only in North America and eastern Australia, is herein also recorded in the South China Block, and thus may play an important role in intercontinental biostratigraphical correlation. By shedding light on the age of the upper limit of the underlying Lianhuashan Formation at the Lingli section, the present study indicates that the Kwangsian Orogeny ended before the late Lochkovian. This date is slightly earlier than the previously estimated late Lochkovian based on studies of fossil plants from the siliciclastic rocks deposited after the Kwangsian Orogeny.

UUID: http://zoobank.org/8010f983-4f6f-43dd-949f-de4653e53d9d

Introduction

The Kwangsian Orogeny, which is thought to be a Caledonian tectonic orogeny occurring in the South China Block (including Guangxi and eastern Yunnan) (Ting, 1929), caused erosion of exposed pre-Devonian strata and deeply influenced subsequent deposition of the widespread earliest Devonian (or Lochkovian) terrestrial siliciclastic rocks over the southern part of the South China Block. From the Pragian onwards, an epicontinental sea flooded the southern margin of the South China Block, resulting in deposition of carbonate-siliciclastic rocks in the shallow shelf zone, which is marked by mudstone and siltstone intercalated with thin-bedded limestone and argillaceous limestone. According to Lu and Chen (2016), the onset of a widespread carbonate succession occurred in the South China Block during the early Emsian (during the *excavatus* Zone).

The rarity of Lochkovian and Pragian conodont material from siliciclastic rocks in the South China Block impedes documentation of a well-established conodont biostratigraphy. Pragian conodonts were reported only by Wang and Wang (1978), Lu et al. (2016, 2017), and Wang et al. (2016) from the Nahkaoling Formation in central Guangxi, whereas Lochkovian conodonts in the South China Block have never been reported. As a result, an unequivocal determination of the ages of some related lithological units is impossible, which further hampers accurate regional and global biostratigraphical correlations. Moreover, it is also difficult to accurately date the ending time of the Kwangsian Orogeny, because the previous work using the fossil plants from Lower Devonian siliciclastic rocks can date the fossil horizons to only a stage level of precision (Xu et al., 2019), instead of the bio-zone or sub-stage level of precision based on conodont biostratigraphy. During this research, we studied Early Devonian conodonts from the Nahkaoling Formation at Lingli, central Guangxi, to demonstrate the age of the lower limit of the Nahkaoling Formation based on conodont biostratigraphy, and to discuss the ending time of the Kwangsian Orogeny in the South China Block.

Geological setting

The Lower Devonian, which is widely distributed and well exposed in the Nanning-Liujing district (Wang and Rong, 1986) along the Yukiang River between Nanning and Liujing (Fig. 1.1), is subdivided into five lithological units in ascending order (Fig. 1.2): the Lianhuashan Formation, Nahkaoling Formation (= Nagaoling or Nakaoling Formation), Yukiang Formation (= Yujiang Formation), Moding Formation, and the

*Corresponding author.

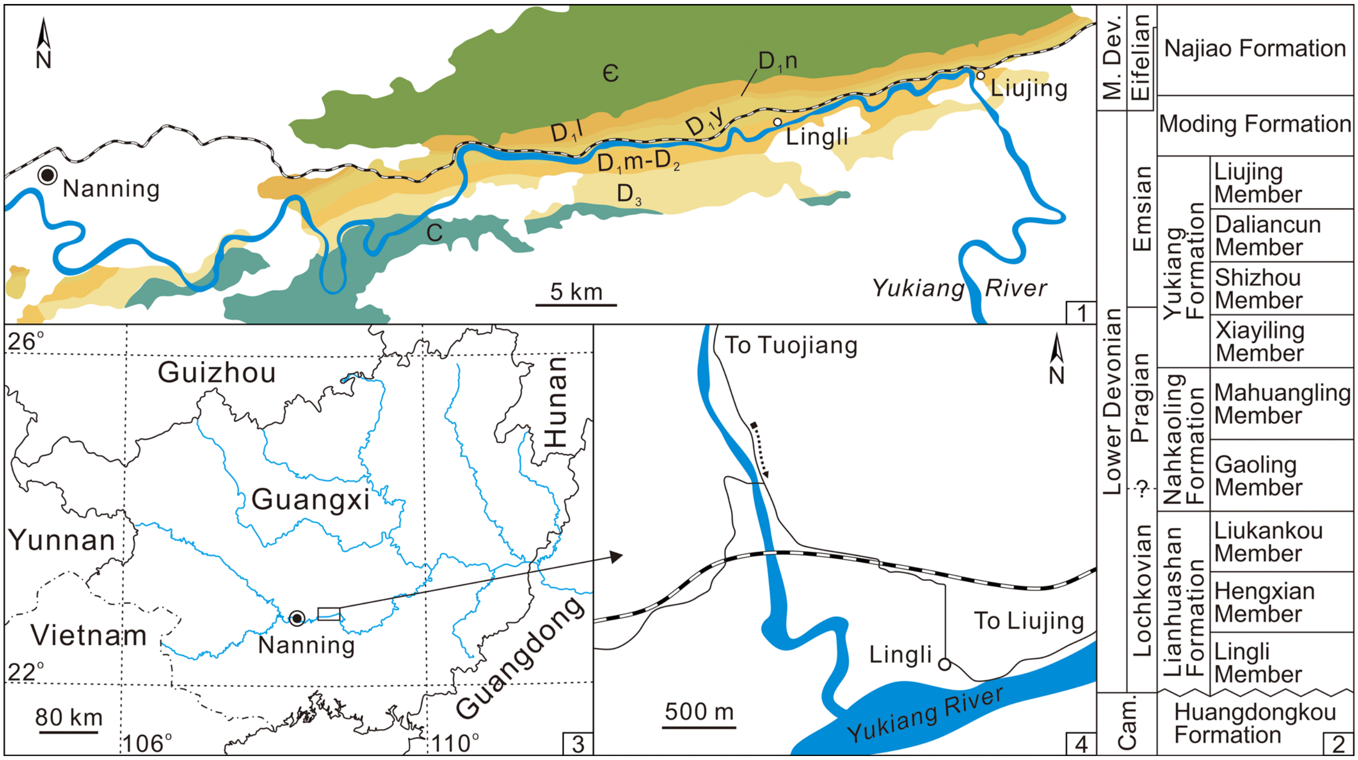

Figure 1. (**1**) Geologic map showing the exposed Paleozoic strata in the Nanning-Liujing district along the Yukiang River. Є: Cambrian; D_1l: Lianhuashan Formation; D_1n: Nahkaoling (Nagaoling) Formation; D_1y: Yukiang (Yujiang) Formation; D_1m-D_2: Lower Devonian Moding Formation and the Middle Devonian; D_3: Upper Devonian; C: Carboniferous. (**2**) Stratigraphic sequence of the Lower Devonian in the Nanning-Liujing district. Cam.: Cambrian; M. Dev.: Middle Devonian. (**3**) Location of the study area, with a rectangle showing the investigated Nanning-Liujing district in central Guangxi. (**4**) Location of the Lingli section, with the dashed line indicating the investigated interval of the Nahkaoling Formation exposed along the country road.

lower part of the Najiao Formation (Wang et al., 1964; Kuang et al., 1989; Zhong et al., 1992). Consisting of red sandstone, siltstone, and mudstone intercalated with several beds of dolostone in the middle part, the Lianhaushan Formation represents nearshore or delta deposition after the Kwangsian Orogeny and was once correlated with upper Lochkovian by Wang (1996) based on the study of ostracodes. The Nahkaoling Formation conformably overlies the Lianhuashan Formation. It comprises a lower member (the Gaoling Member) characterized by alternating mudstone and limestone in its upper part and an upper member (the Mahuangling Member) of mudstone and siltstone. Interpreted to be deposited in a littoral to neritic sea, the Nahkaoling Formation witnessed the first flourish of benthic and pelagic faunas. Based on extensive investigations of the abundant fossils such as brachiopods (Hou, 1959; Hou and Xian, 1975; Bai et al., 1982; Kuang et al., 1989; Qiao et al., 2021), corals (Bai et al., 1982; Kuang et al., 1989), bivalves (Zhang et al., 1988, 2015; Kuang et al., 1989), tentaculitids (Ruan et al., 1979; Xian et al., 1980; Kuang et al., 1989; Wei et al., 2019), ostracodes (Kuang et al., 1989; Wang, 1996), fish (Pan and Wang, 1978; S.F. Liu, 1982; Y.H. Liu, 1985; Kuang et al., 1989; Wang, 1992), spores (Gao, 1978), chitinozoans (Hou, 1978), and conodonts (Wang and Wang, 1978; Kuang et al., 1989; Lu et al., 2016, 2017; Wang et al., 2016), the Nahkaoling Formation in the Nanning-Liujing district was dated as Pragian (Ruan et al., 1979; Wang et al., 1979; Lu et al., 2016, 2017), perhaps even early Pragian (Wang et al., 2016). The Yukiang Formation, which conformably overlies the Nahkaoling Formation, is represented by mudstone and siltstone intercalated with thin beds of limestone in the lower half and by limestone in the upper half. According to Lu et al. (2016, 2017, 2018, 2019), the Yukiang Formation is upper Pragian to lower Emsian in age.

The Lingli section (108°44′50″E, 22°52′1″N) is situated ∼45 km east of Nanning (Fig. 1.3) and ∼2 km northwest of Lingli (Fig. 1.4), a small town on the north bank of the Yukiang River. The Lianhuashan and Nahkaoling formations are continuously and well exposed along the country road heading north from Lingli to Tuojiang village. Consisting of 8.3 m of thin-bedded mudstone, the basal part of the Nahkaoling Formation is conformably underlain by purple-red mudstone and siltstone belonging to the upper part of the Lianhuashan Formation. The investigated interval of the lower part of the Nahkaoling Formation is ∼35.37 m thick and composed of mudstone alternating with thin- to medium-bedded limestone and argillaceous limestone (Fig. 2). This interval belongs to the Gaoling Member. The strata overlying the investigated interval consist of thin-bedded mudstone and siltstone belonging to the Mahuangling Member of the Nahkaoling Formation.

Materials and methods

Forty-seven samples, each weighing 0.90–4.01 kg, were collected from the Lingli section (Fig. 3). Limestone samples were crushed mechanically into small pieces (∼2–5 cm diameter) and dissolved in dilute acetic acid (5–10%). The insoluble residues were then washed, air-dried, and finally concentrated by

Figure 2. Exposure of the lower part (from sample 20LL-1 to sample 20LL-19) of the Nahkaoling Formation, which was measured and sampled in 2020 but was partially destroyed by road construction in 2021, at the Lingli section. The white lines indicate the bases of the sampled limestone beds.

heavy-liquid separation using sodium polytungstate. Specimens coated with gold were photographed using a Scanning Electron Microscope (SEM) in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

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

Systematic paleontology

The section on systematic paleontology is authored by Jian-Feng Lu.

Order Ozarkodinida Dzik, 1976
Family Spathognathodontidae Hass, 1959
Genus *Amydrotaxis* Klapper and Murphy, 1980

Type species.—*Spathognathodus johnsoni* Klapper, 1969.

Amydrotaxis praejohnsoni Murphy and Springer, 1989
Figure 4.1–4.6

1969 *Spathognathodus johnsoni* Klapper, p. 18, pl. 5, figs. 11–13.
1980 *Amydrotaxis johnsoni* (Klapper) alpha morphotype; Klapper and Murphy, p. 498, fig. 2, no. 1–3, 5–14, 16, fig. 3, no. 1–20.
1980 *Ozarkodina johnsoni* (Klapper) alpha morphotype; Klapper and Johnson, p. 450, pl. 1, figs. 5, 6, 17.
1980 *Ozarkodina johnsoni* (Klapper) gamma morphotype; Klapper and Johnson, p. 450.
1983 *Amydrotaxis johnsoni* (Klapper) alpha morphotype; Murphy and Matti, p. 34.
1986 *Amydrotaxis johnsoni* (Klapper) alpha morphotype; Mawson, p. 50, pl. 8, figs. 1–23.
1989 *Amydrotaxis praejohnsoni* Murphy and Springer, p. 349, fig. 2.1–2.41.
2016 *Amydrotaxis praejohnsoni*; Murphy, p. 14, pl. 4, figs. 4–8.

Holotype.—Specimen 8765 iv/11 (Murphy and Springer, 1989, pl. 2, fig. 2.33, 2.34) in University of California, Riverside type collection.

Occurrences.—Restricted to the middle Lochkovian, or from the lower Lochkovian to middle Lochkovian, contingent upon varying definitions for the base of the middle Lochkovian; reported in western North America, eastern Australia, and South China.

Description.—The carminiscaphate Pa element is slightly deflected inward anteriorly and posteriorly. The free blade takes one-third of the whole element, and a strikingly asymmetrical platform is developed in the posterior two-thirds. In the middle third of the element, the inner platform consists of two weakly developed and smooth lobes that are separated by a weak sinus in the margin and more or less equal in length. Therefore, the lateral margin of the inner lobes tends to be parallel to the blade in the middle third. On the opposite side, a smooth and tongue-shaped outer lobe, strongly projecting laterally at a right angle to the blade, is almost twice as wide as the inner lobes. It meets the free blade at the same position as the inner anterior lobe but terminates posteriorly at a more anterior position than the inner posterior lobe. Posterior of the inner posterior and outer lobes, the platform narrows toward the posterior tip and is delimited from the posterior part by a more or less marked indentation

https://doi.org/10.1017/jpa.2023.2 Published online by Cambridge University Press

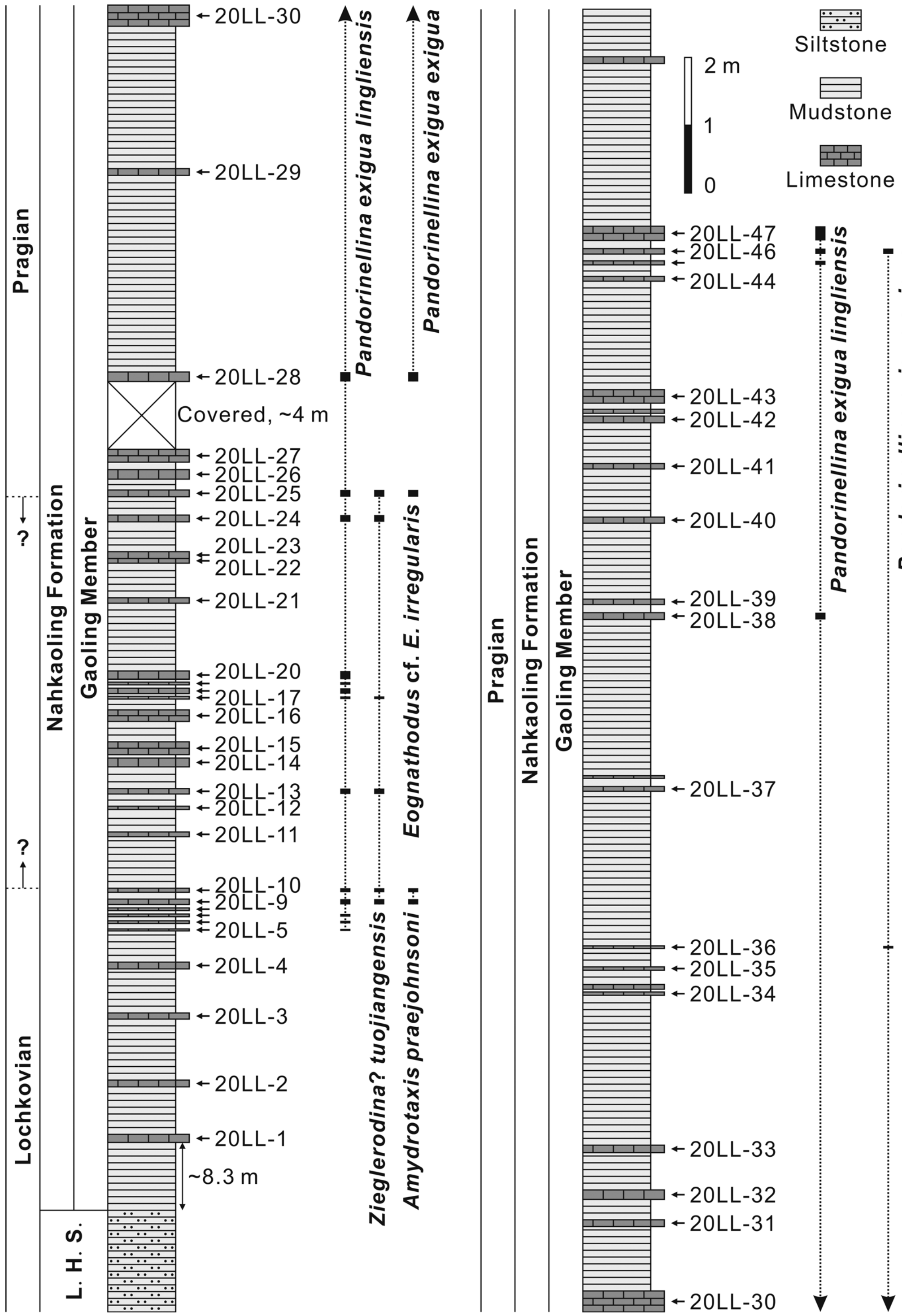

Figure 3. Distribution of conodonts in the Gaoling Member of the Nahkaoling Formation at the Lingli section, central Guangxi. Due to the lack of index fossils for the base of the Pragian, the precise level of the Lochkovian-Pragian boundary at the Lingli section is temporarily unknown and probably lies in the interval between sample 20LL-10 and sample 20LL-25. L. H. S.: Lianhuashan Formation.

in both the inner and outer margins. The broken free blade in the anterior third of the element is followed in the middle third by four well-differentiated denticles that are uniform in height. There is a steep decline in height in the posterior third, where only one to two lower denticles are developed. The lower margin of the element is in a concave arc, with the anterior and posterior ends being the lowest. In lateral view, the inner lobes are characterized by a lateral profile that slopes gradually to the lower margin. On the lower side, the large and moderately excavated basal cavity is L-shaped. It narrows gradually toward the posterior end and extends anteriorly beneath the free blade as a narrow groove.

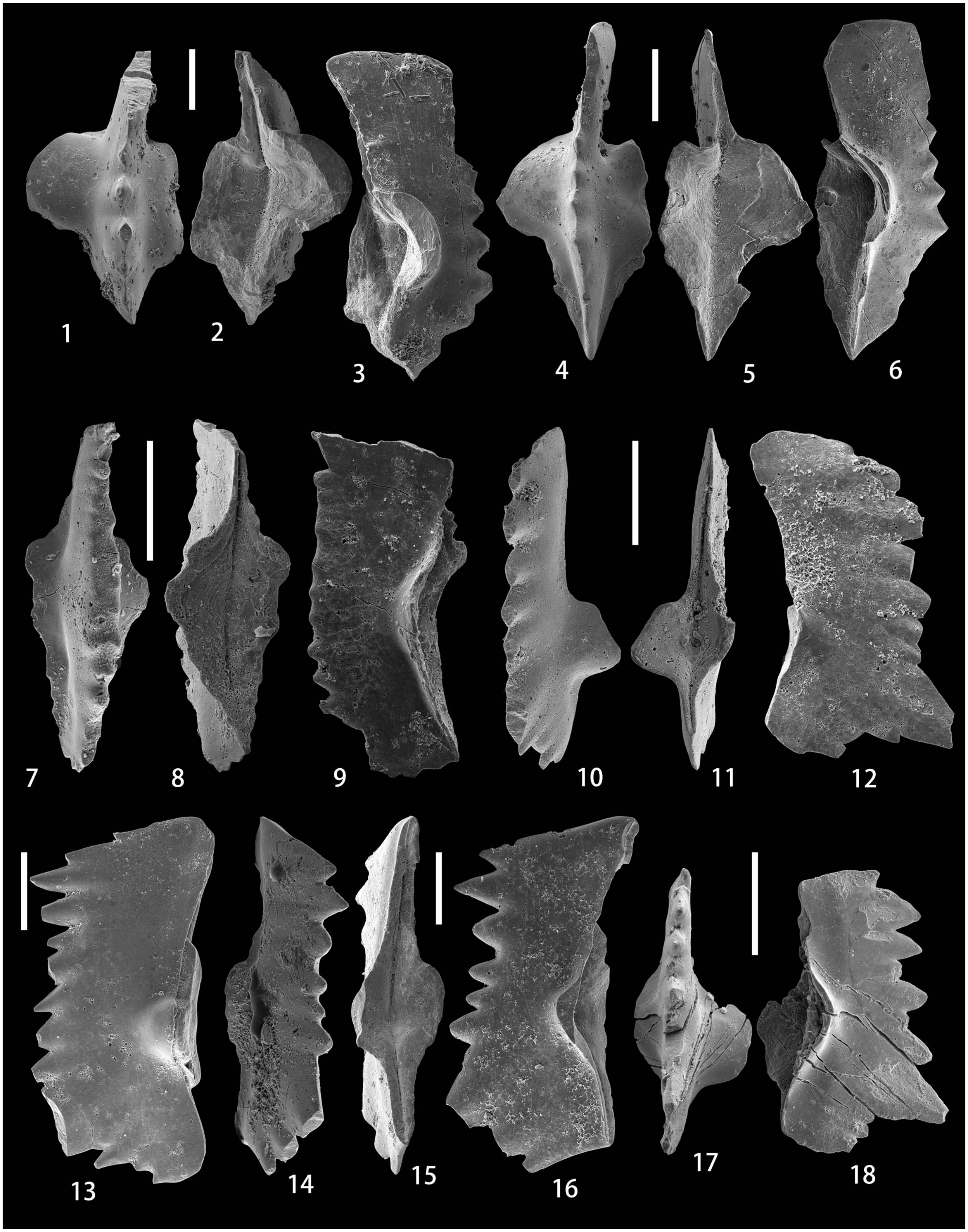

Figure 4. (**1–6**) *Amydrotaxis praejohnsoni* Murphy and Springer, 1989; (**1–3**) upper, lower, and lateral views of NIGP 180672, sample 20LL-9; (**4–6**) upper, lower, and lateral views of NIGP 180673, sample 20LL-10. (**7–9**) *Eognathodus* cf. *E. irregularis* Druce, 1971, upper, lower, and lateral views of NIGP 180674, sample 20LL-25. (**10–18**) *Zieglerodina*? *tuojiangensis* Lu n. sp.; (**10–12**) upper, lower, and lateral views of NIGP 180675, sample 20LL-9, paratype; (**13**) lateral view of NIGP 180676, sample 20LL-13, paratype; (**14–16**) upper, lower, and lateral views of NIGP 180677, sample 20LL-24, holotype; (**17, 18**) upper and lateral views of NIGP 180678, sample 20LL-24, paratype, a juvenile specimen. Scale bar is 200 μm across.

Materials.—Two specimens, from samples 20LL-9 (1) and 20LL-10 (1).

Remarks.—As suggested by Murphy and Springer (1989), the Pa element of *Amydrotaxis praejohnsoni* differs from the Pa element of *A. johnsoni* (Klapper, 1969) in having a sloping or angulate transverse profile through the smaller lobe of the platform. In contrast, the upper surface of the smaller lobe in the Pa element of *A. johnsoni* drops abruptly at the lobe margin downward to the lower margin, thus forming a shouldered transverse profile. In the holotype of the Pa element of *A. praejohnsoni*, the smaller platform has a straight margin, whereas in some of illustrated specimens it is composed of two lobes separated by a weak sinus in the margin (Murphy and Springer, 1989, pl. 2, figs. 15, 17). The Pa element of *Amydrotaxis praejohnsoni* is strikingly close to that of *A. druceana* (Pickett, 1980) in the configuration of the basal cavity and the lateral profile of the inner platform. Initially named *Spathognathodus philipi* Druce, 1971 (*S. philipi* Druce, 1971, is a junior homonym of *S. exigua philipi* Klapper, 1969, and thus invalid according to the ICZN, 1999), the Pa element of *A. druceana* is characterized by strongly fused denticles in the median third of the blade, the tips of which are completely fused to form a long ridge in the holotype and in two of the three paratypes. Moreover, as suggested by Murphy and Springer (1989), in contrast to the margin of the smaller platform lobe in the Pa element of *A. praejohnsoni*, which is parallel to the blade or tapers posteriorly, the margin of the smaller lobe generally tapers toward the anterior end of the element in the Pa element of *A. druceana*. Specimens illustrated as the Pa element of *A. druceana* by Farrell (2003, pl. 4, figs. 13–21) closely resemble the Pa element of *A. praejohnsoni* in possessing discrete denticles in the middle third of the blade, but mainly differ by their smaller inner lobe tapering towards the anterior end of the platform.

Genus *Eognathodus* Philip, 1965

Type species.—Eognathodus sulcatus Philip, 1965.

Eognathodus cf. *E. irregularis* Druce, 1971
Figure 4.7–4.9

Occurrences.—Lower Pragian; reported from South China.

Description.—The carminiscaphate Pa element is straight, with a broken anterior blade consisting of three remnant denticles that are rounded in cross-section. In the middle part of the element, a narrow and flat platform is developed; the sulcus is completely absent. This narrow platform does not extend to the posterior end of the element but is followed posteriorly by a short and chevron-shaped transverse ridge and then a denticle that has an elliptical cross-section with its long axis perpendicular to the element. There are three denticles with a rounded cross-section in the posteriormost part of the element. On the lower side, the symmetrical and moderately large basal cavity narrows gradually toward the posterior end of the element and extends anteriorly as a narrow groove. In lateral view, the upper margin of the middle part of the element is flat, with a smooth and straight platform margin on one side and a waved platform margin showing blunt and rounded tips of denticles on the other side. The posterior blade is arched downward.

Materials.—One specimen, from samples 20LL-25.

Remarks.—According to Druce (1971, text-fig. 2) and Pickett (1980, figs. 7D–F), the holotype of the Pa element of *Eognathodus irregularis* Druce, 1971, is characterized by having denticles in the middle third of the element, which are elliptical in cross-section with their axes at right angles with the element. Later, Murphy (2005, p. 199) suggested that in the early Pragian the Pa element of *E. irregularis* has various morphs but is mainly characterized by a medium- to large-sized basal cavity, irregular denticles or tubercles, and the absence of a sulcus. The present specimen differs greatly from the holotype of the Pa element of *E. irregularis* in the development of a narrow and flat platform in the middle part of the element. Other specimens similar to the present one were illustrated by Murphy (2005, fig. 6.15, 6.17) as *E. irregularis*. However, the present specimen has a much narrower basal cavity, which is different from those two specimens whose basal cavity has a rounded and wide outline.

Genus *Zieglerodina* Murphy, Valenzuela-Ríos, and Carls, 2004

Type species.—Spathognathodus remscheidensis Ziegler, 1960.

Zieglerodina? *tuojiangensis* Lu new species
Figure 4.10–4.18

Holotype.—Specimen NIGP 180677 (Fig. 4.14–4.16) in the collections of the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Paratypes.—Specimens NIGP 180675 (Fig. 4.10–4.12), NIGP 180676 (Fig. 4.13), NIGP 180678 (Fig. 4.17, 4.18), and 12 other unfigured specimens.

Diagnosis.—A species provisionally assigned to *Zieglerodina* with a Pa element that has a prominently high, broad, and posteriorly inclined cusp in the posterior part of the blade. The cusp is preceded anteriorly by 4–8 irregularly shaped and discrete denticles and succeeded posteriorly by 2–4 lower denticles. The shallow basal cavity is situated posterior of the mid-length of the blade.

Occurrences.—From the lower or middle Lochkovian to lower Pragian; reported from South China.

Description.—The blade of the carminate Pa element is normally straight. Two small, slightly or distinctly asymmetrical, and tongue-shaped lobes are confined to the posterior part of the blade. A distinctly high and large cusp is situated in the posterior third of the blade and is inclined posteriorly. Anterior of the cusp are 4–8 irregular and discrete denticles, which may be erect or posteriorly inclined. In most of the studied specimens, the second denticle at the anterior

https://doi.org/10.1017/jpa.2023.2 Published online by Cambridge University Press

end is a bit larger or higher than the adjacent ones. Posterior of the cusp are 2–4 lower denticles, whose heights drop rapidly from the high cusp, thus forming a steep upper margin posterior of the cusp. The lower margin is more or less straight in small specimens but tends to be concave in larger ones. On the lower side, the shallow and posteriorly situated basal cavity extends anteriorly and posteriorly as a narrow groove reaching the end.

Etymology.—Named after Tuojiang village, which is close to the Lingli section.

Materials.—Sixteen specimens, from samples 20LL-9 (1), 20LL-10 (1), 20LL-13 (2), 20LL-17 (2), 20LL-24 (9), and 20LL-25 (1).

Remarks.—Murphy et al. (2004) classified the Pridoli and Lochkovian Spathognathodontidae by the restriction of *Ozarkodina* Branson and Mehl, 1933, to forms similar to its type species and by the establishment of new genera *Wurmiella* Murphy, Valenzuela-Ríos, and Carls, 2004, *Zieglerodina* Murphy, Valenzuela-Ríos, and Carls, 2004, and 'New Genus *W*' Murphy, Valenzuela-Ríos, and Carls, 2004 (the genus *W*, however, has not been accepted according to ICZN, 1999, rules, as noted by Corriga and Corradini, 2009; Corradini and Corriga, 2010; Corriga et al., 2014, 2016). According to Murphy et al. (2004), *Ozarkodina* has a Pa element characterized by a high cockscomb in the anterior part and a small basal cavity with its anterior margin in the anterior half of the blade; the Pa element of *Wurmiella* has denticles on the anterior and posterior processes without obvious size variation; whereas in the Pa element of 'New Genus *W*', the lobes are commonly ornamented by a ridge or denticle. The Pa element of *Cuspigrandiosa* Murphy, 2016, is characterized by short or rudimentary small denticles behind the cusp that increase in size posteriorly. In contrast, *Zieglerodina* is probably the most suitable genus to accommodate this new species described herein, because the Pa element of *Zieglerodina* is characterized by small, subcircular lobes without ornament, unequal denticles, an enlarged cusp, and a posterior position of basal denticles, an enlarged cusp, and a posterior position of basal cavity, all of which can be seen in the described new species. *Zieglerodina*? *tuojiangensis* Lu n. sp. is readily distinguishable from other species of this genus by its high, broad, and posteriorly inclined cusp, long anterior blade, and distinctly short posterior blade whose height decreases greatly from the high cusp. *Zieglerodina*? *tuojiangensis* Lu n. sp. probably belongs to a new genus, whose other elements of the apparatus need further investigation.

Genus *Pandorinellina* Müller and Müller, 1957

Type species.—*Pandorina insita* Stauffer, 1940.

Pandorinellina exigua lingliensis Lu new subspecies
Figure 5.1–5.15

Holotype.—Specimen NIGP 180681 (Fig. 5.7–5.9) in the collections of the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Paratypes.—Specimens NIGP 180679 (Fig. 5.1–5.3), NIGP 180680 (Fig. 5.4–5.6), NIGP 180682 (Fig. 5.10–5.12), NIGP 180683 (Fig. 5.13–5.15), and 89 other unfigured specimens.

Diagnosis.—A subspecies of *Pandorinellina exigua* having a Pa element with an extremely enlarged and high denticle in the anterior third of the blade. The basal cavity has two slightly asymmetrical lobes that are clearly delimited posteriorly from a progressively tapering groove that reaches the posterior end. The lower margin anterior of the basal cavity expansion is normally straight to slightly convex, whereas that posterior of the basal cavity expansion is in a concave arc.

Occurrences.—From the lower or middle Lochkovian into Pragian; reported from South China.

Description.—The blade of the carminate Pa element is straight or slightly deflected anteriorly or posteriorly. Two rounded, tongue-shaped, and slightly asymmetrical lobes are confined to the middle part of the blade. The anterior margin of the two lobes is located at the posterior end of the anterior third of the blade. The anterior third of the blade, which is prominently offset to the right side, is usually occupied by only one extremely high and enlarged denticle. In some specimens, one or two very small denticles may be developed anterior of this prominent denticle. The posterior edge of the prominent denticle drops vertically to a position just in front of the convex arc of the posterior two-thirds of the blade. Denticles on the posterior arc are commonly irregular in size and much lower; no distinctly high denticle exists even in the middle third of the blade above the basal cavity. The lower margin of the anterior third of the blade is straight to slightly convex, with the anterior end of the blade being higher than the anterior end of the basal cavity expansion. In the posterior two-thirds, the lower margin is in a concave arc. Therefore, the lowest point of the lower margin is situated at the anterior end of the basal cavity expansion right below the junction of the anterior third of the blade and the posterior arc. On the lower side, the basal cavity is shallow. It is narrowly expanded beneath the anterior and posterior blade and reaches the ends. In larger specimens, the anterior and posterior grooves are much wider than the corresponding structures in the smaller specimens.

Etymology.—Named after the Lingli town.

Materials.—Ninety-five specimens, from samples 20LL-5 (7), 20LL-6 (11), 20LL-7 (1), 20LL-9 (3), 20LL-10 (10), 20LL-13 (2), 20LL-17 (2), 20LL-18 (3), 20LL-19 (2), 20LL-20 (1), 20LL-24 (32), 20LL-25 (13), 20LL-28 (2), 20LL-38 (1), 20LL-45 (1), 20LL-46 (2), and 20LL-47 (2).

Remarks.—Although specimens of the Sa element have not been obtained, the new taxon is assigned to the genus *Pandorinellina* and treated as a new subspecies of *P. exigua* (Philip, 1966) due to the close similarity of its Pa element to those of *P. exigua exigua* (Philip, 1966) and *P. exigua philipi* (Klapper, 1969) in having a similar high anterior third of the blade, an identical convex arc in the posterior two-thirds, and

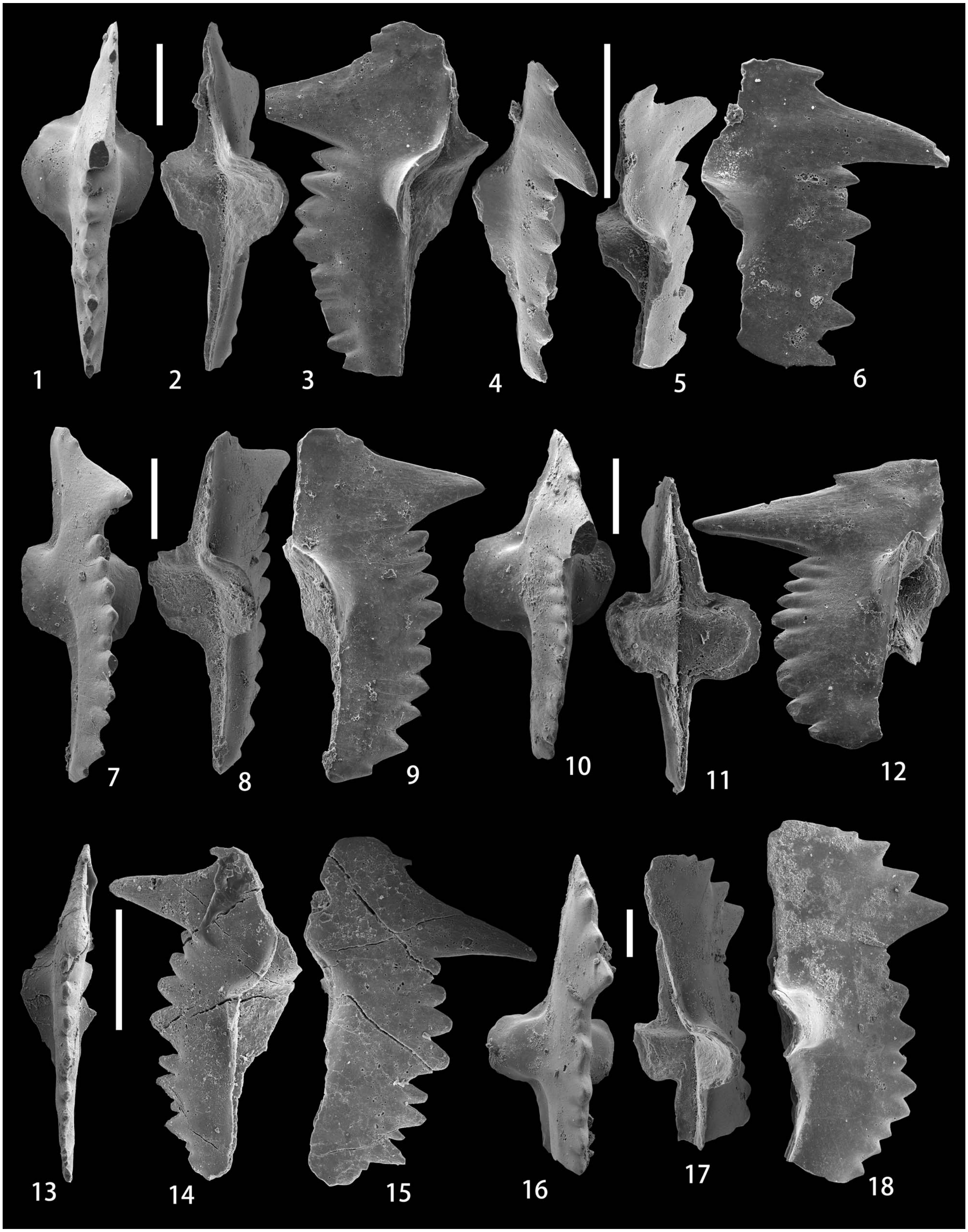

Figure 5. (**1–15**) *Pandorinellina exigua lingliensis* Lu n. subsp.; (**1–3**) upper, lower, and lateral views of NIGP 180679, sample 20LL-5, paratype; (**4–6**) upper, lower, and lateral views of NIGP 180680, sample 20LL-5, paratype, a juvenile specimen; (**7–9**) upper, lower, and lateral views of NIGP 180681, sample 20LL-6, holotype; (**10–12**) upper, lower, and lateral views of NIGP 180682, sample 20LL-17, paratype; (**13–15**) upper, lower-lateral, and lateral views of NIGP 180683, sample 20LL-25, paratype, a juvenile specimen. (**16–18**) *Pandorinellina exigua exigua* (Philip, 1966), upper, lower, and lateral views of NIGP 180684, sample 20LL-28. Scale bar is 200 μm across.

the same configuration of the lower margin. However, the Pa element of *P. exigua lingliensis* Lu n. subsp. possesses one extremely high and enlarged denticle occupying the whole anterior third of the blade. In this respect, it readily differs from the Pa elements of *P. exigua exigua* and *P. exigua philipi*, both of which have at least three much smaller and lower denticles in the anterior third of the blade (Fig. 5.3, 5.9, 5.12 vs. Fig. 5.18). In addition, the adult Pa element of *P. exigua lingliensis* Lu n. subsp. has inner and outer lobes clearly delimited posteriorly from a gradually tapering groove that is narrowly expanded beneath the entire portion of the anterior and posterior blades. In contrast, the inner lobe of the Pa element of *P. exigua exigua* is not clearly delimited posteriorly from the groove, whereas in the holotype of the Pa element of *P. exigua philipi* the cavity is not expanded beneath the posterior blade but replaced by a much narrower groove. The Pa element of *Pandorinellina*? *boucoti* (Klapper, 1969) is also highly distinguishable by possessing only one high and broad denticle in the anterior third of the blade. However, in the Pa element of *P.*? *boucoti* the lower margin in the anterior third of the blade is flat, resulting in the anterior end of the blade being lower than or at the same level as the anterior end of the basal cavity expansion, whereas in the Pa element of *P. exigua lingliensis* Lu n. subsp., the anterior end of the blade is higher than the anterior end of the basal cavity expansion. Moreover, the Pa element of *P.*? *boucoti* has distinctly asymmetrical lobes, on the larger one of which a single, high node may be developed.

Conodont biostratigraphy

Only 18 of the 47 samples yielded conodont elements (Table 1, Fig. 3). The conodont fauna from the Gaoling Member of the Nahkaoling Formation is dominated by *Pandorinellina exigua lingliensis* Lu n. subsp., which is recorded in sample 20LL-5 and ranges upwards into the highest sample 20LL-47. *Zieglerodina*? *tuojiangensis* Lu n. sp. ranges from sample 20LL-9 to sample 20LL-25. Both new taxa are endemic forms restricted to South China. Although globally reported, *P. exigua exigua* has a rather long stratigraphic range, and thus is also of less biostratigraphical significance. Based on the stratigraphic ranges of *Amydrotaxis praejohnsoni* and *Eognathodus* cf. *E. irregularis*, the interval from the base of the Nahkaoling Formation to the level of sample 20LL-10 belongs to the Lochkovian, whereas the interval from sample 20LL-25 to sample 20LL-47 belongs to the Pragian (Fig. 3).

At the Lingli section, *Amydrotaxis praejohnsoni* first occurs in sample 20LL-9, which is ~11.51 m above the lithological boundary between the Lianhuashan Formation and the Nahkaoling Formation, and ranges upwards into sample 20LL-10, which is 0.1 m above sample 20LL-9. Previously, the lowest occurrence of *A. praejohnsoni* (= *Ozarkodina* sp. C Klapper, 1977) was used by Klapper (1977, p. 40) to define the lower boundary of the third Lochkovian conodont zone in central Nevada, the *O.* n. sp. D Zone (= *delta* Zone of Klapper and Johnson, 1980). However, this species has a restricted geographical distribution and was only reported in western North America (Klapper, 1969; Klapper and Johnson, 1980; Klapper

Table 1. Occurrence of conodont taxa from the Gaoling Member of the Nahkaoling Formation at the Lingli section.

Sample no. (20LL)	5	6	7	9	10	13	17	18	19	20	24	25	28	36	38	45	46	47	Total number
Sample level (m)	3.12–3.15	3.23–3.27	3.33–3.37	3.51–3.59	3.69–3.75	5.14–5.22	6.54–6.60	6.62–6.72	6.75–6.79	6.83–6.95	9.05–9.15	9.42–9.52	14.12–14.26	24.72–24.74	29.57–29.67	34.80–34.86	34.96–35.04	35.16–35.37	
Sample weight (kg)	1.92	2.67	2.09	2.78	1.97	2.62	3.22	3.12	3.01	3.02	3.51	2.70	2.18	1.68	2.03	2.91	3.38	3.46	
Pandorinellina exigua lingliensis n. subsp.	7	11	1	3	10	2	2	3	2	1	32	13	2		1	1	2	2	**94**
Zieglerodina? *tuojiangensis* n. sp.				1	1	2	2				9	1							**16**
Amydrotaxis praejohnsoni				1	1														**2**
Eognathodus cf. *E. irregularis*												1							**1**
Pandorinellina exigua exigua													1	1			20		**22**
Total number	**7**	**11**	**1**	**5**	**12**	**4**	**4**	**3**	**2**	**1**	**41**	**15**	**3**	**1**	**1**	**1**	**22**	**2**	**135**

and Murphy, 1980; Murphy and Matti, 1983; Murphy and Springer, 1989; Murphy, 2016) and eastern Australia (Mawson, 1986). Accordingly, great difficulty was encountered in the global application of the central Nevada *delta* Zone to the Lochkovian in other regions. Subsequently, the *delta* Zone was subdivided into numerous zones by different conodont researchers (Valenzuela-Ríos, 1994a, b; Valenzuela-Ríos and Murphy, 1997; Murphy and Valenzuela-Ríos, 1999; Corradini and Corriga, 2012; Slavík et al., 2012; Valenzuela-Ríos et al., 2015) based on studies in the Spanish Central Pyrenees, the Prague Synform, the Carnic Alps, and Sardinia. However, *Amydrotaxis* has not been reported so far in Europe, as pointed out by Valenzuela-Ríos et al. (2015), except for the unfigured *Amydrotaxis* sp. reported by Corriga et al. (2009, fig. 3) from Sardinia.

Valenzuela-Ríos and Murphy (1997) subdivided the Lochkovian into the lower, middle, and upper parts: the bases of the middle and upper Lochkovian were suggested to be defined by the first occurrences of *Ancyrodelloides omus* Murphy and Matti, 1983 α morphotype (= *Lanea omoalpha* Murphy and Valenzuela-Ríos, 1999) and *Criteriognathus pandora* (= *Masaraella pandora*) Murphy, Matti, and Walliser, 1981 β morphotype, respectively. Slavík (2011), Slavík et al. (2012), and Corradini and Corriga (2012) shifted the position of the base of the middle Lochkovian to the entry of *Ancyrodelloides carlsi* (Boersma, 1973) (= *Lanea carlsi* Boersma, 1973) because they demonstrated that *L. omoalpha* has a much longer range than previously supposed, even extending downwards into the lower Lochkovian in the Carnic Alps and Bohemia. However, due to the fact that *A. carlsi* only works as a good marker for the basal middle Lochkovian in Europe and cannot be applied in North America, Murphy and Valenzuela-Ríos (2017) proposed that *A. transitans* (Bischoff and Sannemann, 1958) is a better marker for the base of the middle Lochkovian on a global scale. This suggestion was subsequently supported by Corriga and Corradini (2019). Apparently, the definition of the base of the middle Lochkovian has been the subject of numerous studies and remains controversial. As shown by Murphy and Valenzuela-Ríos (1999, text-fig. 1), *A. praejohnsoni* ranges from the *omoalpha*-*transitans* Zone into the *trigonicus*-*pandora* β Zone. In other words, the occurrence of *A. praejohnsoni* is restricted to the middle Lochkovian no matter whether the base of the middle Lochkovian is marked by *L. omoalpha* or by *A. carlsi*; however, the range of *A. praejohnsoni* extends downwards into the lower Lochkovian if *A. transitans* is proposed to mark the base of the middle Lochkovian. Therefore, the interval from sample 20LL-9 to sample 20LL-10 belongs to the middle Lochkovian or even lower Lochkovian, contingent upon different definitions for the base of the middle Lochkovian. This is the first time that *A. praejohnsoni* has been reported from China, and the first time that Lochkovian conodonts have been recorded from the South China Block. *Amydrotaxis praejohnsoni* plays an important role in global biostratigraphical correlation, especially when other contemporaneous taxa of great biostratigraphical significance cannot be obtained.

Eognathodus cf. *E. irregularis* only occurs in sample 20LL-25 at the Lingli section. As noted previously, the Pa element of this taxon closely resembles that of *E. irregularis* in the presence of irregular denticles on the blade and the absence of a sulcus. However, it differs from the holotype of the Pa element of *E. irregularis* in having a narrow and flat platform in the middle part of the blade; it also differs from two specimens of the Pa element of *E. irregularis* illustrated by Murphy (2005, fig. 6.15, 6.17) in having a much narrower basal cavity. As suggested by Murphy (2005, p. 199), various morphs of the Pa element of *E. irregularis* in the early Pragian are characterized by a medium- to large-sized basal cavity, irregular denticles or tubercles, and the absence of a sulcus. Accordingly, the occurrence of *E.* cf. *E. irregularis* in sample 20LL-25 indicates that this level is assignable to the lower Pragian and may be very close to the Lochkovian-Pragian boundary. The precise determination of this boundary needs further investigation.

Discussion

First named and identified by Ting (1929, p. 157) as a Caledonian tectonic orogeny in South China, the Kwangsian Movement (= Guangxi Movement) is evinced by a widespread disconformity or distinct angular unconformity between the Devonian and the underlying strata. Chen et al. (2010, 2012, 2014) determined that the duration of the Kwangsian Orogeny extended from the Late Ordovician to the Silurian-Devonian transition. However, the precise time of the Kwangsian Orogeny termination on the South China Block remains unknown. Recently, after having investigated the major hiatus in middle Paleozoic rocks at 126 sections in South China, Wang et al. (2021) pointed out, based on the studies of fossil plants from the siliciclastic rocks in northern Guangxi, that the Kwangsian Orogeny ended in the late Lochkovian, and that the starting time of the deposition of the post-orogeny strata shows a stepwise delay northeastward. This diachrony results from the gradually strengthened transgression northeastwards after the Kwangsian Orogeny from the Early Devonian to the Late Devonian in the South China Block (Xu et al., 2019).

As noted previously, the interval from sample 20LL-9 to sample 20LL-10 in the lower part of the Nahkaoling Formation at the Lingli section belongs to the middle Lochkovian or even lower Lochkovian, contingent upon varying definitions for the base of the middle Lochkovian. Therefore, the age of the Lianhuashan Formation cannot be younger than middle Lochkovian. At the Lingli section, the basal part of the Lianhuashan Formation is marked by a conglomerate bed ∼0.1 m thick and unconformably overlies the Cambrian Huangdongkou Formation. Additionally, at the Liujing section, which is located ∼14 km east of the Lingli section, an angular unconformity between the underlying Huangdongkou Formation and the overlying Lianhuashan Formation is also observed. The thickness of the basal conglomerate bed of the Lianhuashan Formation at the Liujing section is 0.3 m (Kuang et al., 1989, p. 14). The Lianhuashan Formation, mainly consisting of purple-red thick quartzitic sandstones and siltstones with a basal conglomerate bed, represents rapid deposits in shallow water after the Kwangsian Orogeny. The corroborated age of the Lianhuashan Formation at the Lingli section in central Guangxi indicates that the Kwangsian Orogeny ended before the late Lochkovian, which is an earlier date than indicated by fossil plants from the siliciclastic rocks deposited after the Kwangsian Orogeny.

After the Kwangsian Orogeny, the northeastwards marine transgression resulted in a stepwise delay in the onset of deposition of the post-orogeny strata northeastwards in the South China Block. Therefore, the post-orogeny transgression flooded the southernmost areas of the South China Block first, including southern Guangxi and, more importantly, northeastern Vietnam. A more precise temporal calibration of the termination of the Kwangsian Orogeny relies on detailed investigations on the Lochkovian and Pragian biostratigraphy in northeastern Vietnam where deposition after the Kwangsian Orogeny took place first. Northeastern Vietnam, especially the East Bac Bon Zone of the Bac Bo Region, was part of Cathaysian Land (a southeastern component of the South China Block) during the Devonian (Thanh and Hoe, 1988; Thanh et al., 2013). In the East Bac Bon Zone, the Lower Devonian is subdivided in ascending order into the Si Ka Formation, Bac Bun Formation, Mia Le Formation, and the lower part of the Ban Pap Formation. The Si Ka, Bac Bun, and Mia Le formations show a close similarity in lithology and fossil composition to the Lianhuashan, Nahkaoling, and Yukiang formations, respectively, in Guangxi (Thanh et al., 2013). More importantly, the Si Ka Formation, the basal part of which is marked by the conglomerate beds locally up to 5–10 m thick, unconformably overlies the Lower Ordovician Lutxia Formation. The presence of a conglomerate bed and distinct unconformity parallel the present findings in the South China Block and agree with what was emphasized by Thanh et al. (2013, p. 184), specifically that the red coarse clastic continental or subcontinental deposits of the Si Ka Formation indicate the influence of the Kwangsian Orogeny. In order to investigate the ending time of the Kwangsian Orogeny in northeastern Vietnam, the conodont biostratigraphy of the overlying Bac Bon Formation, a lithological unit represented by the interfingering of limestone and siliciclastic deposits, needs to be studied in the future.

Conclusions

An early or middle Lochkovian to early Pragian conodont fauna is reported from the Gaoling Member of the Nahkaoling Formation at the Lingli section, central Guangxi. These are the first Lochkovian conodonts reported from the South China Block. A new species, *Zieglerodina*? *tuojiangensis* Lu n. sp., and a new subspecies, *Pandorinellina exigua lingliensis* Lu n. subsp., are described herein.

The lower boundary of the Nahkaoling Formation, which previously was correlated roughly with the base of the Pragian, is dated more accurately to be approximately the middle Lochkovian or even much older. This suggests that the age of the upper boundary of the underlying Lianhuashan Formation in central Guangxi is not younger than the middle Lochkovian, meaning that the Kwangsian Orogeny ended before the late Lochkovian. This date is earlier than the previously estimated late Lochkovian end for the Kwangsian Orogeny based on the studies of fossil plants from siliciclastic rocks deposited after the Kwangsian Orogeny (Wang et al., 2021).

Amydrotaxis praejohnsoni, which previously had been reported only from North America and eastern Australia, is reported for the first time from the South China Block. This species plays an important role in middle Lochkovian intercontinental biostratigraphical correlation when other biostratigraphically important taxa, which have a wide distribution in the peri-Gondwana (e.g., Spanish Central Pyrenees, Prague Synform, Sardinia, and Carnic Alps), have not yet been recorded.

Acknowledgments

We thank S.X. Zhang (Associate Editor), M.A. Murphy (California), S. Gouwy (Calgary) and C. Corradini (Trieste) for providing important and useful comments that greatly improved the manuscript. T.H. Gao is acknowledged for critically reading and meticulously polishing the manuscript. Sincere thanks also go to H.Y. Zhang for his assistance in processing limestone samples in the laboratory. This work is supported by the Youth Innovation Promotion Association Chinese Academy of Sciences, the National Natural Science Foundation of China (41702009), and the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB26000000).

Declaration of competing interests

The authors declare none.

References

Bai, S.L., Jin, S.Y., and Ning, Z.S., 1982, The Devonian Biostratigraphy of Guangxi and Adjacent Area: Beijing, Peking University Press, 203 p. [in Chinese]

Bischoff, G., and Sannemann, D., 1958, Unterdevonische conodonten aus dem Frankenwald: Notizblatt des Hessischen Landesamtes für Bodenforschung, v. 86, p. 87–110.

Boersma, K.T., 1973, Description of certain Lower Devonian platform conodonts of the Spanish Central Pyrenees: Leidse Geologische Mededelingen, v. 49, p. 285–301.

Branson, E.B., and Mehl, M.G., 1933, Conodonts from the Bainbridge Formation (Silurian) of Missouri: University of Missouri Studies, v. 8, p. 39–52.

Chen, X., Zhang, Y.D., Fan, J.X., Chen, J.F., and Li, Q.J., 2010, Ordovician graptolite-bearing strata in southern Jiangxi with a special reference to the Kwangsian Orogeny: Science China Earth Sciences, v. 53, p. 1602–1610.

Chen, X., Zhang, Y.D., Fan, J.X., Tang, L., and Sun, H.Q., 2012, Onset of the Kwangsian Orogeny as evidenced by biofacies and lithofacies: Science China Earth Sciences, v. 55, p. 1592–1600.

Chen, X., Fan, J.X., Chen, Q., Tang, L., and Hou, X.D., 2014, Toward a stepwise Kwangsian Orogeny: Science China Earth Sciences, v. 57, p. 379–387.

Corradini, C., and Corriga, M.G., 2010, Silurian and lowermost Devonian conodonts from the Passo Volaia area (Carnic Alps, Italy): Bollettino della Societa Paleontologica Italiana, v. 49, 237–253.

Corradini, C., and Corriga, M.G., 2012, A Přídolí–Lochkovian conodont zonation in Sardinia and the Carnic Alps: implications for a global zonation scheme: Bulletin of Geosciences, v. 87, p. 635–650.

Corriga, M.G., and Corradini, C., 2009, Upper Silurian and Lower Devonian conodonts from the Monte Cocco II Section (Carnic Alps, Italy): Bulletin of Geosciences, v. 84, p. 155–168.

Corriga, M.G., and Corradini, C., 2019, Ontogeny of *Ancyrodelloides carlsi* (Boersma) and comments on its generic attribution (Conodonta, Lower Devonian): Geobios, v. 57, p. 25–32.

Corriga, M.G., Corradini, C., Ferretti A., 2009, Silurian conodonts from Sardinia: an overview: Rendiconti della Società Paleontologica Italiana, v. 3, p. 95–107.

Corriga, M. G., Corradini, C., and Walliser, O.H., 2014, Upper Silurian and Lower Devonian conodonts from Tafilalt, southeastern Morocco: Bulletin of Geosciences, v. 89, p. 183–200.

Corriga, M.G., Corradini, C., Schönlaub, H.P., and Pondrelli, M., 2016, Lower Lochkovian (Lower Devonian) conodonts from Cellon section (Carnic Alps, Austria): Bulletin of Geosciences, v. 91, p. 261–270.

Druce, E.C., 1971, Conodonts form the Garra Formation (Lower Devonian): Bureau of Mineral Resources, Geology and Geophysics, Bulletin, v. 116, p. 29–64.

Dzik, J., 1976, Remarks on the evolution of Ordovician conodonts: Acta Palaeontologica Polonica, v. 21, p. 395–455.
Farrell, J.R., 2003, Late Pridolian, Lochkovian, and early Pragian conodonts from the Gap area between Larras Lee and Eurimbla, central western NSW, Australia: Courier Forschungsinstitut Senckenberg, v. 245, p. 107–181.
Gao, L.D., 1978, Early Devonian spores and acritarchs from the Nakaoling Stage of Liujing, Kwangsi, *in* Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, ed., Symposium on the Devonian System of South China: Beijing, Geological Publishing House, p. 346–358. [in Chinese]
Hass, W.H., 1959, Conodonts from the Barnett Formation of Texas: United States Geological Survey Professional Papers, v. 243-F, p. 365–400.
Hou, H.F., 1959, Lower Devonian and Eifelian spiriferid brachiopods from southern Guangxi: Acta Palaeontological Sinica, v. 7, p. 450–462. [in Chinese with Russian abstract]
Hou, H.F., and Xian, S.Y., 1975, Lower to Middle Devonian brachiopods from Guangxi and Guizhou: Professional Papers of Stratigraphy and Palaeontology, v. 1, p. 1–85. [in Chinese with English abstract]
Hou, J.P., 1978, Early Devonian chitinozoans from the Nakaoling Formation of Liujing, Heng County, Kwangsi, *in* Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, ed., Symposium on the Devonian System of South China: Beijing, Geological Publishing House, p. 359–396. [in Chinese]
ICZN, 1999, International Code of Zoological Nomenclature. 4th Edition: London, The International Trust for Zoological Nomenclature, 306 p.
Klapper, G., 1969, Lower Devonian conodont sequence, Royal Creek, Yukon Territory, and Devon Island, Canada: Journal of Paleontology, v. 43, p. 1–27.
Klapper, G., 1977, Lower and Middle Devonian conodont sequence in central Nevada, *in* Murphy, M.A., Berry, W.B.N., and Sandberg, C.A., eds., Western North America: Devonian: University of California, Riverside Campus Museum Contribution, v. 4, p. 33–54.
Klapper, G., and Johnson, J.G., 1980, Endemism and dispersal of Devonian conodonts: Journal of Paleontology, v. 54, p. 400–455.
Klapper, G., and Murphy, M.A., 1980, Conodont zonal species from the *delta* and *pesavis* Zones (Lower Devonian) in central Nevada: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 8, p. 490–504.
Kuang, G.D., Zhao, M.T., and Tao, Y.B., 1989, The Standard Devonian Section of China: Liujing Section of Guangxi: Wuhan, China University of Geosciences Press, 154 p. [in Chinese with English summary]
Liu, S.F., 1982, Preliminary note on the Arthrodira from Guangxi, China: Vertebrata PalAsiatica, v. 20, p. 106–114. [in Chinese with English summary]
Liu, Y.H., 1985, A galeaspid (Agnatha), *Antiquasagittaspis cornuta* gen. et sp. nov., from Lower Devonian of Guangxi, China: Vertebrata PalAsiatica, v. 23, p. 247–254. [in Chinese with English summary]
Lu, J.F., and Chen, X.Q., 2016, New insights into the base of the Emsian (Lower Devonian) in South China: Geobios, v. 49, p. 459–467.
Lu, J.F., Qie, W.K., and Chen, X.Q., 2016, Pragian and lower Emsian (Lower Devonian) conodonts from Liujing, Guangxi, South China: Alcheringa, v. 40, p. 275–296.
Lu, J.F., Qie, W.K., Yu, C.M., and Chen, X.Q., 2017, New data on the age of the Yukiang (Yujiang) Formation at Liujing, Guangxi, South China: Acta Geologica Sinica (English Edition), v. 91, p. 1438–1447.
Lu, J.F., Valenzuela-Ríos, J.I., Liao, J.-C., and Kuang, G.D., 2018, Conodont biostratigraphy of the Yujiang Formation (Emsian, Lower Devonian) at Shizhou, Guangxi, South China: Palaeoworld, v. 27, p. 170–178.
Lu, J.F., Valenzuela-Ríos, J.I., Liao, J.-C., and Wang, Y., 2019, Polygnathids (Conodonta) around the Pragian/Emsian boundary from the Dacun-1 section (central Guangxi, South China): Journal of Paleontology, v. 93, p. 1210–1220.
Mawson, R., 1986, Early Devonian (Lochkovian) conodont faunas from Windellama, New South Wales: Geologica et Palaeontologica, v. 20, p. 39–71.
Müller, K.J., and Müller, E.M., 1957, Early Upper Devonian (Independence) conodonts from Iowa, part I: Journal of Paleontology, v. 31, p. 1069–1108.
Murphy, M.A., 2005, Pragian conodont zonal classification in Nevada, western North America: Revista Española de Paleontología, v. 20, p. 177–206.
Murphy, M.A., 2016, *Cypricriodus hesperius* (Klapper and Murphy)—taxonomy and biostratigraphy: University of California, Riverside Campus Museum Contribution, v. 8, p. 1–24.
Murphy, M.A., and Matti, J.C., 1983, Lower Devonian conodonts (*hesperius–kindlei* Zones), central Nevada: University of California Publications in Geological Sciences, v. 123, p. 1–83.
Murphy, M.A., and Springer, K.B., 1989, Morphometric study of the platform elements of *Amydrotaxis praejohnsoni* n. sp. (Lower Devonian, conodonts, Nevada): Journal of Paleontology, v. 63, p. 349–355.
Murphy, M.A., and Valenzuela-Ríos, J.I., 1999, *Lanea* new genus, lineage of Early Devonian conodonts: Bollettino della Societa Paleontologica Italiana, v. 37, p. 321–334.
Murphy, M.A., and Valenzuela-Ríos, J.I., 2017, Reconstruction of the skeletal apparatus of *Flajsella* Valenzuela-Rios and Murphy 1997 (Devonian conodont): Stratigraphy, v. 14, p. 285–297.
Murphy, M.A., Matti, J.C., and Walliser, O.H., 1981, Biostratigraphy and Evolution of the *Ozarkodina remscheidensis-Eognathodus sulcatus* lineage (Lower Devonian) in Germany and central Nevada: Journal of Paleontology, v. 55, p. 747–772.
Murphy, M.A., Valenzuela-Ríos, J.I., and Carls, P., 2004, On classification of Pridoli (Silurian)–Lochkovian (Devonian) Spathognathodontidae (conodonts): University of California, Riverside Campus Museum Contribution, v. 6, p. 1–25.
Pan, K., and Wang, S.T., 1978, Devonian Agnatha and Pisces of South China, *in* Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, ed., Symposium on the Devonian System of South China: Beijing, Geological Publishing House, p. 298–333. [in Chinese]
Philip, G.M., 1965, Lower Devonian conodonts from the Tyers area, Gippsland, Victoria: Proceedings of the Royal Society of Victoria, v. 79, p. 95–118.
Philip, G.M., 1966, Lower Devonian conodonts from the Buchan Group, eastern Victoria: Micropaleontology, v. 12, p. 441–460.
Pickett, J., 1980, Conodont assemblages from the Cobar Supergroup (Early Devonian), New South Wales: Alcheringa, v. 4, p. 67–88.
Qiao, L., Chen, B., and Shen, S.Z., 2021, Lower Devonian (Pragian) brachiopods from the Dashatian section, Guangxi, South China: Rivista Italiana di Paleontologia e Stratigrafia, v. 127, p. 1–16.
Ruan, Y.P., Wang, C.Y., Wang, Z.H., Rong, J.Y., Mu, D.C., Kuang, G.D., Yin, B.A., and Su, Y.B., 1979, On the age of Nahkaoling and Yukiang formations: Acta Stratigraphica Sinica, v. 3, p. 225–229. [in Chinese]
Slavík, L., 2011, *Lanea carlsi* conodont apparatus reconstruction and its significance for subdivision of the Lochkovian: Acta Palaeontologica Polonica, v. 56, p. 313–327.
Slavík, L., Carls, P., Hladil, J., and Koptíková, L., 2012, Subdivision of the Lochkovian Stage based on conodont faunas from the stratotype area (Prague Synform, Czech Republic): Geological Journal, v. 47, p. 616–631.
Stauffer, C.R., 1940, Conodonts from the Devonian and associated clays of Minnesota: Journal of Paleontology, v. 14, p. 417–435.
Thanh, T.D., and Hoe, N.D., 1988, Outline of paleogeographical reconstruction of Vietnam and adjacent regions during the Devonian, *in* McMillan, N.J., Embry, A.F., and Glass, D.J., eds., Devonian of the World Volume I: Regional Syntheses: Canadian Society of Petroleum Geologists Memoir, v. 14, p. 591–595.
Thanh, T.D., Phương, T.H., Janvier, P., Hùng, N.H., Cúc, N.T.T., and Dương, N.T., 2013, Silurian and Devonian in Vietnam—stratigraphy and facies: Journal Geodynamics, v. 69, p. 165–185.
Ting, V.K., 1929, The orogenic movements in China: Bulletin of the Geological Society of China, v. 8, p. 151–170.
Valenzuela-Ríos, J.I., 1994a, Conodontos del Lochkoviense y Praguiense (Devónico Inferior) del Pirineo Central Español: Memorias del Museo Paleontológico de la Universidad de Zaragoza, v. 5, 178 p.
Valenzuela-Ríos, J.I., 1994b, The Lower Devonian conodont *Pedavis pesavis* and the *pesavis* Zone: Lethaia, v. 27, p. 199–207.
Valenzuela-Ríos, J.I., and Murphy, M.A., 1997, A new zonation of middle Lochkovian (Lower Devonian) conodonts and evolution of *Flajsella* n. gen. (Conodonta), *in* Klapper, G., Murphy, M.A., and Talent, J.A., eds., Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson: Geological Society of America Special Paper, v. 321, pp. 131–144.
Valenzuela-Ríos, J.I., Slavík, L., Liao, J.-C., Calvo, H., Hušková, A., and Chadimová, L., 2015, The middle and upper Lochkovian (Lower Devonian) conodont successions in key peri-Gondwana localities (Spanish Central Pyrenees and Prague Synform) and their relevance for global correlations: Terra Nova, v. 27, p. 409–415.
Wang, C.Y., and Wang, Z.H., 1978, Early and Middle Devonian conodonts of Kwangsi and Yunnan Province, *in* Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, ed., Symposium on the Devonian System of South China: Beijing, Geological Publishing House, p. 334–345. [in Chinese]
Wang, C.Y., Ruan, Y.P., Mu, D.C., Wang, Z.H., Rong, J.Y., Yin, B.A., Kuang, G.D., and Su, Y.B., 1979, Subdivision and correlation of the Lower and Middle Devonian series in different facies of Guangxi: Acta Stratigraphica Sinica, v. 3, p. 305–311. [in Chinese]
Wang, C.Y., Chen, B., and Kuang, G.D., 2016, Lower Devonian conodonts from the Nagaoling Formation of the Dashatian section near Nanning, Guangxi, South China: Acta Micropalaeontologica Sinica, v. 33, p. 420–435. [in Chinese with English abstract]
Wang, N.Z., 1992, Microremains of agnathans and fishes from Lower Devonian of central Guangxi with correlation of Lower Devonian between central Guangxi and eastern Yunnan. South China: Acta Palaeontologica Sinica, v. 31, p. 298–307. [in Chinese with English summary]

Wang, S.Q., 1996, Leperditiid Sinoleperditiini (Ostracoda) from the Early Devonian of Liujing and Liujia, Guangxi, China: Acta Palaeontologica Sinica, v. 35, p. 331–348. [in Chinese with English summary]

Wang, Y., and Rong, J.Y., 1986, Yukiangian (Early Emsian, Devonian) brachiopods of the Nanning-Liujing District, central Guangxi, southern China: Palaeontologia Sinica, Series B, v. 172, p. 1–282. [in Chinese with English summary]

Wang, Y., Yu, C.M., and Fang, D.W., 1964, On the age of Nahkaoling Formation and subdivision of Yukiang Formation in central-eastern Guangxi: Chinese Science Bulletin, v. 11, p. 1013–1015. [in Chinese]

Wang, Y., Rong, J.Y., Tang, P., Huang, B., Zhang, X.L., Xu, H.H., Liu, F., Jiang, Q., and Wang, Y., 2021, Characteristics of major hiatus in middle Paleozoic rocks of South China and their significance of geotectonics: Scientia Sinica Terrae, v. 51, p. 218–240. [in Chinese]

Wei, F., Zong, P., and Gong, Y.M., 2019, Tentaculitids and their evolutionary significance in the Early Devonian Dashatian section, South China: Palaeobiodiversity and Palaeoenvironments, v. 99, p. 7–28.

Xian, S.Y., Wang, S.D., Zhou, X.Y., Xiong, J.F., and Zhou, T.R., 1980, Nandan Typical Stratigraphy and Paleontology of Devonian in South China: Guiyang, Guizhou People's Press, 135 p. [in Chinese]

Xu, H.H., Wang, Y., Tang, P., Fu, Q., and Wang, Y., 2019, Discovery of Lower Devonian plants from Jiangxi, South China and the pattern of Devonian transgression after the Kwangsian Orogeny in the Cathaysia Block: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 531, 108982. https://doi.org/10.1016/j.palaeo.2018.11.007.

Zhang, R.J., Yan, D.P., Cao, X.P., and Zhao, MT., 1988, The Early–Middle Devonian bivalve faunas, life-habits and depositional environments of Guangxi: Geology of Guangxi, v. 1, p. 1–86. [in Chinese with English summary]

Zhang, R.J., Yao, H.Z., Yao, J.X., Tu, B., Yan, D.P., Wang, J.X., Duan, Q.F., and Tang, C.Y., 2015, Devonian Bivalves of Guangxi and Biodiversity Changes of Devonian Bivalves in South China: Wuhan, China University of Geosciences Press, 296 p. [in Chinese with English abstract]

Zhong, K., Wu, Y., Yin, B.A., Liang, Y.L., Yao, Z.G., and Peng, J.L., 1992, The Devonian System of Guangxi, China: Wuhan, China University of Geosciences Press, 384 p. [in Chinese]

Ziegler, W., 1960, Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinisches Schiefergebirge): Paläontologische Zeitschrift, v. 34, p. 169–201.

Accepted: 19 December 2022