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Middle Visean (Mississippian) conodonts from shallow-water deposits in the Yashui section, Guizhou, South China, and their stratigraphic significance

Qiulai Wang,* ⓘ Yuping Qi, and Le Yao

State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China <qlwang@nigpas.ac.cn>, <ypqi@nigpas.ac.cn>, <lyao@nigpas.ac.cn>

Non-technical Summary.—In southern Guizhou, South China, there are well-exposed shallow-water deposits of the Jiusi and Shangsi formations, which consist of platform limestones mixed with shales and sandstones. Conodonts, ancient tooth-like fossils, were found in the limestones and were dominated by two groups: the *Cavusgnathus* aff. *Cav. unicornis* and *Clydagnathus windsorensis* in the upper Jiusi Formation and the *Cavusgnathus unicornis* in the lowest Shangsi Formation. *Vogelgnathus campbelli* with small lateral denticles was found for the first time in Eastern Paleotethys. The *Cavusgnathus unicornis* is used as a marker for the regional Shangsian stage and correlated to other conodont zones marked by similar species in North America and Europe of middle Visean.

Abstract.—The typical Mississippian shallow-water deposits of the Jiusi and Shangsi formations are well exposed in the Yashui section in southern Guizhou, South China. The strata are composed mainly of platform limestones intercalated with shales and sandstones. Conodonts obtained from the limestones are dominated by two assemblages of cavusgnathids: the *Cavusgnathus* aff. *Cav. unicornis* and *Clydagnathus windsorensis* assemblage from the upper Jiusi Formation and the *Cavusgnathus unicornis* assemblage from the lowest Shangsi Formation. *Vogelgnathus campbelli* (Rexroad, 1957) is reported for the first time in Eastern Paleotethys and is characterized by small lateral denticles. The evolutionary first occurrence of *Cavusgnathus unicornis* Youngquist and Miller, 1949 is recognized as a marker for the regional Shangsian stage. This biostratigraphic datum is interpreted to be correlative with other shallow-water conodont zones marked by *Cavusgnathus unicornis* s.l. and similar species from North America and Europe.

Introduction

Carboniferous shallow-water conodont assemblages from open marine shallow-water environments (e.g., carbonate platform and outer shelf) are typically diverse and accompanied by other benthic taxa such as corals, brachiopods, and foraminifers (e.g., the late Tournaisian conodonts with short ranges; Tian and Coen, 2005). More-restricted environments (e.g., inner shelf, back reef, and lagoon) are highly influenced by sea level, temperature, and salinity, which makes these conodont faunas different from their open-marine counterparts. Genera belonging to Cavusgnathidae (mentioned in the following) are the typical representatives of the restricted shallow-water-environment faunas (Austin and Davies, 1984). Although they may be found in deeper-water environments, such as slopes and outer shelves, they are uncommon and make up a small portion of these assemblages. In these cases, reworking of these fossils due to downslope transport should be considered (Austin and Davies, 1984). The globally recognized *Cavusgnathus* biofacies (Mississippian) and *Adetognathus* biofacies (Pennsylvanian) are based on these dominant euryhaline genera (Merrill and Martin,

1976; Davis and Webster, 1985). Their early homomorphic relatives *Clydagnathus* and *Patrognathus* represent similar facies during Late Devonian (Sandberg and Dreesen, 1984). *Taphrognathus* is also very useful in correlation of Visean sequences (Purnell et al., 2002).

China was composed of several independent tectonic blocks during the Carboniferous. Most of these tectonic units were scattered around the eastern rim of the Paleotethys Ocean in low- and middle-latitude belts (e.g., Am, An, NC, SC, Si, T, and Ti in Fig. 1). Diverse conodont assemblages are documented from different depositional settings along a dip profile. Salinity appears to be one of the most important ecological factors for the Carboniferous conodonts in China because high salinity levels are associated with low-diversity faunas (Wang and Clark, 1990). Most of the Carboniferous shallow-water conodont faunas in China are reported from the Mississippian. A conodont zonation based on index species of *Siphonodella* has been recognized in Guizhou, Hunan, Guangxi, and Guangdong and is a useful tool for regional correlation of the early Tournaisian successions (Ji, 1987a; Ji and Ziegler, 1992; Qie et al., 2016). In Yunnan and Hunan, *Finognathodus* and *Dollymae* are shallow-water benthonektonic representatives of the late Tournaisian and probably early Visean (Ji, 1987b; Coen et al., 2004; Tian and Coen, 2005). There are some scattered records

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*Corresponding author.

of *Clydagnathus*, *Bispathodus*, and *Rhachistognathus* from Tarim and Junggar areas in Xinjiang (Zhao et al., 2000), but most of them are from borehole data without reliable stratigraphic control. Species of *Neognathodus* from Xainza, Tibet, may be shallow-water representatives of Bashkirian and Moscovian strata in the Lhasa block (Ji et al., 2007).

The reconstructed temperature shows that the Visean may have been a relatively warm period before the main stage of the late Paleozoic ice age (Yao et al., 2020). This was inferred mainly from the compiled oxygen isotope curve based on calcitic brachiopod shells (Veizer and Prokoph, 2015). Statistics on the distributions and dimensions of the glaciers and reef-like bioconstructions also support such deduction (for more references, see Isbell et al., 2012; Yao et al., 2020). Shallow-water environments are widely distributed in South China with abundant macrofaunas. To clarify the coevolution of life and environments, it is important to develop techniques that allow precise stratigraphic correlation. The foraminifer-based stratigraphy in shallow-water deposits is conventionally used, but the scarcity of shallow-water taxa in deep-water deposits makes the correlation between the two realms difficult. The nektobenthic conodont species are highly cosmopolitan, less diverse, and provide clearer correlation across different lithological facies. The conodont assemblages described here are from the restricted shallow-water environment at Yashui, Guizhou, and are dominated by cavusgnathids. Similar assemblages in South China have been reported previously only from the boreholes in Shaoguan, Guangdong (Ding and Wan, 1989). These new conodont assemblages elucidate the evolution of *Cavusgnathus unicornis* Youngquist and Miller, 1949, which is an important species for biostratigraphic correlation, from *Cavusgnathus* aff. *Cav. Unicornis* Youngquist and Miller, 1949, allowing for a proposed global correlation based on the reported taxa.

Geological setting

The South China Block is located in the northeastern Paleotethys Ocean at low latitude, and the old lands of Yangtze and Cathaysia were connected during the Visean to Serpukhovian (Fig. 1). Marine-to-terrestrial alternations are widely recognized in the present northeastern regions such as Jiangsu, Anhui, and Hubei provinces (e.g., the Gaolishan Formation, mainly shales and siliciclastics with brachiopods and plants). In the southwestern regions, carbonates vary between nearshore (e.g., the Jiusi and Shangsi formations, intercalated with shales and abundant macrofossils) and basinal (e.g., the Nandan Formation, intercalated with siliceous cherts and few macrofossils) settings. Classic separation of the carbonates in Guizhou was based partly on their distinct colors, with the "white" and "black" carbonates indicating the shallow-water and deep-water deposits, each with mainly benthic and planktic organisms, respectively (Xiong and Zhai, 1985). The regional subdivisions of the Carboniferous in China are based mainly on the shallow-water sections from the white carbonate regions (Shen and Wang, 2015).

The section at Yashui is well exposed along the road near the town of Yashui and consists of the typical white carbonate and some shaly strata (Fig. 2). The composite stratigraphic section is composed of three outcrops: A, B, and C, in ascending order, and consists of the Jiusi, Shangsi, Baizuo, and Huashiban formations (Wu, 1987). The continuous sections B and C are the reference sections of the regional Dewuan Stage, characterized by the thick limestone with abundant corals and brachiopods (Wu, 2008; Lin et al., 2012; Lin, 2013). The beds with paleokarsts or storm-sorted brachiopods may indicate intervals of disturbed deposition (Chen et al., 2016; Yao et al., 2016a). Conodonts are rare in this section, and foraminifers are the primary biochronostratigraphic indexes. The Visean–Serpukhovian boundary was tentatively put within a paleokarst bed in the upper part of Shangsi Formation, about 5 m below the regional Shangsian–Dewuan boundary (Wu, 2008; Groves et al., 2012; Chen et al., 2016).

The studied interval consists of section A (Yashui-A; 25.9889°N, 106.7501°E). The top of section A is correlated with the bottom of section B by a marker bed with a fossiculate coral biostrome. It consists of the upper part of Jiusi Formation and the lowermost part of Shangsi Formation (Wu, 1987) (Fig. 2). The upper Jiusi Formation is composed mainly of gray to dark gray, thick-bedded limestones and shaly marls intercalated with a few sandstones. Brachiopods, corals, gastropods, and crinoids are abundant in pure limestones and sometimes also in laminated marls. Foraminifer assemblages with *Eoparastaffella*, *Dainella*, and *Archaediscus* can be roughly correlated with the MFZ11 to MFZ12 foraminiferal zones in Western Europe (Wu, 1987; Poty et al., 2006). The lower Shangsi Formation is composed of a higher number of limestone beds with lesser shales. The boundary between the Jiusi and Shangsi formations (roughly correlated with the regional Jiusian stage and Shangsian boundary) at this site is marked by a distinct coral biostrome bed (Wu, 1987; Yao et al., 2016b, and our bed 100 in Fig. 3). New foraminifera data from this biostrome bed and the overlying strata include *Pojarkovella nibelis* (Durkina, 1959), *Koskinobigenerina breviseptata* Eickhoff, 1968, and *Koskinotextularia cribriformis* Eickhoff, 1968, referring to the MFZ12 foraminiferal zone of the middle Visean (Yao et al., 2016b).

Methods and materials

We sampled every limestone bed within the 65 m outcrop, spanning the boundary of the Jiusi and Shangsi formations. In total, 58 conodont samples (4–5 kg each) were collected and processed by acetic acid dissolution (∼10% vol) and heavy-liquid separation (ρ ∼2.8 g/mL). Conodonts are rare, and the diagnostic specimens were extracted from only 18 samples (Fig. 3). All of the specimens are black in color (CAI 4∼5), and most of them are Pa pectiniform elements, which are the most robust elements in the conodont apparatus. Discrete fragments of the ramiform elements are common, and this may indicate a high-energy environment where less-robust elements were crushed and washed away. The specimens were photographed by a Hitachi SU3500 scanning electron microscope (SEM) after gold coating.

Repository and institutional abbreviation.—The illustrated specimens are stored in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, China, under the catalog numbers NIGP 201189–201236.
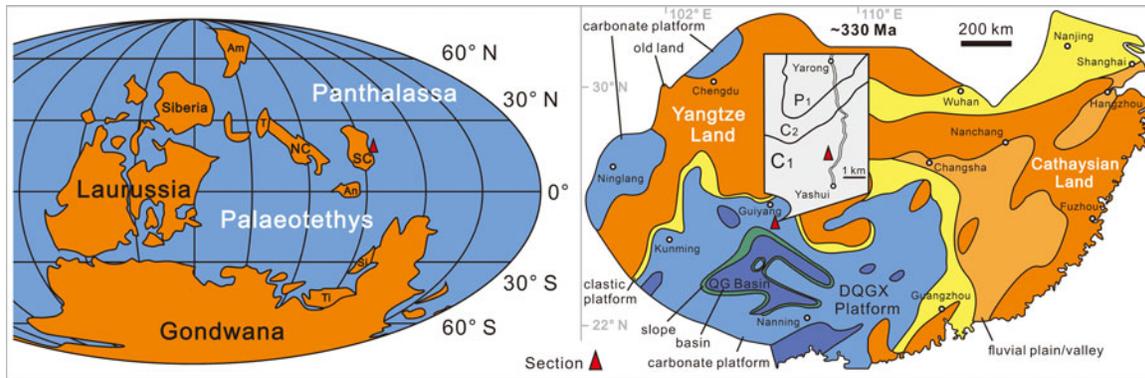
Figure 1.   Paleogeographic reconstructions of the globe (Am = Amuria; An = Annamia; NC = North China; SC = South China; Si = Sibumasu; T = Tarim; Ti = Tibet; modified from Torsvik and Cocks, 2017) and South China (DQGX Platform = Yunnan–Guizhou–Guangxi–Hunan Platform; QG Basin = Guizhou–Guangxi Basin; C_1 = Mississippian; C_2 = Pennsylvanian; P = Permian; modified from Wu, 1987; Feng et al., 1998) during Visean to Serpukhovian.

Systematic paleontology

In this paper, the systematic study is based mainly on the Pa elements because other elements are scarce and not well preserved. We follow Sweet (1988) and Purnell (1992) for the classification and detailed synonyms.

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Phylum Chordata Bateson, 1886
Class Conodonta Pander, 1856
Subclass Conodonti Branson, 1938
Order Ozarkodinida Dzik, 1976
Family Cavusgnathidae Austin and Rhodes in Robison, 1981

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Remarks.—Cavusgnathidae was erected by Austin and Rhodes (Robison, 1981) and originally included seven genera:

Cavusgnathus Harris and Hollingsworth, 1933, *Adetognathus* Lane, 1967, *Clydagnathus* Rhodes, Austin, and Druce, 1969, *Patrognathus* Rhodes, Austin, and Druce, 1969, *Taphrognathus* Branson and Mehl, 1941, *Capricornognathus* Austin in Austin and Mitchell, 1975, and *Cloghergnathus* Austin in Austin and Mitchell, 1975. According to the current study, this family includes eight genera. *Cloghergnathus* and *Capricornognathus* are considered junior synonyms of *Patrognathus* and *Taphrognathus*, respectively (Purnell, 1992), and the endemic genus *Montognathus* Crane in Jenkins et al., 1993 that was recognized from eastern Australia is included. Dzik (2006) noted that this family may be polyphyletic and includes three early genera: *Pseudopolygnathus* Branson and Mehl, 1934, *Alternognathus* Ziegler and Sandberg, 1984 and *Scaphignathus* Helms, 1959.
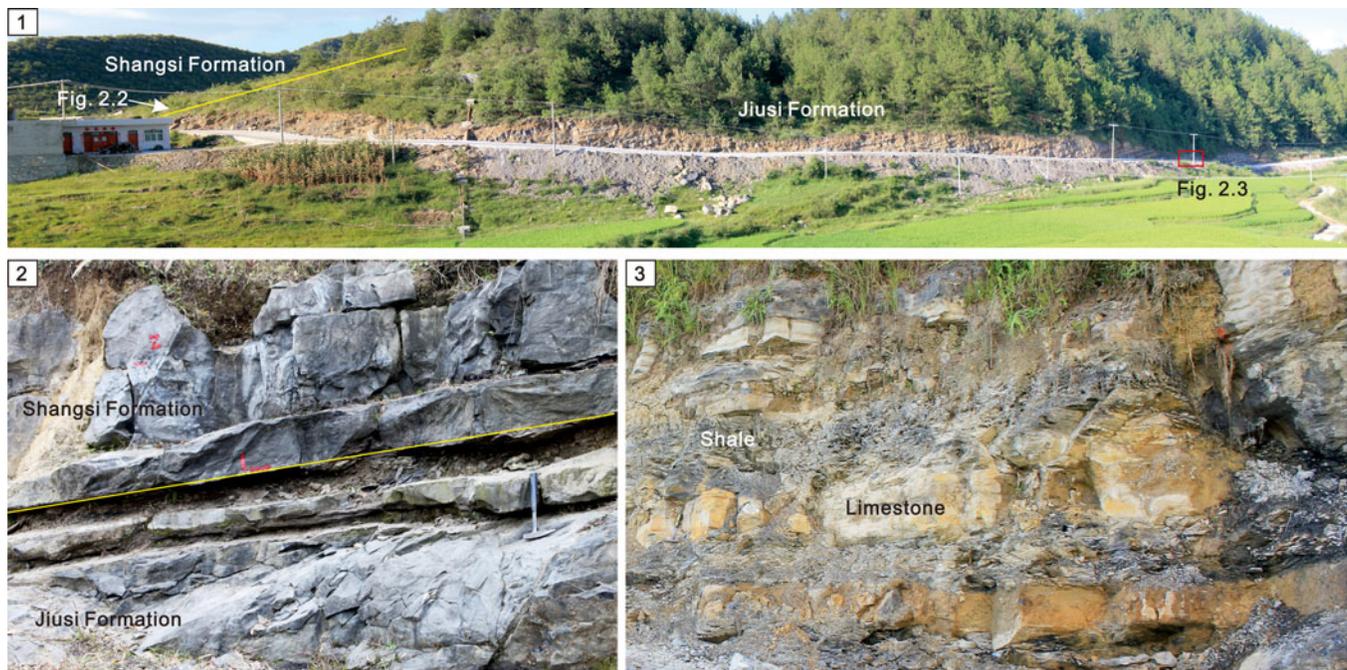
Figure 2.   Outcrop pictures of the Yashui-A section. (**1**) Distant view of the section. (**2**) Detail of the section showing the boundary between the Jiusi Formation and the Shangsi Formation. (**3**) Typical lithostratigraphic succession of the Jiusi Formation.
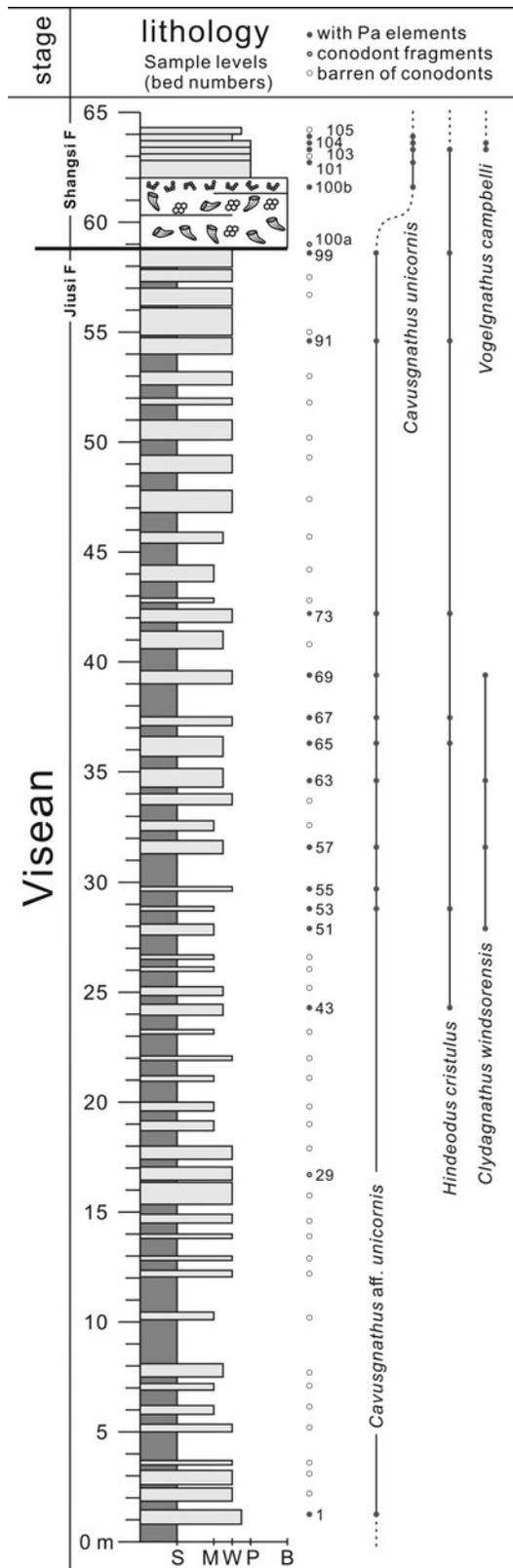
Figure 3. Lithostratigraphic column and conodont distributions of the Yashui-A section. F = formation; S = shaly marls; M = mud limestone; W = wackestone; P = packstone; B = biostrome.

This extends the family to the mid-Famennian of the Late Devonian. The conventional terms of "left" and "right" used here refer to the relative locations of certain parts when the cavusgnathid Pa element is situated venter (anterior) up and dorsal (posterior) down in oral view.

Genus *Cavusgnathus* Harris and Hollingsworth, 1933

Type species.—*Cavusgnathus alta* Harris and Hollingworth, 1933.

Remarks.—As the first described cavusgnathid, early interpretations of *Cavusgnathus* had a wide range of variation and a nearly global distribution. Since the erection of new morphological groups, many species originally included in this genus have been reassigned (e.g., Lane, 1967 considered all representatives of the Pennsylvanian *Cavusgnathus* to belong to his new genera *Adetognathus*). Although the phylogeny of these similar genera is far from being resolved (Lane, 1967; Rhodes et al., 1969; von Bitter and Austin, 1984; Brown et al., 1990; Jenkins et al., 1993), the morphological differences in Pa elements are relatively distinct. The Pa element of *Cavusgnathus* has a shorter blade and shows Class IV or Class IIIa symmetry while *Adetognathus* shows Class II or IIIb and *Taphrognathus* shows Class II or III symmetry (Lane, 1967; Purnell, 1992). *Cavusgnathus* differs from *Clydagnathus* in having platform ornament with ridges rather than discrete nodes. The reassignment of *Cly. hudsoni* Metcalfe, 1981 to *Cavusgnathus* extended the range of this genus into the late Tournaisian.

Cavusgnathus unicornis Youngquist and Miller, 1949
Figures 4.27–4.35, 5.1–5.8

1949 *Cavusgnathus unicornis* Youngquist and Miller, 1949, p. 619, pl. 101, figs. 18–23 (Pa element, α morphotype). [Iowa]

1949 *Cavusgnathus regularis* Youngquist and Miller, p. 619, pl. 101, figs. 24, 25 (Pa element, β morphotype). [Iowa]

1957 *Cavusgnathus convexa* Rexroad, p. 17, pl. 1, figs. 3–6 (Pa element, γ morphotype). [Illinois]

1957 *Ozarkodina compressa* Rexroad, p. 36, pl. 2, figs. 1, 2 (Pb element). [Illinois]

Holotype.—The University of Iowa 4174 from Pella beds at Pella South West, Marrion County, Iowa, USA (Youngquist and Miller, 1949, pl. 101, figs. 18, 19).

Occurrence.—Lower Shangsi Formation in the Yashui-A section, Guizhou; mid-Visean.

Description.—Both dextral and sinistral Pa elements of *Cavusgnathus unicornis* are recognized at Yashui. There is a difference between them, thus a Class IIIa symmetry is supported. The ventral (anterior) blade is about 35%–40% of the whole element length and occupied mostly by the fixed part. Three to eight denticles are on the blade, laterally compressed and normally with lower part fused. The dextral element has fewer denticles (usually three to five) on the
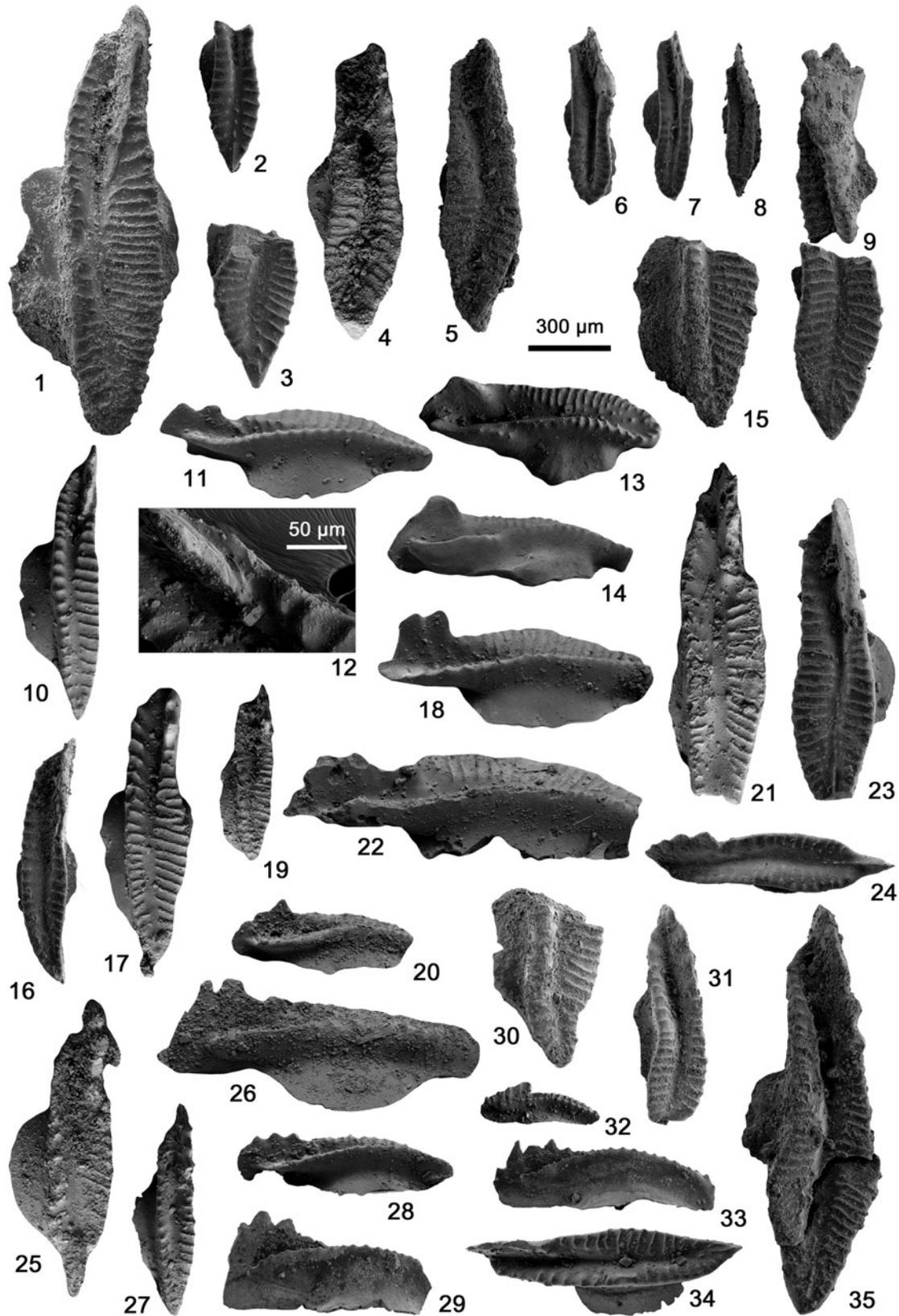
Figure 4. Conodonts from Yashui-A section (**1, 10–22, 25, 27–30, 33, 34** are sinistral Pa elements; **2–9, 23, 24, 26, 31, 32, 35** are dextral Pa elements). (**1–26**) *Cavusgnathus* aff. *Cav. unicornis* Youngquist and Miller, 1949: (**1, 2, 7, 8, 10–14**) 201189, 201190, 201195, 201196, 201198, 201198, 201198, 201199, 201199, bed 63; (**3**) 201191, bed 1; (**4, 26**) 201192, 201192, bed 55; (**5, 6**) 201193, 201194, bed 57; (**9, 15**) 201197, 201200, bed 67; (**16–18**) 201201, 201202, 201202, bed 69; (**19, 20**) 201203, 201203, bed 91; (**21–24**) 201204, 201204, 201205, 201206, bed 99; (**25**) 201207, bed 53. (**27–35**) *Cavusgnathus unicornis* Youngquist and Miller, 1949: (**27, 28**) 201208, 201208, bed 100b; (**29, 33–35**) 201209, 201213– 201215, bed 104; (**30–32**) 201210–201212, bed 103. (**1–11, 13–35**) Scale bars = 300 µm; (**12**) scale bar = 50 µm.
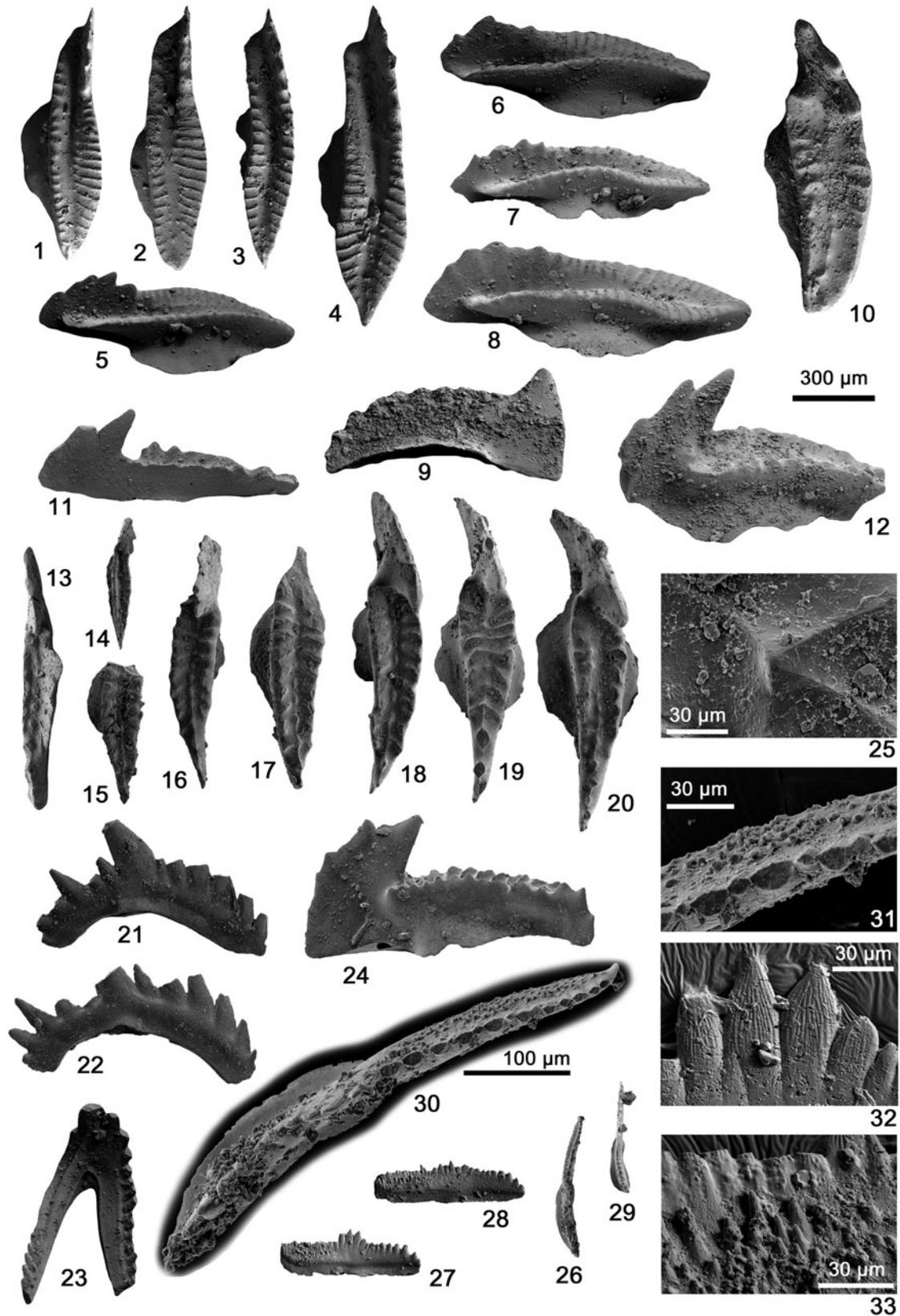
Figure 5. Conodonts from Yashui-A section (**1, 2, 5, 6, 14–17, 26, 29–31** are sinistral Pa elements; **3, 4, 7–13, 18–20, 24, 25, 27, 28, 32, 33** are dextral Pa elements; **21, 22** are Pb elements; **23** is S element). (**1–8**) *Cavusgnathus unicornis* Youngquist and Miller, 1949: (**1, 2, 4–6, 8**) 201216, 201217, 201219, 201216, 201217, 201219, bed 105; (**3, 7**) 201218, 201218, bed 104. (**9**) *Hindeodus cristulus* (Youngquist and Miller, 1949), 201220, bed 57. (**10–20, 24, 25**) *Clydagnathus windsorensis* (Globensky, 1967): (**10, 12**) 201221, 201221, bed 57; (**11, 13, 14**) 201222, 201222, 201223, bed 51; (**15–18, 24**) 201224–201227, 201227, bed 63; (**19, 20, 25**) 201228, 201229, 201228, bed 69. (**21**) *Ozarkodina* sp., 201230, bed 69. (**22**) *Ozarkodina* sp., 201231, bed 63. (**23**) *Apatognathus* sp., 201232, bed 105. (**26–33**) *Vogelgnathus campbelli* (Rexroad, 1957): (**26–28, 30–33**) 201233–201235, 201233, 201233–201235, bed 104; (**29**) 201236, bed 103. (**1–24, 26–29**) Scale bars = 300 μm; (**25, 31–33**) scale bars = 30 μm; (**30**) scale bar = 100 μm.

relatively shorter blade. In lateral view, the blade height is greater than length, and we accept the typical α (e.g., Fig. 4.32), β (e.g., Fig. 4.27, 4.28), γ (e.g., Fig. 5.1–5.8), or other intergradational morphotypes of *C. unicornis* summarized by Rexroad (1981). The blade is attached to the caudal side for sinistral elements and to the rostral side for dextral elements. Thus, it always appears that the blade connects to the "right" side. The junction between the blade and the parapet is smooth for dextral elements but has a slight notch in most sinistral elements. Both parapets are ornamented with transverse ridges and usually expanded most at the dorsal two-thirds of the whole length. The flat platform in the dextral element can be clearly seen from the "left"-lateral view (Fig. 5.7, 5.8) while in the sinistral element, the "left" parapet is uplifted with less lateral expansion and upper outline of the platform seems gradually arched (Fig. 5.5, 5.6). The medial trough is very shallow ventrally where the "left" parapet decreases in height. Several linear-situated nodes may fill in the dorsal trough and extend as a dorsal blade. The parapets may occasionally taper at the end (Fig. 4.30). The basal cavity is fully open and widest near the middle length of the element. The basal cavity is slightly asymmetric with the caudal (inner) half extending farther ventrally, and this may help to recognize the chirality of the elements.

Materials.—Thirteen Pa elements, including some broken specimens (201208–201219).

Remarks.—*Cavusgnathus unicornis* from Yashui contains dextral and sinistral elements of various blade morphotypes. The comparable species *Cav. hudsoni* was commonly found in older strata of the Tournaisian and was originally assigned to *Clydagnathus* (Metcalfe, 1981). *Cav. hudsoni* has a relatively longer free blade and a trough that may close ventrally, which is different from all other *Cavusgnathus* species. *Cav. naviculus* (Hinde, 1900) is also a cosmopolitan species but was found in younger strata, mostly Serpukhovian, with a nearly filled medial trough. The platform of *Cav. altus* (i.e., *Cav. alta*) has a rather flat upper outline in lateral view and a basal cavity not extended to the dorsal end. *Cav. charactus* Rexroad, 1957 is diagnosed by the significant notch between the blade and parapet, which is not prominent in *Cav. unicornis*.

Cavusgnathus aff. *Cav. unicornis* Youngquist and Miller, 1949
Figure 4.1–4.26

? 1982   *Cavusgnathus regularis* type Youngquist and Miller, 1949; von Bitter and Plint-Geberl, 1982, pl. 3, figs. 14, 17, 18 only (Pa elements).
? 1984   *Cavusgnathus unicornis* Youngquist and Miller, 1949; von Bitter and Austin, 1984, pl. 19, figs. 12–14, 16–28 only (Pa elements).

Occurrence.—Upper Jiusi Formation in the Yashui-A section, Guizhou; mid-Visean.

Description.—*Cavusgnathus* aff. *Cav. unicornis* from Yashui shows Class IIIa symmetry. The ventral blade is about 25%–35% of the whole element length with very small free part.

One to five laterally compressed denticles lie on the blade with their most basal part fused. The sinistral element usually has fewer denticles as one or two large denticles. The blades of the specimens show similarity of the α (e.g., Fig. 4.6–4.8, 4.13, 4.14, 4.19, 4.20, 4.24), β (e.g., Fig. 4.9–4.12), and intermediate morphotypes of the *Cav. unicornis*. The ventral blade is always close to or connected with the "right" parapet but usually more medially situated. Thus, a notch commonly occurs between the blade and "right" parapet because of this misalignment, and the dorsal end of the blade ends abruptly (e.g., Fig. 4.10–4.14, 4.21–4.25). The element is slim in general, ornamented with transverse ridges on both parapets, and a trough almost straight in the sinistral and slightly twisted in the dextral. The parapets in the dextral element constrict at the middle length and expand at the dorsal part when the specimens are small (e.g., Fig. 4.6, 4.7); in larger specimens, these parts are more ventrally situated (e.g., Fig. 4.23). In the sinistral element, the "left" parapet is uplifted and the "right" parapet is laterally expanded. The widest place of the platform is at the middle length. Dorsal blades in some specimens are significantly extended beyond the platform (Fig. 4.24, 4.25).

Materials.—Twenty-three Pa elements, including some broken specimens (201189–201207).

Remarks.—In all aspects, *Cavusgnathus* aff. *Cav. Unicornis* is similar to *Cav. unicornis*, but the relatively low number of specimens makes it difficult to understand what morphological changes should be considered interspecific. Because the diagnostic characteristics of *Cavusgnathus* aff. *Cav. unicornis* are restricted stratigraphically, we maintain the distinction between the two and interpret them as closely related species. The Pa element of *Cavusgnathus* aff. *Cav. unicornis* has a slimmer platform with relatively shorter blade and more significant parapet notch. These characters also show similarity with *Cav. hudsoni*, but the latter has a relatively longer free blade (more information in Purnell, 1992, table 2). The morphometric changes from small specimens to large specimens may be explained by allometric ontogeny, in which the dorsal part of platform grows faster than the ventral in *Cavusgnathus*. Thus, the length proportion of the ventral blade may decrease during growth as shown in Figure 6.

The lineage from *Taphrognathus* to *Cavusgnathus* (i.e., *Cav. unicornis*) has long been suggested on the basis of specimens from the lower and upper St. Louis formations (Rexroad and Collinson, 1963) in the United States and from Avon Gorge (von Bitter and Austin, 1984) in the United Kingdom. However, after the reassignment of *Cly. hudsoni* as the earliest *Cavusgnathus*, the former lineage seems unreliable stratigraphically, thus a lineage from *Clydagnathus* to *Cavusgnathus* early forms was suggested (Purnell, 1992). Because no small specimens were collected, the ontogenetic patterns proposed by Austin (1973) and Purnell (1992) could not be tested. Jenkins et al. (1993) considered the right attachment of the blade and the openness of the ventral trough as two successive phylogenetic modifications in *Cavusgnathus*.

A new species, *Cav. altifrons* Jenkins in Jenkins et al., 1993, has been recognized as the intermediate between *Cav. hudsoni* and other Chesterian *Cavusgnathus* species (e.g.,
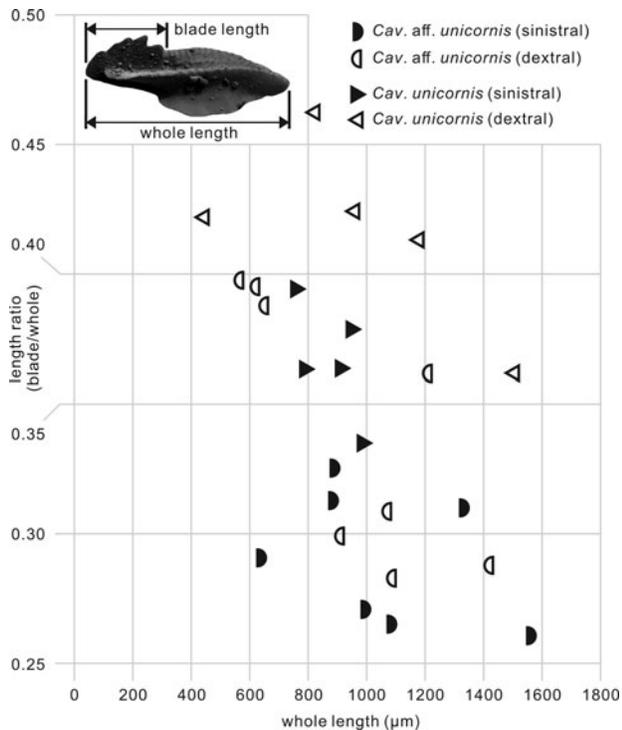
Figure 6. Plot of the dimensional ratios of *Cavusgnathus unicornis* and *Cavusgnathus* aff. *Cav. unicornis*

Cav. unicornis). *Cav. altifrons* has a similar platform shape and parapet notch. The dorsal blade in *Cav. Altifrons* is also quite like those of some of our specimens (e.g., Fig. 4.24, 4.25). *Cav. altifrons* differs from *Cavusgnathus* aff. *Cav. unicornis* by having a relatively longer free blade, smaller basal cavity, parapets ornamented with nodes rather than transverse ridges, and in lateral view the "left" parapet joints with the ventral blade at about half the height of the blade. Meanwhile, *Cav. altifrons* seems to lack a clear chirality.

Considering the dimensional ratios plot by Jenkins et al. (1993), *Cavusgnathus* aff. *Cav. unicornis* may be morphologically similar to *Cav. unicornis* and *Cav. charactus*. Since there are few illustrations of *Cav. charactus*, it is difficult to make a comparison. The Pb element of *Cavusgnathus* aff. *Cav. unicorns* may be represented by two *Ozarkodina* sp. found within the same stratigraphic range. Our *Ozarkodina* sp. is similar to the holotype of *Ozarkodina compressa* (thought as the Pb element of *Cav. unicornis*) but with less-fused denticles and more arched profile in lateral view (Fig. 5.21, 5.22). Thus, it is more similar to the older Pb element of *Cav. hudsoni* illustrated by Purnell (1992; pl. 1, fig. 9).

The early *Cavusgnathus* record in South China is from the upper Jinling Formation, accompanied with the late Tournaisian species *Polygnathus communis communis* (Ni, 1984, identified as *Cly. unicornis* Rhodes, Austin, and Druce, 1969, but the single illustrated specimen is more like *Cav. altifrons* or *Cav. hudsoni* and reassigned to *Cavusgnathus*). Recently, several similar specimens have been found from Guizhou and Guangxi, with *Polygnathus* (probably *Polygnathus dujieensis* Qie et al., 2014 spanning the Tournaisian– Visean boundary) (unpublished).

These specimens are ornamented with elongated nodes or transverse ridges on both parapets. The difference between *Cav. altifrons* and *Cav. hudsoni* is blurred, if only by these ornaments on parapets, and the low-resolution SEM figures may also cause such confusion. Because of the preceding comparison, *Cavusgnathus* aff. *Cav. unicornis* is considered as an intermediate between *Cav. hudsoni* and *Cav. unicornis*.

Genus *Clydagnathus* Rhodes, Austin, and Druce, 1969

Type species.—*Clydagnathus cavusformis* Rhodes, Austin, and Druce, 1969.

Remarks.—When Rhodes et al. (1969) recognized this genus from early Tournaisian strata, they distinguished it from *Cavusgnathus* by the merging of the parapet and ventral blade, the closure of the medial trough ventrally, and a laterally, rather than longitudinally, expanded basal cavity. Later conodont workers found these characters not practical and proposed using parapet ornaments with nodes rather than ridges to distinguish them from *Cavusgnathus* instead (Nicoll and Druce, 1979; von Bitter and Plint, 1987). The long-ranging *Clydagnathus* may be polyphyletic (Rhodes et al., 1969; Sandberg and Ziegler, 1979; Purnell, 1992). The reassignment of *Cav. windsorensis* Globensky, 1967 to *Clydagnathus* extends the range of this genus into Visean.

Clydagnathus windsorensis (Globensky, 1967)
Figure 5.10–5.20, 5.24, 5.25

1967   *Cavusgnathus windsorensis* Globensky, p. 439, pl. 57, figs. 3, 4, 7, 9, 11, 19; pl. 58, fig. 1 (Pa element).
1967   *Cavusgnathus* cf. *windsorensis* Globensky, 1967, p. 439, pl. 57, figs. 2, 6, 10, 12; pl. 58, fig. 8 (Pa element).
? 1983   *Clydagnathus*? cf. *cavusformis* Rhodes, Austin, and Druce, 1969; Briggs, Clarkson, and Aldridge, p. 3, figs. 1–3 (whole animal).
1987   *Clydagnathus windsorensis* (Globensky, 1967); von Bitter and Plint, p. 350, pl. 57, figs. 2.1–2.7, 2.10, 2.11, 2.14–2.17 (Pa element).

Holotype.—University of New Brunswick 64-F-235 from Windsor Limestone at Skir Dhu, Cape Breton, Nova Scotia, Canada (Globensky, 1967, pl. 57, figs. 3, 4, 7).

Occurrence.—Upper Jiusi Formation in the Yashui-A section, Guizhou; mid-Visean of the Mississippian.

Description.—The Pa element has a lanceolate platform with parapets ornamented by discretely spaced nodes. The nodes are laterally elongated in oral view and pointed in lateral view. The ventral blade is a little less than one-third of the whole element, with the height greater than the length. Two to six laterally compressed blade denticles are present, almost fully fused at the base. Only the last two denticles are easily recognizable. The ventral blade is almost free and medially situated. The ventral blades connect with the "right" parapet for both sinistral and dextral elements, and this Class IIIa

symmetry is distinguishable in oral view (e.g., Fig. 5.16, 5.18). The medial trough is closed ventrally by the merging of the "left" parapet with the blade and dorsally by the carina and dorsal blade. Occasionally, the elongated nodes on the parapets may connect with the carina and cross at the trough (Fig. 5.19, 5.25). The basal cavity is mainly restricted at the middle length of the element. The stoutest and slimmest specimens studied here are considered as two ends of the morphometric range of this species (Fig. 5.10–5.13), and the similar situation of *Cly. unicornis* Rhodes, Austin, and Druce, 1969 has been illustrated by Varker and Higgins (1979, pl. 16, figs. 8, 9).

Materials.—Eighteen Pa elements, including some broken specimens (201221–201229).

Remarks.—*Clydagnathus windsorensis* has limited records outside of North America. There is a long temporal gap between this species and its early counterparts. Purnell (1992) considered it as a possible progenetic offshoot of *Cavusgnathus*. The known conodont animal *Clydagnathus*? cf. *Cly. cavusformis* might belong to this species (Briggs et al., 1983). The possible Pb element is similar to that of *Lochriea* rather than *Cavusgnathus* (*Ozarkodina* sp. A. in Globensky, 1967, pl. 55, figs. 1, 5, 12), and a cladistic study based on the complete apparatus may yield similar results (Donoghue et al., 2008). Unfortunately, no similar Pb element was recovered. Compared with the published materials, our Pa element shows intermediate characters of the parapet denticles between the typical *Clydagnathus* and *Cavusgnathus*, which probably adds more confusion on the phylogeny of this genus.

<div align="center">

Family Uncertain
Genus *Vogelgnathus* Norby and Rexroad, 1985

</div>

Type species.—*Spathognathodus campbelli* Rexroad, 1957.

Remarks.—The apparatus of this genus is based on bedding plane materials (Norby and Rexroad, 1985; Purnell and Donoghue, 1997; Sanz-Lopez et al., 2019). *Vogelgnathus* is similar to several genera (e.g., *Lochriea*, *Gnathodus*, and *Hindeodus*) but is easily differentiated by the Pa elements (Norby and Rexroad, 1985; Sweet, 1988; Donoghue et al., 2008). Dzik (2006) included several Devonian species within this genus and under the family Francodinidae. The evolution of this genus is not clear. As for the conventional Mississippian representatives, the phylogeny pattern is probably complicated by geographical differentiation (Purnell and von Bitter, 1992a; Sanz-Lopez et al., 2019).

<div align="center">

Vogelgnathus campbelli (Rexroad, 1957)
Figure 5.26–5.33

</div>

1957 *Spathognathodus windsorensis* Rexroad, p. 37, pl. 3, figs. 13–15 (Pa element).
1985 *Vogelgnathus campbelli* (Rexroad, 1957); Norby and Rexroad, p. 3, pl. 1, figs. 1, 2 (assemblage), pl. 2, figs. 3–10 (Pa element), pl. 2, figs. 1, 2, pl. 3, figs. 5, 9, 10 (Pb element).

Holotype.—Illinois State Geological Survey 2P75 from Ridenhower Shale of the Paint Creek Formation at Floraville, St. Clair County, Illinois, USA (Rexroad, 1957, pl. 3, fig. 15). *Occurrence.*—Lower Shangsi Formation in the Yashui-A section; mid-Visean.

Description.—The paired dextral and sinistral Pa elements are mirrored in general, except for locations of the lateral nodes on the blade. The free blade occupies less than half of the whole element in length, with ~15 denticles of varying size inclined ventrally. The basal cavity is longitudinally elongated and extends to the dorsal end. There is a constriction at the ventral one-third, which separates the platform into two parts. The ventral part is slightly less expanded in the smaller specimen but more in the larger specimens (Fig. 5.26, 5.29). Between four and seven denticles are on the carina, with the highest ones upright at the middle length and inclined dorsally. The dorsal part occupies two-thirds of the platform and with around seven to 10 denticles, slightly inclined dorsally. The denticles on the blade and ventral carina are laterally compressed in cross section with a flatter outline on the "left" side and usually fused or with germ denticles inserted between larger denticles (Fig. 5.31). The denticles on the dorsal carina are round in cross section, narrowly spaced ventrally, and widely spaced dorsally. In both dextral and sinistral Pa elements, small nodes occur on the "left" side of the blade above the lateral ridge, more ventrally inclined than the blade denticles (Fig. 5.33). The microtexture of coarse fibrous crystals is exhibited around the denticles but is not apparent on the small lateral nodes (Fig. 5.32, 5.33). In lateral view, the lower outline of the basal cavity is flat.

Materials.—Four Pa elements (201233–201236)

Remarks.—*Vogelgnathus campbelli* is cosmopolitan and has been reported from many regions of middle and low latitudes (e.g., North America: Rexroad, 1957; Globensky, 1967; Purnell and von Bitter, 1992a; western Europe: Rhodes et al., 1969; Park, 1983; van den Boogaard, 1992; Purnell and von Bitter, 1992a; Nemyrovska and Samankassou, 2005; eastern Europe: Kabanov et al., 2009; East Asia: Igo, 1973; Qi et al., 2014; north coast of Gondwana: Jenkins et al., 1993; Nemyrovska et al., 2006; Medina-Varea, 2018; Atakul-Ozdemir et al., 2019; south Urals of central Asia: unpublished materials of the authors). We accept the recently revised phylogeny (Purnell and von Bitter, 1992a; Nemyrovska and Samankassou, 2005; Sanz-Lopez et al., 2019), and the profiles of our specimens are more like the possible ancestor *V. simplicatus* (Rhodes, Austin, and Druce, 1969) rather than the possible descendant *V. postcampbelli* (Austin and Husri, 1974). Our specimens closely resemble the holotype and other specimens from the type area in Illinois and also in Atlantic Canada, possessing distinct lateral nodes (Norby and Rexroad, 1985; Purnell and von Bitter, 1992a, b). Almost all previous records of *V. campbelli* outside of North America do not have such characters, except for some specimens from Morocco (Medina-Varea, 2018). Purnell and von Bitter (1992b) studied these unusual asymmetrical-placed nodes and thought they were functional. The paring pattern for ozarkodinid Pa elements

might be that the sinistral lies behind the dextral element (Purnell, 1995). More evidence is still needed to reveal why only some specimens of this species have such lateral nodes, excluding the interference of age and sedimentary setting. The asymmetry of the denticles in cross section is also found in many other ozarkodinids without lateral nodes (especially for the blade denticles). As the microtexture is well developed on both sides of the denticles, it is difficult to determine whether it is functional or just a wear structure.

Stratigraphic correlations

Conodonts are most abundant in the middle (bed 63; ∼34.5 m) and upper (bed 104; ∼63.5 m) parts of the Yashui-A section, including Pa elements of *Cavusgnathus* aff. *Cav. unicornis*, *Cavusgnathus unicornis*, *Clydagnathus windsorensis*, *Hindeodus cristulus* (Youngquist and Miller, 1949), and *Vogelgnathus camp-belli*. Two assemblages, described in the following, are recognized: the *Cavusgnathus* aff. *Cav. unicornis*–*Cly. windsorensis* assemblage from the upper Jiusi Formation and the *Cav. unicornis* assemblage from the lowermost Shangsi Formation (Figs. 3, 7).

In the Yashui-A section, common Visean conodont representatives of deep-water facies (e.g., *Gnathodus* and *Lochriea*) are absent. The *Cavusgnathus* aff. *Cav. unicornis* assemblage contains the nominate species through the lower part of the studied section, but its real first occurrence is not clear. *Cavusgnathus* aff. *Cav. unicornis* occurs with *Clydagnathus windsorensis* or *Hindeodus cristulus* in the relatively productive samples of beds 43–69. The *Cav. unicornis* assemblage is present in the uppermost part of the section. It is marked by the phylogenetic first occurrence of *Cav. unicornis* and also includes *Vogelgnathus campbelli*. *Hindeodus cristulus* is in both assemblages.

The aforementioned foraminifers of the MFZ11 to MFZ12 foraminiferal zone suggest a possible early to middle Visean age for the studied interval at the Yashui-A section. As for the conodonts, *Hindeodus cristulus* and *Vogelgnathus campbelli* are common in the late Visean and early Serpukhovian, but their first occurrences are much lower, from late Tournaisian (Metcalfe, 1981; Zhuravlev, 2017; Sanz-Lopez et al., 2019). Invasions of *V. campbelli* were considered indicators of rapid sea-level-rise events in the Cantabrian Mountains, Spain (van den Boogaard, 1992; Nemyrovska and Samankassou, 2005); however, their occurrence in shallow-water facies is sparse and therefore not useful to correlate sea-level change. The shallow-water conodonts are particularly prone to facies control; thus, correlation between restricted and endemic faunas is complicated (Austin and Davies, 1984; Barrick et al., 2022). However, conodont zonations for shallow-water facies have been recognized globally, based mainly on the cavusgnathids (*Taphrognathus*, *Clydagnathus*, *Cavusgnathus*, and *Adetognathus*). At Yashui, the only cosmopolitan species with potential for regional or long-distance correlations is *Cav. unicornis*, which also marks the base of the regional Shangsian stage.

In the central United States, this widespread species first occurred from the middle St. Louis breccia at the base of the *Apatognathus scalenus*–*Cavusgnathus* Zone (Collinson et al., 1962, 1971; ∼base of Faunal Unit 8 *scitulus*–*scalensus* Zone of Lane and Brenckle, 2005). Near the zonal boundary, there is a short interval with co-occurrence of *Cav. unicornis* and *Taphrognathus varians* Branson and Mehl, 1941 (including the "*Taphrognathus*–*Cavusgnathus* transitions" of Rexroad and Collinson, 1963). We correlate the *Cavusgnathus* aff. *Cav. unicornis* assemblage at Yashui with this interval and above the main hosting horizons for *T. varians* of the Warsaw and Salem formations (Fig. 7).
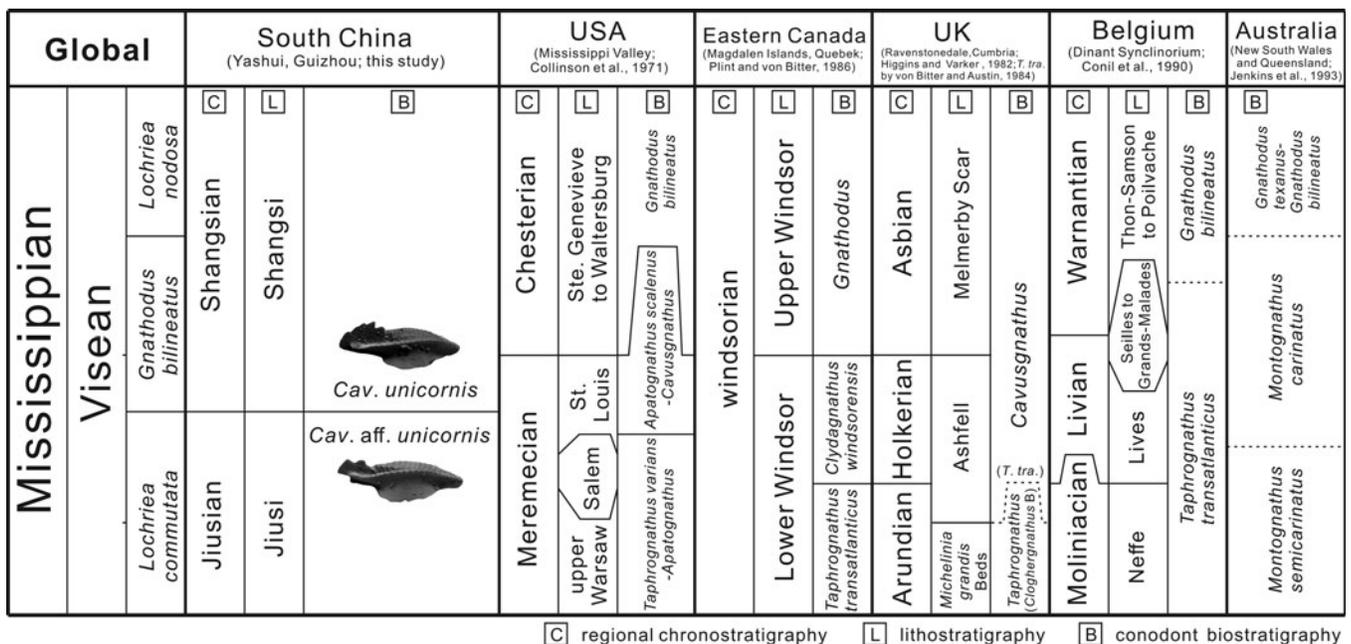
Figure 7. Correlation of the biozonations based on the shallow-water conodonts during the Visean of different regions.

In eastern Canada, the shallow-water conodont succession incudes the *T. transatlanticus* (von Bitter and Austin, 1984) (the generic assignment is suspect; see Purnell et al., 2002), *Cly. Windsorensis*, and *Gnathodus* zones in the Windsor Group, in ascending order (Plint and von Bitter, 1986). The *Cav. unicornis* associated with *Cly. windsorensis* often occurred in the *Gnathodus* Zone (e.g., von Bitter and Plint-Geberl, 1982). The illustrated *Cav. unicornis* from the lower horizons within the *T. transatlanticus* Zone are similar to *Cavusgnathus* aff. *Cav. unicornis* in this study with blade-parapet notches (e.g., von Bitter and Plint-Geberl, 1982, pl. 3, figs. 14, 17, 18). We propose that the *Cavusgnathus* aff. *Cav. unicornis* and *Cav. unicornis* assemblages may be correlative with the *Cly. windsorensis* Zone in Canada, although the original concept of this zone includes no *Cavusgnathus* (Fig. 7).

The shallow-water conodont succession in the United Kingdom is similar to that of eastern Canada. In Ravenstonedale of Cumbria, Higgins and Varker (1982) erected the *Taphrognathus* Zone marked by the co-occurrence of *T. varians* and *T. carinatus* (Higgins and Varker, 1982) (originally as *Cloghergnathus carinatus*). The overlying *Cloghergnathus* Zone is marked by the extinction of *T. carinatus*. Above this is the *Cavusgnathus* Zone that is marked by the first occurrence of *Cav. unicornis*. The lower two zones are hard to differentiate with the proposed markers (Purnell et al., 2002), and there was a conodont-barren interval within the Ashfell Sandstone between the top of *Cloghergnathus* Zone and the base of the *Cavusgnathus* Zone. This barren interval was later filled by the *T. transatlanticus* Zone recognized in the Avon Gorge (von Bitter and Austin, 1984). This zone is correlative with the same-name zone in eastern Canada but different in that the nominated species co-occurred with the *Cly. windsorensis* and probably the real first occurrence of *Cav. unicornis* s.l. in the United Kingdom. We think their *Cav. unicornis* (e.g., von Bitter and Austin, 1984, pl. 19, figs. 12–14, 16–28) resembles our *Cavusgnathus* aff. *Cav. unicornis* and use this in our correlation (Fig. 7).

The *T. transatlanticus* Zone of Belgium is not very clear, but as Conil et al. (1990) stated, "a few specimens of small taphrognathid-like conodonts have been found at the top of the Moliniacian as well as some cavusgnathids at the base of the Livian." Some of the Australian *Adetognathus* from the early to middle Visean (e.g., *Adetognathus taphrognathoides* Jenkins in Jenkins et al., 1993, fig. 10A–C, H, I) might be *Taphrognathus*, and this is considered in the proposed correlation here (Fig. 7).

Considering all the preceding factors, the studied interval at Yashui could be tentatively correlated with Visean conodont zones from other regions that include the first occurrence of *Cavusgnathus unicornis* s.l. (Fig. 7). This horizon consistently occurs above the widespread *Taphrognathus varians* assemblage in multiple regions (e.g., the United States and the United Kingdom). The primitive type *Cavusgnathus* aff. *Cav. unicornis* commonly co-occurs with *Clydagnathus windsorensis* and occasionally with the suspect *T. transatlanticus*. The *Cavusgnathus* aff. *Cav. unicornis* to *Cav. unicornis* lineage is now recognized only in this single section. More work studying the lineage of *Cav. unicornis* will test our proposed phylogeny

and may significantly improve global correlations of Visean shallow-water deposits.

Conclusion

Conodonts from the typical Visean shallow-water platform deposits in southern Guizhou have been studied. Two conodont assemblages are described, one from the upper Jiusi Formation and the other from the lowest Shangsi Formation of the Yashui-A section. The conodont faunas of this interval are dominated by cavusgnathids, and the yield is low. The first occurrences of Pa elements of *Cavusgnathus* aff. *Cav. unicornis*, *Hindeodus cristulus*, *Clydagnathus windsorensis*, *Cav. unicornis*, and *Vogelgnathus campbelli* occur successively. The *Cavusgnathus* aff. *Cav. unicornis* assemblage and the *Cav. unicornis* assemblage are associated with the lithological boundary between the two formations. Judging from the intermediate features of the Pa and possible Pb elements, *Cavusgnathus* aff. *Cav. unicornis* is likely a direct ancestor of *Cav. unicornis* and a possible descendant of *Cav. hudsoni*. The first occurrence datum of *Cav. unicornis* near the base of the Shangsi Formation is constrained by the most abundant data here compared with neighboring regions and is suggested to mark the beginning of the middle Visean and regional Shangsian. Although the underlying zone with *Taphrognathus varians* has not been reported from South China, this work shows potential in finding biostratigraphically significant conodonts in other shallow-water sections. More work is needed in this region to refine the temporal scheme.

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Declaration of competing interests

The authors declare none.

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