Alatoconchids: giant Permian bivalves from South China

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Highlights

Giant alatoconchid bivalves, a highly distinctive Tethyan fauna, are identified for the first time in the Permian of South China.

Alatoconchids range from the lower Kungurian to the uppermost Capitanian in South China.

Dense concentrations of the clams signify their gregarious habit.

Abstract

Alatoconchidae, a unique bivalve family from the Permian, are characterized by a giant body size (up to 100 cm long), and unusual shell form with wing-like flanges and coarse prismatic outer layer of the shell wall. Palaeogeographically, they are restricted to low-latitude Tethyan and Panthalassan regions. However, the clams have not been previously been reported from South China even though this is one of the main, eastern Palaeotethyan terranes. Here we show that these giant clams were in fact widely distributed in South China, but they have been previously misidentified as phylloid algae. The present study verifies their occurrence in the region using reconstruction of shell forms from a series of transverse sections, as well as their characteristic shell microstructure. The alatoconchids occur commonly as coquina beds. Over thirty occurrences, ranging from the early Kungurian to probably the latest Capitanian in time, have been found. Based on detailed lithological and microfacies observation at more than ten fossil localities, most alatoconchid-bearing horizons (ABH) are autochthonous deposits, confined to medium- to thick-bedded limestones (often wackestone) of shallow water carbonate platforms. Two occurrences from an intra-platform basin are allochthonous deposits shed from the nearby carbonate platform by gravity flows, and featured by completely disintegrated fragments. Autochthonous and condensed accumulation of the fossil materials with great lateral persistence imply a gregarious habit of the clam, although slightly reworking might be involved. Its absence of from high energy conditions, as well as the completeness of shell preservation, suggests it was not a reef dweller. To obtain giantism in the tropical oligotrophic environment, alatoconchids may have harboured photosymbionts, like present-day tridacnids, facilitated by its transparent shell texture, although this notion is challenged by Asato et al. (2017). Their association with calcareous algae and corals in the ABH indicates that the optimum belt of the clams is likely within the euphotic zone, but below that of calcareous green algae judging from the lithological succession and skeletal grain association.

Keywords: Alatoconchidae, habit and habitat, Guadalupian, Tethyan fauna, South China.

1. Introduction

The Alatoconchidae is a giant bivalve family that was restricted to the Permian, with the largest individuals reaching lengths of 100 cm (Yancey and Boyd, 1983). Like other giant, aberrant bivalves such as the extant tridacnids, and the ancient rudists and megalodonts, they lived in warm, shallow-marine environments and are often interpreted to have housed photosynthetic algae in their tissues (Yancey and Boyd, 1983; Isozaki and Aljinović, 2009). However, they typically have very thick shells and some have suggested this attribute makes it unlikely that they housed photosymbionts (Asato et al. 2017). The shells have unusual, wing-like flanges and were first described as problematica from Japan (Ozaki, 1968). Subsequent research in Afghanistan, Malaysia, Croatia, Tunisia and Iran showed their bivalve nature (Termier et al., 1973; Runnegar and Gobbett, 1975; Kochansky-Devidé, 1978; Boyd and Newell, 1979; Thiele and Ticky, 1980). With additional collections from Malaysia, Japan and Tunisia, Yancey and Boyd (1983) and Yancey and Ozaki (1986) revised the systematic scheme of the family and proposed identification criteria based on their morphology and hinge structure. Alatoconchids have also been reported from Philippines, Oman and Alaska (Kiessling and Flügel, 2000; Wiedlich and Bernecker, 2007; Blodgett and Isozaki, 2013). Yancey and Boyd (1983) identified their reclining habit and described a unique double-layered microstructure of the shell wall. Findings from Japan, Thailand and Croatia identified their biostratigraphic range (Isozaki, 2006; Udchachon et al., 2007, 2014; Aljinović et al., 2008) as ranging from the Artinskian (middle Cisuralian) to a level slightly before the Guadalupian–Lopingian boundary (GLB) (Isozaki and Aljinović, 2009).

The Alatoconchidae are confined palaeogeographically to low-latitude Tethyan and Panthalassan regions and thus have a similar distribution to the contemporaneous, warm-water fusulinid family Verbeekinidae and coral family Waagenophyllidae (Fig. 1; Yancey and Boyd, 1983; Isozaki and Aljinović, 2009). Curiously, the alataconchids have never been reported from South China even though it is one of the best known terranes in the eastern part of the Tethyan province. Yancey and Boyd (1983) postulated that they should occur in this region and here we show, for the first time, over 30 years later, that this prediction was correct.

South China has one of the best known tropical, marine Permian successions with well-known biostratigraphic and palaeogeographic context. Based on our investigation and published sources (which have misidentified alatoconchids as phylloid algae), we show that alatoconchids occur at over thirty localities in the region, mostly from shallow-water facies but also as transported fragments in deep intra-platform basins. These records offer an opportunity to learn more about the ecology of these giant bivalves. This paper aims to

(1) describe the general features of the alatoconchids in the region; (2) identify their habitats and facies occurrences and spatial distribution.

2. Geological setting

The South China Craton is bordered by the Qinling–Dabie–Sulu orogen to the north, the Longmenshan fault to the northwest, and the Jinshajiang–Ailaoshan–Songma suture zone to the west and south, and almost includes the whole of southern China (Cawood et al., 2017; Wan, 2010). The craton was formed by the amalgamation of the Yangtze and Cathaysian blocks during the Caledonian orogeny (Cawood et al., 2017). During Middle and Late Permian four major palaeogeographic basins developed: the Yangtze carbonate Platform (YCP), the Cathaysian littoral clastic basin, the Jiangnan chert basin, and the Dian–Qian–Gui carbonate basin (Liu and Xu, 1994; Feng et al., 1997; Ma et al., 2009) (Fig. 2). The alatoconchids studied here occurred on the YCP, as well as on isolated carbonate platforms (ICPs) in the Dian–Qian–Gui basin (Fig.2).

South China was located in the eastern part of Palaeotethys in the Permian (Scotese and Langford, 1995; Ziegler et al., 1997), where it was subject to warm climatic conditions, and belongs to the blocks with Cathaysian affinity (Scotese and Langford, 1995; Ziegler et al., 1997). Permian strata are divided by two unconformities into three major units. The lower unit is the Maping Formation of the late Carboniferous to the Artinskian stage (Permian). The Chihsia and Maokou formations compose the middle unit and contain the alatoconchids discussed here (Fig. 3). The upper unit mainly includes the Wuchiaping and Changhsing formations, dominated by limestone on the YCP, while the coal-bearing Lungtan and Heshan formations occur in the lowermost part (Fig. 3). The Kungurian Chihsia Formation is a monotonous, widespread black limestone that records the expansion of marine deposition. The Guadalupian Maokou Formation is dominated by limestones in the middle and upper Yangtze valley (Fig. 2). However, there is considerable lithofacies differentiation and, by the late Guadalupian (late Wordian to Capitanian stage), there were both platform carbonates and deeper water argillaceous/siliceous facies found in intra-platform basins. Accordingly, the YCP is divided into three belts, the eastern, western and central belts, during Guadalupian time.

The central belt was characterized by relatively deep water marl–limestone alternations and thicker-bedded limestone with nodular and banded chert, possibly of carbonate shelf to basin environments. In the late

Guadalupian, deep-water argillaceous and siliceous facies occurred interbedded with thin-bedded micrite and/or manganese carbonates in intra-platform basins: the Central Guizhou Trough and Eastern Chongqing–Western Hubei Basin (Fig. 2). In the western belt, the Maokou Formation consists of massive dolomite with algae laminae and intercalated basalt flows (the Emeishan Basalt). Along the southern margin of the YCP, there are reefs constructed of sponges and Archaeolithoporella (Fig. 2). Although a reef belt was depicted in many published palaeogeographical maps, reefs are limited to just a few localities. To the south is the Dian–Qian–Gui Basin, which is characterized by shallow-water ICPs surrounded by thin-bedded chert and claystone basinal facies.

Permian correlation in South China is achieved using conodont and fusulinid zonation (Fig. 3), complemented by sequence stratigraphic analysis. Additionally, the Maokou Formation is subdivided into three or four members in the central belt of the YCP. The first member is dominated by alternating marl and limestone and overlain by grey limestone (partly dolomitized) of the second member. The third member is grey limestone, differing the second member in the presence of thin-bedded chert and/or discrete nodules. It extends to the top of the Formation in northern Guizhou, e.g. in Zunyi city. The uppermost (fourth) member is mainly a bioclastic limestone. Chronologically, the first and second members correspond to the Roadian and Wordian epochs respectively, whilst the third and fourth members are of Capitanian age (Fig. 3; Xiao et al., 1986; Zhang N et al., 2007; Cai, 2017). The two boundaries separating the three Guadalupian third-order sequences coincide with the top boundary of the first and second members (Chen et al., 1997; Wang et al., 1998).

3. Overview of the Alatoconchidae and their presence in South China

3.1 Overviews of the Alatoconchidae

The Alatoconchidae possess large equivalve shells that are compressed dorsoventrally and elongated in the anteroposterior direction (Yancey and Boyd 1983; Fig. 4A, B). Beaks of the shells are commonly terminal, and the extension of the umbonal carina forms their distinctive wing-like flanges (Fig. 4D). There is a dorsal crest extending along the plane of commissure, while the ventral surface is flat and perpendicular to the commissural plane. The height and width of the shell reach the maximum in the anterior half, before decreasing abruptly in the mid-shell and the width reduces gradually towards the posterior end. The duplivincular ligament field covers the ventral half or the whole of the cardinal area. Below the cardinal area, a byssal groove is present (Figs. 4B, C) and a byssal collar is well-developed in some species. The umbone and outer edges of the shells are usually massive. The shell form of Shikamaia perakensis is one of the best known (Yancey and Boyd, 1983; Figs. 4A, B).

Shell microstructure is also a diagnostic feature of the alatoconchids. Their shell wall consists of two parts. The external part is an easily recognizable prismatic layer composed of large calcite prisms, as long as 3 mm, set perpendicular to the shell surface. Although prismatic structures are very common in bivalve shells, coarse prisms of such size are rare. The Inoceramidae and Pinnidae both possess similar prismatic layers (Elorza and Garca-Garmilla, 1998; Checa et al., 2005). The former are not known from the Palaeozoic whilst pinnids have been reported from Permian strata (e.g. Biakov, 2013). However, both these groups differ from alataoconchids because they are compressed in the dorsoventral direction rather than laterally. The internal part is usually recrystallized into mosaic of calcite crystals that have a large size range. In Shikamaia akasakaensis and S. ozakii this part of the shell is subdivided into two layers of different crystal sizes (Asato et al., 2017), although their primary texture is unknown.

The Alatoconchidae are proposed to have their closest relationship with Myalinidae, in the superfamily Ambonychiacea, as indicated by their duplivincular ligament and thick shell wall (Yancey and Boyd, 1983). They are divided into two subfamilies, the Saikraconchinae and the Alatoconchinae. Saikraconchinae are characterized by a small cardinal area, large byssal collar and simple ligament pattern with ligament grooves extending along nearly all the hinge line. The Alatoconchinae have a large cardinal area, small to absent byssal collar and ligament area confined to the ventral half of the cardinal area. Saikraconchinae and Alatoconchinae respectively contain only one genus, Saikraconcha and Shikamaia. Saikraconcha comprises two subgenera Saikraconcha and Dereconcha. Dereconcha differs from Saikraconcha (Saikraconcha) in the absence of an umbonal septum. In other words, its byssal groove runs along the dorsal margin of the byssal collar instead of the middle of the collar. Shikamaia also consists of two subgenera, Shikamaia and Alatoconcha, with Tanchintongia considered to be a junior synonym of Shikamaia. Alatoconcha is distinguished from Shikamaia (Shikamaia) by a larger dorsal niche and a subcircular rather than elongate shell outline.

3.2 Alatoconchid sections in South China

The alatoconchids occur commonly as coquinas in South China. Extraction of the bivalves from the generally very resistant limestone is very difficult and has inhibited detailed taxonomic work. Nevertheless, available transverse sections (perpendicular to the commissure plane) are sufficient to reconstruct the morphology with partial interior details. Profiles revealed by these transverse sections are in consistent with diagnostic features of the alatoconchids. The symmetry of the articulated shells helps to select the sections perpendicular to the commissural plane. Then the direction and position of these sections across the single valves could be roughly determined by the features of the shell form or by the related structures (e.g., hinge structure).

Sections across the cardinal area (Fig. 5) show that the wall of a single valve defines a triangular area largely or completely infilled by the material of the internal shell layer (mosaic calcite). This is internal infilling of the umbonal cavity. The shortest side of triangle outline corresponds to the cardinal area of the shell while the other two sides are the dorsal (upside) and ventral (underside) wall respectively. The sector filled by micrite in the interior of the section displays the form of the body cavity near its apical end (Fig. 5C–H).

The cardinal area shows morphological variation in these sections. On the ventral side, the cardinal area transits to the ventral wall sharply or gradually. The byssal groove observed in many individuals displayed as a small concave area at the ventral margin of the cardinal area (Fig. 5E, F, I). On the dorsal half, the configuration of the cardinal area in the sections is distinguished into two types. For the first type, the cardinal area bows laterally at a 0° to 45° angle with the plane of commissure (Fig. 5A, B, G, H). This character is comparable to that seen in Shikamaia akasakaensis, S. perakensis (Fig. 4A, C) and S. (Alatoconcha) vampyra (Ozaki, 1968; Termier et al., 1973; Runnegar and Gobbett, 1975) which possess a more or less bowed-out cardinal area (especially reported in Shikamaia (Alatoconcha) vampyra by Yancey and Boyd (1983)). Instead of bowing outward, the second type is subhorizontal to the commissure on the dorsal side (Fig. 5C–F). This feature is seen in Saikraconchia tunisiensis (Yancey and Boyd, 1983), which has non-terminal and ventrally down-turned beaks resulting in the curvature of the cardinal area to the commissural plane at the dorsal side. Although the taxonomy is not determinable, the variation in the pattern of cardinal area suggests the alatoconchids in South China were diverse.

Moving posteriorly to the hingeline, the connected body cavities of the two valves are displayed in the transverse section (analogous to Fig. 4D). A transverse section of an articulated shell shown in figures 6A and B is probably near the hingeline as it displays only a small gap on the dorsal side of each valve that connects the body cavities. In this section, the wall of the shell is still massive at the ventral side, near the commissural plane, and there is a lamina on the ventral surface of the valve representing the posterior extension of the byssal collar or the ventral margin of the cardinal area.

Many transverse sections of the articulated shells are roughly an isosceles triangle with the dorsal wall curving outward (Fig. 6C–F). Appearances with half of the isosceles triangular profile preserved are common. The high crest indicated by the height of the triangle and the large body cavity represented by the inner sector with micrite infilling imply these sections were cut through the middle of the shells. In these sections, the height tapers abruptly from the dorsal crest (denoted by the peak of the section), then extends subhorizontally to the edges and results in a narrow flange on each valve. This feature conforms to the general pattern of alatoconchid bivalves.

Some specimens show wall thickening at the position where the slope of the dorsal shell changes (Figs. 7A, B). A similar thickening is seen in transverse sections of Shikamaia perakensis (Fig. 4D; Runnegar and Gobbett, 1975). In Shikamaia akasakaensis, the heavy thickening is near the dorsal margin (Ozaki, 1968), but this appearance may be because its dorsal crest is relatively low. The ventral surface is usually flat in middle transverse sections but occasionally the outer portion of the flange undulates (Figs. 6E, F). The edges of the shell are often massively infilled by sparry calcite and extend horizontally or upward. Undulate flanges are known in Saikraconcha ogulineci, and the edges of Saikraconcha (Dereconcha) kamparensis are obviously upturned (Yancey and Boyd, 1983). In several individuals from the Lengshuixi section, the infilling at the edge of the flanges is incomplete and leaves crescent cavities (Figs. 7A, B). This feature is similar to that of Shikamaia (Alatoconcha) vampyra (Termier et al., 1973) and specimens from Philippines (Kiessling and Flügel, 2000, p. 50, Fig. 5). Yancey and Boyd (1983) suggested that compartmentalization of the flange could be caused by trauma, but this feature is rare amongst alatoconchids including those from South China.

A group of sections in our observation have an overall flat profile (Figs. 7C, D). The bilateral symmetry of these sections, and the wall thinning near the symmetry line suggest they cut through the shells along a direction perpendicular to the commissural plane. The height of alatoconchids along the anteroposterior axis usually reaches the maximum in the anterior half, then reduces abruptly (Fig. 4B). Thus the posterior portion of the shell is flat without a dorsal crest. Some taxa may possess a very low crest in the entire shell, but such forms are currently poorly known. Therefore, sections with flat outline are probably across the posterior part of the alatoconchid shell (Figs. 7C, D). A distinctive section is seen in figures 7E and F. The flat appearance and bilateral symmetry indicate it is a slightly oblique transverse section across the posterior of an articulated shell. However, the body cavities of the two valves in this section are separated by an abapical septum in each valve that encloses the body cavity of the valve. Such a septum has not been described previously indicating the presence of an undescribed taxon in South China.

3.3 Shell texture feature

Besides the morphological features reconstructed from transecting profiles, unique shell microstructure provides another diagnostic clue. The fossil shells from South China commonly preserve the easily identifiable microstructure previously reported from alatoconchids. The prismatic layer on the outside consists of coarse calcite prisms aligning perpendicular to the shell surface (Figs. 8A, B). The prisms vary in length from 0.3 mm to more than 3 mm and in diameter from 20 μm to 150 μm. A single crystal usually extends throughout the whole layer (Fig. 8A). In cross section, the calcite prisms are polygonal and present a honeycomb pattern together (Fig. 8C). Detached constituent prisms and prism clusters are commonly scattered in the host rocks.

The usually recrystallized inner part is a mosaic of granular calcite crystals that vary widely in diameter from about 30 μm to a centimeter scale (Fig. 8D). The subdivision of this part is not evident in the specimens of this study. In thickness, the inner part ranges from 0.3 mm to more than 20 mm, and often become massive in the umbonal or the edge part of the shell. The thickness ratio of the internal to external parts is uncertain, the former is thinner occasionally, but is usually several times thicker than the latter (Figs. 8B, D).

3.4 Previous misidentification

Despite their wide distribution, these giant bivalves in South China have been absent from the list of Alatoconchidae for decades due to the misidentification. The earliest written record in China by Dai et al.,

(1978) assigned the fossils to the Pinnidae (bivalve family) in consideration of the large size and the prismatic external layer of the shell wall. This identification, present only as a footnote, received little attention in the following studies. As the abundant flat-shaped fossils are exposed on the outcrops just like a stack of flat plates, and no complete specimens were found, most of the literature has assumed they were a type of large phylloid algae with a form like lotus leaves (e.g. Li and Yuan, 1983; Zhao, 1991a, b, c; Zhou et al., 2014; Luo et al., 2015). Although the early studies did not have the right classification, they did disseminate the presence of these fossils, resulting in their wide recognition in the region. The informal name “lotus leaf algae” was usually used to record these fossils, and it has made the literature survey of this study much easier even though most of the records are only short descriptions.

4. Occurrences in South China

After our systematic scrutiny, alatoconchid-bearing horizon (ABH) has been identified from over thirty localities, including ~10 discovered in this study from the YCP and the Dian–Qian–Gui Basin (Fig. 2). Most of the localities investigated in this study are reliably constrained to biozones.

Most of the alatoconchid occurrences are in the shallow-water carbonate successions where they are found as coquina beds that range from less than 10 cm to about 200 cm in thickness and form from 5% to more than 50% shell content. Although the boundary between the alatoconchid beds and its underlying strata is usually clear, no erosional structure has been found below the beds, or truncation above the bed. The beds are dominated by the pairs of shell-wall with both the walls parallel to the bedding (like Figs. 7C, E). Such appearances are the sections through the flanges of the giant bivalves. Inserted among these pairs are the triangular profiles of the transverse sections (Figs. 5, 6, 7A), and also a small number of scattered flat shell plates. The plates vary in dimension from 1 cm to more than 20 cm and are usually parallel to the bedding. Almost all of the transverse sections are arranged with the ventral shell on the underside, indicating an orientation consistent with the life position. In contrast, those shells preserved in the gravity flow deposits of deep water environment are mostly fragments shorter than 5 cm and lack articulated valves or complete single valves (see the Jiangjiazhai and Pianpozhai sections below).

4.1 Details at the localities

A total of twelve alatoconchid-bearing successions are selected here and divided into three groups according to the palaeogeography and stratigraphical correlation. The five sections of the first group are from the shallow water environment of the YCP. The second group, including five sections as well, is distributed in central Guizhou, where the relative deep water siliceous and argillaceous deposits of intra-platform trough were developed during the Capitanian (Central Guizhou Trough in Fig. 2). While those two composing the third group are from the Dian–Qian–Gui Basin.

4.1.1 Shallow-water platform occurrences

(1) Wenjiangsi of Guiding, southern Guizhou

This locality is situated in the transition between the central and eastern belts of the YCP (WJS in Fig. 2), and was the first alatoconchid occurrence the authors (JX and WQ) encountered in August, 2007. Here the Maokou Formation is about 180 m thick, and unconformably overlain by the Wuchiaping Formation with poorly exposed coal, siltstone and claystone at the boundary interval (A in Fig.9; Shao et al., 1998). The ABH is in the upper part of the Maokou Formation, 16.1 m below the base of the Wuchiaping Formation.

Bed 64, 4.8 m below the ABH, is 10.8 m thick massive bioclastic grainstone dominated by peloids, indicating a shoal environment (Fig. 10A). Overlying the grainstone, Bed 65 and 66 are thick-bedded packstone with silicified limestone interbeds. Above the ABH there is medium- and thick-bedded skeleton wackestone (Fig. 10C) with interbedded chert (Bed 68 and 69). The alatoconchid-bearing Bed 67 is 2.9 m in thickness (A in Fig. 9). The clam shells concentrate in two beds, 100 and 70 cm thick respectively (Fig. 11A), interbedded with packstone containing non-fusulinid foraminifers, calcareous algae, ostracods, gastropods and brachiopods. The shells exposed on the outcrop are mainly the sections through the wing-like flanges and the flat shell plates (Fig. 11B). A few transverse sections in living orientation are also present. The biggest single value recognized by the section is about 35 cm wide and 15 cm high. These bivalve shells make up about 40% of the rock volume in the lower bed and 30% in the upper bed. The matrix between the shells is micrite with a few microfossils of ostracods and calcareous algae (Fig.10B). The algal association in the alatoconchid beds and the interbedded packstone are similar and include Gymnocodium, Ungdarella and Mizzia. The problematic fossil Pseudovermiporella is also present.

The unconformity between the Middle and Upper Permian in the western Yangtze Craton has been attributed to uplift prior to eruption of the Emeishan large igneous province (He et al., 2003). However, the Guiding section is in He et al.'s outer zone, where erosion was supposedly minor (He et al., 2003). In sequence stratigraphic correlation, the ABH is in the lower part of the third sequence in the Maokou Formation, thus the alatoconchids at this locality are probably of the Capitanian age, although biostratigraphic study is still required.

(2) Xingwen, eastern Sichuan

The Xingwen area is within the central belt of the YCP (XG, SiL in Fig. 2). The ABH occurs at the bottom of the second member of the Maokou Formation, and is a clear marker bed (B in Fig. 9; Fig. 11C). Fusulinids, Neoschwagerina craticulifera and N. margaritae occur in the same member suggesting a Wordian age for the alatoconchid horizon (Zhang et al., 1986). In sequence correlation, the ABH is in the second third-order sequence of the Maokou Formation which also corresponds to the Wordian stage (Chen et al., 1997; Wang et al., 1998).

At the Xingwen Global Geopark, alatoconchid shells occur on the cliff of a large karst funnel (more than 500 m in diameter). The ABH, containing four alatoconchid beds, is about 3 m thick (Fig. 11C–E). A 20 cm thick marlstone layer is developed below the bottom of the ABH. The first alatoconchid bed is about 30 cm above the marlstone. It is a single bed that contains only 1–3 shells in vertical orientation (Fig. 11E). Most shells observed in this bed are flanges or flat plates arranged parallel to the bedding plane. Chert nodules are common just above the first alatoconchid bed.

About 150 cm above the first bed, there is the second alatoconchid bed with a thickness of 80 cm (Fig. 11D). In the second bed, the sections of the clams are mostly through their flanges. A few triangular transverse sections are also present, with the largest one reaching a width of about 60 cm (Fig. 6E). All these sections are parallel to the bedding. The alatoconchid shells account for about 30% of the volume of the limestone. The third bed is about 50 cm above the second bed and has a thickness of 10 cm. A small number of the clam shells, including the articulated ones (Fig. 6A), are dispersed in the interval between the second and the third beds. A layer of chert bands forms a clear upper border for the third bed (Fig. 11D). About 40 cm above the third bed is the fourth alatoconchid bed that is 40 cm thick. The preservation and proportion of the shells in the third and fourth beds are similar to the second bed. Massive rugose coral colonies are present in the ABH (Fig. 11F). The matrix supporting the alatoconchid shells is micritic and contains microfossils of calcareous algae (Mizzia), foraminifers, ostracods as well as calcite prisms or clusters detached from alatoconchid shells (Fig. 10D). The intervals between the alatoconchid beds are packstone with Mizzia and Eogoniolina and minor foraminifers, ostracods and Pseudovermiporella (Fig. 10E).

This alatoconchid-bearing succession described above is well developed in the Xingwen area and has great lateral persistence in the region, including northern Guizhou and southern Sichuan (summarized in discussion below). Alatoconchid shells were also found in quarry scree at Silong town, which is about 5 km away from the Xingwen World Geopark (Fig. 11G). But in situ observation on the cliff were not possible because of safety concerns.

(3) Dapuzi of Nanchuan, southern Chongqing

This location (DPZ in Fig. 2) is situated in the central belt of the YCP like the occurrences at Xingwen and it shows similar lithological features. The ABH is in the second member of the Maokou Formation, which is dominated by gray medium- to thick-bedded packstone (C in Fig. 9). Underlying the ABH, Bed 26 is mainly composed of alternating marl–limestone. As at Xingwen, the alatoconchid shells occur in the second third-order sequence of the Maokou Formation and are probably of Wordian age (Chen et al., 1997; Wang et al., 1998).

In the ABH, the lower portion of the Bed 27, the alatoconchid shells are sparsely scattered in the host rock and parallel to the bedding. The clam flanges vary largely in size with the largest ones being more than 40 cm long (Figs. 12A, C). Massive rugose coral colonies also occur in the same horizon (Fig. 12B). The host rock of these alatoconchid shells is a packstone with foraminifers, ostracods, Pseudovermiporella and unidentifiable mollusk shells (Fig. 10F). Differential compaction in the host rock is evident, e.g., the fitted textures in figure 10F. Packstone overlying the ABH is rich in calcareous algae, including abundant Mizzia and minor Permocalculcus (Fig. 10G).

(4) Lengshuixi of Shizhu, eastern Chongqing

This location is in the central belt of YCP, and near the Eastern Chongqing–Western Hubei Basin (LSX in Fig. 2). At this section, the ABH is at the top of the Maokou Formation, which consists of the dark-grey medium-bedded bioclastic limestone with thin-bedded black marlstone interbeds and a small amount of cherty nodules (D in Fig. 9). Clastic deposits, with economic coal seams of the Lungtan Formation (early Wuchiapingian), unconformably overlie the ABH (Fig. 12D).

The ABH is about 2 m thick in total (Fig. 12D) and contains scattered, well preserved, giant bivalve shells (Fig. 12E). Several transverse sections were also found, and their orientation indicates preservation in life position (e.g. Fig. 7A). The encasing packstones have non-fusulinid foraminifers, ostracods and Pseudovermiporella (Fig. 10H). Underlying the ABH, the packstone contains abundant calcareous algae, minor fusulinids, non-fusulinid foraminifers and ostracods (Fig. 10I). The algae are dominated by Mizzia, and a small number of Eogoniolina and Gymnocodium.

In the area from eastern Chongqing to western Hubei, the Maokou Formation extends upward into the latest Capitanian (Zhang N et al., 2007). Thus, at the well-studied Maoershan section and the Xiakou section from western Hubei, conodont biozones across the Guadalupian–Lopingian boundary are established that correlate well with the Global Stratotype Section and Point of the GLB at the Penglaitan Section, Guangxi, South China (Jin et al., 2006; Xia et al., 2007; Zhang LL et al., 2007). At Maoershan, about 50 kilometers from the Lengshuixi section, the topmost, middle Permian Clarkina postbitteri hongshuiensis occurs in the top of the Maokou Limestone about 10 m below the Late Permian coal seams, and the lowest Upper Permian C. p. postbitteri occurs just above the coal seams (Zhang LL et al., 2007). Furthermore, at the Pengshui section near Lengshuixi, and the Maocaojie section, as well as the Tianqiao section of western Hubei, Jinogondolella granti (found just below the Clarkina postbitteri hongshuiensis, Fig. 3) was found in the upper part of the Maokou Formation (Huang and Zhang, 2004; Yang, 2007; Zhang N et al., 2007). At these sections, the first Jinogondolella granti occur more than 20 m from the top of the Maokou Formation whilst the uppermost part of the Formation in this region is barren of conodonts. Thus, the absence of Clarkina postbitteri hongshuiensis Zone in these sections is thought to record their absence not to be the result of erosion (Huang and Zhang, 2004; Xia et al., 2007; Zhang N et al., 2007). However, at Lengshuixi, the barren interval likely spans a longer time because Jinogondolella shannoni (middle Capitanian) was found only 40 m from the top of the Maokou Formation (the ABH), whilst the strata above are poor in conodonts (Yang, 2007). As indicated by the stratigraphical correlation of the upper Maokou limestone in the neighboring area, the alatoconchids at the Lengshuixi section are likely of Capitanian age, possibly from the late part of this Stage.

(5) Longyin of Pu'an, weastern Guizhou

In contrast to the occurrences above, this location records alatoconchids from the Chihsia Formation. In this area, a relatively complete early Permian succession is developed, from the Asselian to Sakmarian carbonate deposits and Artinskian clastic deposits. The Kungurian stage includes the Liangshan Member and the Chihsia Formation.

At the section, Bed 62 and 63 belong to the Chihsia Formation (E in Fig. 9). Bed 62 is 22 m thick and comprises medium- and thick-bedded limestone and thin-bedded marlstone. The fusulinid Misellina spp. and Staffella spp. occur in Bed 62. Both indicate a lower Kungurian age (Xia, 1994). Bed 63 is 20 m in thickness, and mainly composed of thick-bedded and massive bioclastic limestone with cherty nodules, that yields corals and fusulinids.

The ABH is in the upper part of the Bed 62 where three alatoconchid beds were observed. The lower two beds are respectively 20 and 25 cm thick and separated by a bedding surface (Fig. 12F). The alatoconchid shells are dispersed in these two beds and are only 2–10 cm in length, shorter than that in other occurrences. Due to the smaller body size, the massive umbonal portion of the shell is more commonly exposed on the outcrop. Thus the shell beds here are different in appearance to other occurrences (Fig. 12G). Non-alatoconchid fossils in the beds belong to the cephalopods, with their distinctive septate shells (Fig. 12H) and three-layered shell texture (Fig. 12G), and non-fusulinid foraminifers, ostracods and Pseudovermiporella (Fig. 13A).

About one metre above the second bed, there is a third, 12 cm-thick alatoconchid bed (Fig. 12I). Here, most shells are less than 5 cm in length, except for a few flanges more than 10 cm (Fig. 12I). Many of the small chips intersect obliquely or perpendicularly to the bedding. The random orientation and serious breakage imply reworking and slow sedimentation.

4.1.2 Occurrences in central Guizhou

The area from Zunyi to Shuicheng also belongs to the central belt of YCP, but is characterized by deep water siliceous and argillaceous deposits with manganese ore in the late Guadalupian. These deep water deposits are present as the Central Guizhou Trough (Fig. 2). Our field survey in this region found the giant bivalves not only in the shallow water limestone but also in the deep-water successions from Shuicheng.

(1) Zunyi

Zunyi city is in the northern portion of the Central Guizhou Trough. The first and second members of the Maokou Formation are similar to those in southern Sichuan and Chongqing (e.g. Xingwen and Dapuzi) but the third member is dominated by the thin-bedded chert with manganese claystone interbeds extending to the top of the formation. The limestone of the fourth member in other areas is absent. The alatoconchid beds were found in the second member of the Maokou Formation at the Sangshuwan and Shangji sections in shallow-water carbonates that yield no conodonts (SSW, SJ in Fig. 2). However, the overlying deep-water third member contains conodonts indicating a mid-Capitanian age (Jinogondolella postserrata and J. shannoni) (Cai, 2017), and so the ABHs may be of Wordian age.

At the Sangshuwan section, the ABH (Bed 8) is 9.4 m thick and dominated by grey, medium-bedded wackestone with calcareous algae, foraminifers and ostracods (Fig. 13B). The bivalve shells in the bottom 0.9 m are densely packed and occupy about 20% of the limestone volume (Fig. 14A). Upward, the shells are sparse and discontinuously float in the host rock (Fig. 14B). Among the shell sections exposed on the outcrop, 50% are cut across the flanges whilst triangular, transverse sections and flat shell plates also occur. Other fossils within the ABH are calcareous algae, brachiopods and colonial rugose corals (Fig. 14B). Underlying the ABH, Bed 6 is 3.2 m thick and comprises alternating marl–limestone and Bed 7, 10.9 m thick, consists of medium-bedded wackestone (F in Fig. 9). Above the ABH, Bed 9 is composed of thick-bedded packstone with abundant Mizzia and Eogoniolina (Fig. 13C).

The ABH (Bed 8, Fig. 14C) at the Shangji section is about 2 m thick (G in Fig. 9) with shells throughout occupying about 10% of the volume (Fig. 14D). The host rock is wackestone with non-fusulinid foraminiferas, ostracods and calcareous algae including Mizzia, Gymnocodium and Ungdarella (Fig. 13D). A thick-bedded wackestone underlies the ABH and a thick-bedded, algal packstone overlies it. The next bed (Bed 10), is about 6 m thick and comprises light-grey, massive packstone containing non-fusulinid foraminiferas, echinoderms, calcareous algae (Ungdarella) and the problematica Tubiphytes and Pseudovermiporella (Fig. 13E).

(2) Shuicheng in the south

The third member of the Maokou Formation is seen in southern part of Shuicheng city where it deposited in the late Guadalupian Central Guizhou Trough. The 30–90 m thick unit consists of thin-bedded chert and manganese carbonates interbedded with thin- to medium-bedded limestone. The overlying fourth member is mainly medium-and thick-bedded limestones 0–50 m thick. These two members comprise the third sequence of the Maokou Formation, and the associated fusulinids Yabeina and Neomisellina indicate a Capitanian age (GSGP, 1973). The Maokou Formation is unconformably overlain by the Emeishan basalt of late Capitanian age (Sun et al., 2010) or the early Wuchiapingian Lungtan Formation.

In the Pianpozhai and Jiangjiazhai sections of this region, about 8 km apart (H, I in Fig. 9), an ABH occurs within the third member of the Maokou Formation, intercalated in the thin-bedded chert and manganese carbonates (Fig. 15A). It is about 15 cm thick and mostly consists of shell fragments 1–5 cm in length, and a few about 10 cm (Fig. 15B), in the matrix composed of crinoids and lime mud. These alatoconchid-bearing horizons are interbedded with cherts of the basin facies. Grading in the ABHs suggest deposition from a decelerating sediment-gravity flow (Fig. 15D).

A quarry in Xiaohebian village, about 3 km to the northwest of the Jiangjiazhai section (XHB in Fig. 2), yields alatoconchids from the fourth member of the Maokou Formation (J in Fig. 9). The ABH, Bed 2, is about 3 m thick and consists of grey medium- and thick-bedded wackestone with two alatoconchid levels, 100 and 10 cm thick respectively. Sections of flat flanges dominate the observation on the outcrop (Fig. 15E) and form about 15% of the volume in both beds. The ABH is underlain by a 1.2 m thick packstone with a bed of concentrated solitary corals (Fig. 15F). Thin-bedded wackestone interbedded with medium-bedded packstone (Bed 4) occurs above and this is, in turn, overlain by early Wuchiapingian claystone and coal seams of the

Lungtan Formation (Bed 5), but the contact is not exposed. Noteworthy is that the occurrence here was obviously from a carbonate platform of shallow water condition, despite its proximity to the basinal Jiangjiazhai section.

4.1.3 Dian–Qian–Gui Basin Occurrences

Dian–Qian–Gui Basin development consisted of shallow-water ICPs surrounded by argillaceous and siliceous deep-water facies. Alatoconchids widely occur on the ICPs in the basin, but have not been found in the deep-water facies (Fig. 2). Two representative occurrences were investigated in this study and are introduced below.

(1) Yanpeng of Leye, northwestern Guangxi

The Yanpeng section, located in the interior of the Leye–Tianlin ICP (I in Fig. 2), is one of the most typical sections that has ABHs in both the Chihsia Formation and the Maokou Formation (K in Fig. 9). Along the road-cut section, the alatoconchid shells were observed in a total of thirty beds.

At this section, the Chihsia Formation is about 120 m thick, and overlies massive grainstone and oncoidal limestone of the Maping Formation. Its lower part, about 40 m thick, it is mainly composed of grey, thick-bedded to massive packstone with foraminiferas, Pseudovermiporella and a few ostracods (Fig. 13F). The ABH occurs in the middle, and is about 20 m in thickness, and dominated by dark-grey medium- and thick-bedded wackestone and lime mudstone. The 60 m thick upper part mainly consists of light-grey, thick-bedded to massive packstone and wackestone.

The ABH in the Chihsia Formation include eight, extensive beds that range from 10–50 cm thick. The shells are scattered evenly in the beds (Fig. 16A) and transverse sections on the outcrops indicate the alatoconchids are preserved in life position. The micritic matrix contains minor ostracods, foraminifers and Pseudovermiporella (Fig. 13G).

The overlying Maokou Formation has a thickness of about 480 m. The lower part, about 100 m thick, is dominated by light-grey, thick-bedded bioclastic limestone, the middle part, is ~70 m and mainly medium- and thick-bedded dark-grey wackestone and lime mudstone with alatoconchid beds. The upper part is thick-bedded to massive packstone with lime mudstone and marlstone interbeds, and is unconformably overlain by claystone of the Heshan Formation. Two ABHs are contained in the Maokou Formation. In the lower part, the occurrences are seen in 11 beds but they usually have poor lateral persistence and shells are sparse (<5% of rock volume). The other bioclasts include brachiopods, crinoids, gastropods and fusulinids (Fig. 16B) and common, massive coral colonies. The ABH in the middle part of the Maokou Formation are 20–50 cm in thickness and 10% to 40% in shell content. The thickest bed at the top is about 180 cm and the alatoconchids form half of the total limestone volume (Fig. 16C). In all these beds including the thickest one, what dominates the view are the sections of the flat flanges. A small number of transverse sections of the clams occur and show preservation in life position. Other fossils include foraminifers and calcareous algae (*Ungdarella*, *Gymnocodium*, *Mizzia*) (Fig. 13H).

(2) Laopeng of Tian'e, northwestern Guangxi

This location, on the Tian'e–Mashan ICP (III in Fig. 2), preserves a 520 m-thick section of the Maokou Formation (L in Fig. 9). Its lower and upper parts of the formation are dominated by light-grey, thick-bedded to massive packstone with wackestone interbeds, whilst the middle part, about 60 m, consists of dark-gray thin- to medium-bedded wackestone and lime mudstone.

The ABH occur in the base of the middle part of the Maokou Formation (L in Fig. 9; Fig. 16D) where three alatoconchid beds (of 120, 30 and 50 cm thick in ascending order) are found. The alatoconchids are parallel to the bedding and occupy 10% to 20% of the limestone volume (Fig. 16E). The appearance is dominated by the sections of the flat flanges with a few transverse sections. The host wackestone contains *Mizzia* and *Gymnocodium* (Fig. 13I). Below the ABH, there is 1.2 m thick, light-grey, thick-bedded packstone that changes downward to thick-bedded fusulinid limestone (Fig. 16D). The ABH is overlain by dark-grey, medium-bedded wackestone. The exact age of the ABH at this location is not known.

4.2 Alatoconchid lithofacies

Our observations reveal that the alatoconchid-bearing successions in South China occur in five lithofacies:

LF-1: siliceous deposits: thin-bedded, including siliceous claystone and chert with radiolarians and sponge spicules. In the intra-platform trough (the Central Guizhou Trough), the siliceous deposits is interbedded with thin manganese deposits. Bioclastic beds interbedded between these basinal facies suggest transport and gravity-flow deposition (Figs. 15A–C).

LF-2: alternating marl–limestone beds, including bioclastic limestone and fossiliferous marlstone. This lithofacies is common in the upper Chihsia and lower Maokou formations, and is interpreted to have accumulated in an environment transitional between the carbonate platform and basin.

LF-3: medium- to thick-bedded limestone, often wackestone, occasionally packstone. Nodular, banded or thin-bedded chert and thin-bedded claystone are often interbedded in the limestone. Bioclastic components are ostracods, non-fusulinid foraminifers, brachiopods, gastropods and calcareous algae (e.g. Figs. 10B–D). Pseudovermiporella is also very common. In addition, a few massive rugose coral colonies are contained. This facies probably formed on the outer shelf.

LF-4: massive limestone, thick-bedded to massive, mostly packstone. Abundant bioclasts include calcareous algae, non-fusulinid foraminifers, fusulinids, crinoids, brachiopods, ostracods as well as the problematica Tubiphytes and Pseudovermiporella (Figs. 13E, F). Calcareous green algae (e.g. Mizzia and Eogoniolina) often dominate this lithofacies (Fig. 10E, G, I; Fig. 13C). Corals are present and occur as massive colonies or solitary forms concentrated beds (Fig. 15F). This facies is typical in open platform.

LF-5: thick-bedded to massive grainstone, representing shoal environment. Skeletal grain association is similar to that of LF-4, and peloids are one of the common components (Fig. 10A).

Obviously such a succession of lithofacies represents a series of depositional environments decreasing in water depth (Fig. 17). Additionally, reef facies alternate with LF-5 at the margin of YCP and the ICPs in the Dian–Qian–Gui Basin. The massive dolomite/dolomitic limestone (LF-6) of restricted/evaporitic platform in the western part of YCP is the shallowest facies in the region. Based on areal coverage and stratal thickness, the LF-2, -3 and -4 dominate the the Cisuralian and Guadalupian lithofacies on the YCP and these ICPs , with diverse biota of warm water and normal salinity. The well preserved alatoconchids mostly occur in the LF-3, including all the coquina occurrences, but a few occur in the LF-4, in the massive or thick-bedded packstone. Allochthonous fragments of the shells are confined to LF-1.

Detailed descriptions of 12 sections above (Fig. 9) depict a frequent occurrence of alatoconchid occurrences during the Early-Middle Permian transgressive-regressive cycles (Fig. 17). For example, the ABH at Wenjiangsi is on the top of a sequence from LF-5, LF-4 to LF-3 during transgression (Fig. 17b). While alatoconchids at Xingwen is sandwiched in a sequence of LF-2, LF-3 and LF-4 during regression (Fig. 17d). The ABH in LF-4 is actually thin intercalations of LF-3. Such a vertical pattern of occurrence is consistent with the alatoconchid palaeographical distribution in the region (Fig. 2).

5. Discussion

5.1 Stratigraphic range

Alatoconchids are known to range from the Artinskian to the late Guadalupian with their most common occurrences in the Wordian Stage (Runnegar and Gobbett, 1975; Yancey and Ozaki, 1986; Isozaki and Aljinović, 2009). In Japan, Thailand and Croatia, alatoconchids extend to the upper Capitanian (Yabeina Zone) (Isozaki, 2006; Udchachon et al., 2007; Aljinović et al., 2008) and they are considered to have gone extinct below the GLB (Isozaki and Aljinović, 2009).

In South China, the range of alatoconchids is also confined to the upper Cisuralian and Guadalupian interval (Table 1; Fig. 3). The oldest occurrences in the region are in the Kungurian stage: their co-occurrence with the fusulinid Misellina in the Dian–Qian–Gui Basin suggest an early Kungurian age (Lin, 1979; Zhou et al., 2014). A total of seven localities from the ICPs in the Dian–Qian–Gui Basin yield the clams in the Chihsia Formation (Table 1). Outside of this basin, the only Kungurian occurrence is at the Longyin section of Guizhou (E in Fig. 9).

Alatoconchids were widespread in the Guadalupian of South China on both the ICPs of the Dian–Qian–Gui Basin and the YCP (Fig. 3; Table 1). In the Wangjiaping area (WJP in Fig. 3), at the northwestern margin of the YCP, the alatoconchid beds occur in the bottom of the Maokou Formation (coincident with the first appearance of Neoschwagerina indicating a Roadian age (Zhang et al., 1986)). The Donglin section of Chongqing (DL in Fig. 2) has three ABHs found in Roadian, Wordian and Capitanian as indicated by their sequence correlation (Lin et al., 2004). Wordian alatoconchids are found in northern Guizhou, southern Sichuan and western Chongqing (Xingwen Global Geopark, Silong, Gusong, Leshan, Dapuzi, Donglin, Sangshuwan and Shangji). In this region, the ABH in the lower part of the second sequence of the Maokou Formation has great lateral persistence and is regionally correlatable (Fig. 9; Dai et al., 1978; Song, 1981, Zhang et al., 1986).

Fourteen Capitanian alatoconchid occurrences are known: in the central Guizhou, they are widely distributed in the fusulinid Yabeina–Neomisellina Zone (GSGP, 1973; Zhang et al., 1986; Zhao, 1991a, b), including Jiangjiazhai, Pianpozhai and Xiaohebian of Shuicheng city, Yanbeihou, Dudianzi and Dafang of Bijie city, and Xinpu of Zunyi city (Fig. 3). New conodont data from Sangshuwan and Shangji confirmed the Capitanian age of the siliceous deposits in the Zunyi area (Cai, 2017).

Alatoconchids were still widespread at the time of their final appearance in the late Capitanian. At Wenjiangsi, an ABH is found in the top part of the Maokou Formation (A in Fig. 9) and at the nearby Shuiyuan section (SY in Fig. 3) they occur within the late Capitanian Metadoliolina Zone (Mei et al., 2002). At Lengshuixi, on the northeastern margin of the YCP, their highest occurrence is probably of latest Capitanian age (D in Fig. 9). Alatoconchids also occur in the uppermost part of the Maokou Formation in the adjacent Dianjiang area (DJ in Fig. 3).

Eight Guadalupian occurrences lack detailed age dating including six sites in the Dian–Qian–Gui Basin, (Table 1). In the Pingle area, alatoconchids were reported from the strata corresponding to the Maokou Formation as indicated by Neoschwagerina, but the exact horizon was not described (Li and Yuan, 1983).

5.2 Alatoconchid ecology

Alatoconchids were likely epifaunal suspension-feeders, with a reclining habit that lacked a functional byssal opening in their adult stage (Yancey and Boyd, 1983). Their large flattened form suggests an adaptation to avoid sinking into the soft substrates, and would also help stabilize the shell during current and wave activity (Yancey and Boyd, 1983). Their South China occurrences, with complete individuals observed in life position, often in dark grey micritic host rocks supports these inferences. The upturned lateral terminal of the flange, noted in large specimens in this study (Fig. 6A, E), would facilitate the opening-closing of the two valves, and also avoid being buried by the succeeding sediments: an adaptation reminiscent of the geniculate shell form seen in Leptaena brachiopods.

As they usually occur abundantly, alatoconchids were first considered to be reef builders (Termier et al., 1973), but they have not been observed to construct organic frameworks and they did not have a cementing habit. Thus, the alatoconchids were reinterpreted as gregarious dwellers in low- or moderate-energy environments (Table 2; Yancey and Boyd, 1983). Kiessling and Flügel (2000) interpreted Philippine alatoconchid beds as biostromes constructed in a middle ramp environment under current activity. Storm reworking is an alternative factor commonly suggested to cause concentration of alatoconchid shells (Wiedlich and Bernecker, 2007; Udchachon et al., 2007, 2014). However, at all of the localities investigated in this study, no erosional structures or storm-related beds have been observed. Commonly, the appearance of the alatoconchid beds is a mixture of the flange sections and triangular transverse sections in living orientation, showing little evidence of sorting. Such sedimentary texture, combined with their great lateral persistence, suggests in situ accumulation rather than a result of storm or current reworking. The exceptions are the occurrences at Jiangjiazhai and Pianpozhai where alatoconchid shell fragments were carried by sediment gravity flows into the deeper basinal settings.

Photosymbiosis is an ecological strategy commonly seen in clams that attain giant size and was first suggested by Yancey and Boyd (1983) for the alatoconchids and followed by Isozaki and Aljinović (2009). This idea was mainly based on the conjecture that the mantle edge secreted the transparent prismatic outer shell layer at the growing margins and forming a narrow window along the commissural plane for photosymbionts to receive sunlight. However, Asato et al. (2017) argued that the additional thickness of the internal part of the shell made it unfeasible for sunlight to penetrate the shell. Alternatively, Asato et al. (2017) considered that alatoconchids more likely stuck out the mantle edge from the commissure to obtain light, if they indeed performed photosymbiosis. Therefore it is uncertain whether the alatoconchids utilized symbionts although they usually lived alongside photosynthetic calcareous algae and biota with photosymbionts. In the study region, they are frequently associated with calcareous algae and coral colonies, suggesting a life in the photic zone. While judging from the lithofacies successions, the optimal position of the Alatoconchidae is probably in the lower part of euphotic zone and below the thriving zone of calcareous green algae (Fig. 18).

Isozaki and Aljinović (2009) argued that the body size and shell thickness reached the maximum in the Neoschwagerina Zone and rapidly shrank to a small size in the Capitanian Lepidolina Zone. However, this claim is not supported by observations from South China. Firstly, shell wall thickness does not correlate with body size. Large individuals often possess thin walls (Fig. 6E). Secondly, the Capitanian occurrences in China (e.g. Lengshuixi and Wenjiangsi sections), contain lots of large individuals (more than 50 cm in width) indicating they maintained a giant body size up to their extinction level.

6. Conclusions

This study has identified the frequent, widespread occurrence of giant alatoconchid shells in the Permian of South China. In combination with the lithological and microfacies investigations, as well as a literature search, the following conclusions can be made:

1) Alatoconchids have a wide distribution in South China covering the Yangtze Carbonate Platform (YCP) and the Dian–Qian–Gui Basin. The previous identification of these fossils as phylloid algae is no longer valid.

2) Stratigraphically, the alatoconchids in South China extend from the lower Kungurian to probably the uppermost Capitanian.

3) The giant clams lived in the environment of normal marine salinity and warm water. Whilst they often co-occur with calcareous algae, their optimal position was probably in the lower part of euphotic zone and below the thriving zone of calcareous green algae.

4) Alatoconchids occurrences are usually marked by a great abundance of their shells that probably results from a gregarious life style, but they never formed reefs nor biostromes.

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Figure captions

Fig. 1. Palaeogeographic distribution of alatoconchids (base map modified from Isozaki and Aljinović (2009), occurrences in South China are from this study).

Fig. 2. Late Guadalupian lithofacies map of South China with alatoconchid occurrences marked. The district out of the carbonate lithofacies after Ma et al., (2009). Abbreviation of the localities: BJ, Banjiu; DF, Dafang; DJ, Dianjiang; DL, Donglin; DPZ, Dapuzi; GD, Gengdeng; GG, GanGeng; GS, Gusong; JJZ, Jiangjiazhai; LP, Langping; LaoP, Laopeng; LongP, Longping;LS, Leshan; LSX, Lengshuixi; LY, Longyin; LYa, Longya; LZY, Lianziya; MC, Mingcun; MY, Moyang; NR, Nengrong; PL, Pingle Basin; PPZ, Pianpozhai; SL, Shilin; SiL, Silong; SY, Shuiyuan; WJP, Wangjiaping; WJS, Wenjiangsi; XP, Xinpu; XT, Xiatong; XG, Xingwen Global Geopark; YBH, Yanbeihou; YP, Yanpeng; YLJ, Yangliujing. Abbreviation of the provinces name: AH, Anhui; FJ, Fujian; CQ, Chongqing; GD; Guangdong; GX, Guangxi; GZ, Guizhou; HB, Hubei; HN, Hunan; JX, Jiangxi; SC, Sichuan; SX, Shanxi; TW, Taiwan; ZJ, Zhejiang. The isolated carbonate platforms in the Dian–Qian–Gui Basin: I, Leye–Tianlin; II, Lingyun; III, Tian'e–Mashan; IV, Heshan–Laibin; V, Debao–Jingxi.

Fig. 3. Permian stratigraphic chart of South China. Fusulinid and conodont data from Jin et al. (1999) and Wang et al. (2014). Sequence division (Sq) of the Maokou Formation after Wang et al. (1998). The ordinal number indicates the lithological subdivision of the Maokou Formation into four members.

Fig. 4. Shell form of Shikamaia perakensis (after Runnegar and Gobbett (1975) and Yancey and Boyd (1983)). A. Dorsal view. B. Interior view of the right value with orientation and main features labeled, the outline is the same with the side view of the whole shell. C. transverse section through the anterior portion. D. transverse section through the middle portion.

Fig. 5. Transverse sections through the anterior of the alatoconchids in South China. A. Single valve, interior completely infilled by shell material, cardinal area bows slightly to the lateral on the dorsal side, Maokou Formation, Wenjiangsi. B. Single valve, interior completely infilled by shell material, cardinal area bows obviously to the lateral on the dorsal side, Chihsia Formation, Longyin. C. Single valve, the sector filled by micrite in the interior showing the form of the body cavity near its apical end, cardinal area runs subhorizontal on the dorsal side, Maokou Formation, Wenjiangsi. D. Tracing of C. E. Single valve, blank in the interior showing the form of the body cavity near its apical end, cardinal area runs subhorizontal on the dorsal side, black arrow indicates the byssal groove, Maokou Formation, Xingwen Global Geopark. F. Tracing of E. G. Articulated shell with byssal groove on each valve, cardinal area bows slightly to the lateral on the dorsal side, Maokou Formation, Xingwen Global Geopark. H. Tracing of G. I. Close up of the part in the red box of G.

Fig. 6. Transverse sections through the middle of the articulated alatoconchid shells. All from the Maokou Formation in the Xingwen Global Geopark. B, D and F are tracing of their above. A, across the position near the hingeline, small gap on the dorsal side of each valve connects the body cavity, the wall still massive on the ventral side near the plane of commissure, the arrows indicate the laminas on ventral surface, the edge of the shell turned upward; C, most common form of transverse section across the middle position, the right half is not complete; E, the flange of the right part is undulate with the edge turned upward, the left half is not completely exposed.

Fig. 7. Transverse sections through the middle or posterior portion of the alatoconchids. All from the Maokou Formation. A, across the middle of a single valve, the edge of the flange is incompletely infilled with crescent cavities, the black arrow indicates the position of wall thickening, the coin for scale is 2 cm in diameter, from Lengshuixi. B, tracing of A. C, across the posterior of an articulated shell, showing the overall flat profile, the left half is not completely covered by the photograph, from Xingwen Global Geopark. D, tracing of C, the dashed line indicates the plane of commissure. E, across the posterior of an

articulated shell, showing the septa that encloses the body cavity of each valve, the left half is not complete, from Xingwen Global Geopark. F, tracing of E.

Fig. 8. Shell wall structure of alatoconchids in South China. A from the Xingwen Global Geopark, B–D from Wenjiangsi. A, micrograph showing the mosaic interior layer and prismatic exterior layer, under plane-polarized light. B, field photograph showing the obvious prismatic structure of the exterior layer. C, field photograph showing the coarsely recrystallized interior layer. D, cross section of the prismatic layer, under plane-polarized light.

Fig. 9. Sedimentary succession of the typical alatoconchid occurrences in South China. Letters on lithological scale indicating the limestone classification: m, mudstone; w, wackestone; p, packstone; g, grainstone. Note the scale of strata thickness is not identical. Conodont data from Yang (2007) and Cai (2017).

Fig. 10. Microfacies of the alatoconchid-bearing successions at Wenjiangsi (A–C), Xingwen Global Geopark (D, E), Dapuzi (F, G) and Lengshuixi (H, I). Skeletal grains: a. calcareous algae; f. foraminifera; o. ostracod; v. Pseudovermiporella; p. calcite prism detached from the exterior layer of alatoconchid shells. A. Grainstone of the Bed 64; B. Matrix of the alatoconchid bed; C. Wackestone of the Bed 68; D. Matrix of the alatoconchid bed, the yellow arrow indicates the compacted algae; E. Algal packstone interbedded between the alatoconchid beds; F. Host rock of alatoconchids with fitted texture; G. Algal packstone below the ABH; H. Alatoconchid-bearing packstone; I. Foraminieral-algal packstone below the ABH.

Fig. 11. Outcrops showing alatoconchids from Wenjiangsi (A, B), Xingwen Global Geopark (C–F,) and Silong (G). A. Overview of the alatoconchid beds; B. Close up of the lower bed in A; C. Overall view of the strata relative to the ABH, note the alternating marl–limestone of the first member of the Maokou Formation just below the ABH; D, close up of the upper three alatoconchid beds; E, the first alatoconchid bed; F, coral colony in the alatoconchid bed, the red arrow indicates an articulated shell; G, concentrated alatoconchid shells. The coin is 2 cm in diameter.

Fig. 12. Outcrops of alatoconchids from Dapuzi (A-C), Lengshuixi (D-E) and Longyin (F-I). A. Large alatoconchid shell. B. Rugose coral colony in the ABH. C. Alatoconchid flange. D. Contact between the alatoconchid-bearing limestone of the Maokou Formation and the overlying sandy mudstone of the Lungtan Formation, the field book for scale is 18 cm in length. E. Alatoconchid shells. F. Lower two alatoconchid beds. G. Close up of the first bed, the black arrows indicate transverse sections of alatoconchid shells, the red arrows indicate arc-shaped cephalopod shells. H. Cephalopod shells co-occurring with alatoconchids. I. The third alatoconchid bed, the arrows indicate the flanges of alatoconchid shells. The coin is 2 cm in diameter, the pen is 14 cm in length.

Fig. 13. Microfacies of the alatoconchid-bearing successions at Longyin (A), Sangshuwan (B, C), Shangji (D, E), Yanpeng (F–H) and Laopeng (I). Skeletal grains: a, calcareous algae; e, echinoderm; f, foraminifera; o, ostracod; v, Pseudovermiporella; p, calcite prism detached from the exterior layer of alatoconchid shells; s, alatoconchid shell. A. Host rock of alatoconchids. B. Wackestone in the ABH. C. Algal packstone above the ABH. D. Alatoconchid-bearing wackestone. E. Packstone of the Bed 10. F. Packstone in the lower part of the Chihsia Formation. G. Matrix of the alatoconchid beds in the middle part of the Chihsia Formation. H. Host rock of alatoconchids in the middle part of the Maokou Formation. I. Wackestone hosting the alatoconchid shells.

Fig. 14. Outcrops of alatoconchids from Sangshuwan (A, B) and Shangji (C, D) of Zunyi. A. Alatoconchid shells at the bottom of the ABH, the scale ruler is 1 m in length. B. Sparsely scattered alatoconchid shells near the top of the ABH, the dotted line marks a coral colony and the arrow indicates the transverse section cross the middle of a large clam. Scale ruler is 60 cm in length. C. Overall view of strata with ABH. D. Close up of the alatoconchid bed.

Fig. 15. Outcrops of alatoconchids from Shuicheng. A and B from Pianpozhai. C and D, from Jiangjiazhai. E and F, from Xiaohebian. A. Deep-water lithofacies with ABH. B. Alatoconchid fragments preserved with

abundant crinoids. C. Heavily fragmented alatoconchid shells, circles indicate crinoid stems. The coin is 2 cm in diameter. D. Graded bedding developed near the alatoconchid bed. E. Alatoconchid bed. F. Coral concentrated bed below the ABH.

Fig. 16. Outcrops of alatoconchids in the Dian–Qian–Gui Basin. The penknife for scale is 7 cm in length and the hammer is 35 cm long. A–C from Yanpeng of Leye. D–E, from the Maokou Formation of Laopeng, Tian'e. A. Alatoconchid beds in the middle of the Chihsia Formation, the red arrows indicate articulated individuals in living position. B. Alatoconchids (red arrows) scattered in bioclastic limestone at the bottom of the Maokou Formation. C. The thickest alatoconchid bed seen in the lower part of the Maokou Formation. D. Base of the ABH and its underlying thick-bedded packstone. E. Second alatoconchid bed.

Fig. 17. Conceptual scheme displaying lithofacies associations of the ABHs in South China, in the context of transgression–regression cycle. Corresponding to the successions at a, Shangji, Xiaohebian, Yanpeng and Laopeng; b, Wenjiangsi; c, Lengshuixi; d, Xingwen, Dapuzi, Sangshuwan and Longyin; e, Jiangjiazhai and Pianpozhai.

Fig. 18. Summary of environmental settings inhabited by alatoconchids in the Permian of South China.

Tables

Table 1. Occurrences of alatoconchids in South China. Kun, Kungurian; Road, Roadian; Word, Wordian; Cap, Capitanian.

Locality	Formation	Index fossil/Sequence	Age	Reference
Longyin, Guizhou	Chihsia	Misellina	Kun	Investigated
Mincun, Guangxi	Chihsia	Misellina claudiae	Kun	Lin, 1979
Yangliujing, Guangxi	Chihsia	Misellina, Cancellina	Kun	Lu and Li, 1992
BanJiu, Guangxi	Chihsia		Kun	Zhou et al., 2014
Longya, Guangxi	Chihsia	Misellina	Kun	Zhou et al., 2014
Xiatong, Guangxi	Chihsia, Maokou	Misellina, Cancellina, Neoschwagerina	Kun–? (Gua)	Zhou et al., 2014
Yanpeng, Guangxi	Chihsia, Maokou	Misellina, Neoschwagerina	Kun–? (Gua)	Investigated
Gengdeng, Guangxi	Chihsia, Maokou	Misellina, Neoschwagerina	Kun–? (Gua)	Zhou et al., 2014
Wangjiaping, Sichuan	Maokou	first appearance of Neoschwagerina	Road	Zhang et al., 1986
Donglin, Chongqing	Maokou	Verbeekina, Neoschwagerina	Road–Cap	Lin et al., 2004
Longping, Guizhou	Maokou		? (Gua)	Investigated
Laopeng, Guangxi	Maokou		? (Gua)	Investigated
Gangeng, Guangxi	Maokou		? (Gua)	Zhou and Zhang, 1995
Nengrong, Guangxi	Maokou		? (Gua)	Zhou et al., 2014
Pingle Basin, Jiangxi	–	Neoschwagerina	? (Gua)	Li and Yuan, 1983
Xingwen geopark, Sichuan	Maokou	Second sequence of the Guadalupian;	Word	Investigated
Silong, Sichuan	Maokou	Neoschwagerina craticulifera,	Word	Investigated
Gusong area, Sichuan	Maokou	N. margaritae	Word	Dai et al., 1978
Leshan, Sichuan	Maokou		Word	Song, 1981
Dapuzi, Chongqing	Maokou		Word	Investigated
Sangshuwan, Guizhou	Maokou		word	Investigated
Shangji, Guizhou	Maokou		word	Investigated
Xinpu, Guizhou	Maokou	Yabeina, Neomisellina	Cap	Zhang et al., 1986
Wenjiangsi, Guizhou	Maokou	Third sequence of the Guadalupian	Cap	Investigated
Pianpozhai, Guizhou	Maokou	Yabeina	Cap	Investigated
Jiangjiazhai, Guizhou	Maokou	Yabeina	Cap	Investigated
Xiaohebian, Guizhou	Maokou	Yabeina	Cap	Investigated
Yanbeihou, Guizhou	Maokou	Neomisellina douvilleri	Cap	Zhao, 1991a
Dudianzi, Guizhou	Maokou	Neomisellina douvilleri	Cap	Zhao, 1991b
Dafang, Guizhou	Maokou	Yabeina gubleri	Cap	Zhao, 1991c
Shuiyuan, Guizhou	Maokou	Yabeina, Metadoliolina	Cap	Mei et al., 2002
Langping, Guangxi	Maokou	Yabeina	Cap	Lin, 1979
Shilin, Yunnan	Maokou	Dunbarula, Neomisellina	Cap	Dong et al., 2005
Dianjiang, Chongqing	Maokou	Third sequence of the Guadalupian	Cap	Luo et al., 2015
Lengshuixi, Chongqing	Maokou	Jinogondolella shannoni	Cap	Investigated

Table 2. Summary of previous sedimentary interpretations for alatoconchid occurrences.

Inferred environment/process	Evidence/interpretation	Occurrence	Reference
Reef	The shells are concentrated	Afghanistan	Termier et al. (1973)
Sublittoral environment, probably high-energy, attached by byssus	Impressive shell thickening and extraordinary shell form function to stable the shell, posteriorly gaping indicates byssally-attached habit and a subtidal living environment	Malaysia	Runnegar and Gobbet (1975)
Shallow environment with moderate or intermittent energy and loose sediment surface	Fine-grained matrix and associated diverse molluscs, common foraminifers, ostracods, calcareous algae and echinoderm	Review of previous work	Yancey and Boyd (1983)
Laterally-limited biostrome as a result of gregariousness and current	Abundant alatoconchid shells in alternation with organic-rich limestones and fusulinid wackestones	Philippines	Kiessling and Flügel (2000)
Lagoon facies on ancient seamounts	Host rock with high organic content (black to dark grey color) and fine grain size	Japan	Isozaki (2006)
Storm deposits	The fossil material, including shells in life position and densely packed debris, accumulated in 50–70 cm thick beds	Oman	Wiedlich and Bernecker (2007)
Subtidal environment below fair-weather wave base	Articulated shell was found in life position within the wackestone with abundant micrite and fecal pellets	Thailand	Udchachon et al. (2007, 2014)
Proximal storm deposits in subtidal environment below or around storm wave base	The alatoconchid shells are of various levels of fragmentation (?)	Thailand	Udchachon et al. (2007, 2014)
Subtidal to possibly intertidal regime within photic zone	black packstone or wackestone (host rock) with abundant bioclasts of calcareous algae, fusulinids, Tubiphytes, etc.	Croatia	Aljinović et al. (2008)

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