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On the Morphological Complexity of the Graptolite Tubaria in the Darriwilian (Middle Ordovician)

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1 Introduction

As one of the major zooplanktonic organisms in the Ordovician and Silurian marine ecosystems, graptolites played a unique role in the GOBE (Great Ordovician Biodiversification Event) and underwent a considerable variation of diversities both in lifestyle and in speciation through the Ordovician (Sadler et al., 2011; Cooper et al., 2014). Graptolites are among the early planktic groups that succeeded in reaching into the water column in the earliest Ordovician, possibly due to the growing ecological competition from benthic faunas, and a pursuit for new food sources and new ecological niches. They quickly inhabited the vast and nearly unoccupied marine ecospace by establishing a high-efficiency planktic lifestyle (Maletz, 2017). In the Ordovician, as a major organism of the marine planktic ecosystem, graptolites underwent a series of evolutions, not only through a substantial increase in biodiversity, but also the utilization of new constructional development, such as new colony designs and their suggested lifestyles.

2 Simplifications and complications of tubaria

In general, the simplification of graptolite tubarias pointed out by Elles (1922, 1923, 1933) and Bulman (1933, 1955, 1958), represents the main direction in architectural evolution of graptolites in the Ordovician and Silurian. The early graptolites in the late Cambrian and early Ordovician were of generally pendent to declined, multiramous colonies with simple and straight tubic thecae, but subsequently the number of stipes in graptolite colonies started to decrease. As a manifestation of this directional evolution, those pauciramous to two-stiped taxa of dichograptids and diplograptids were derived and dominated in the Early and Middle Ordovician, and moreover, those of monograptids are typified by retaining only one stipe and dominated in the Silurian. However, some graptolites in the Ordovician took a reverse approach by developing far more complicated tubaria with a large number of stipes and with more complex thecae (Fig. 1). It appears that the complication of tubaria occurs intermittently in some specific time intervals, and represents a side line of evolution in contrast to the tubaria simplification (Mu, 1963).

Mu (1963) summarized seven complication events based mainly on the development of numerous lateral branches or cladia from the main stipes of graptolite tubaria in Ordovician and Silurian. Later studies showed that some new complex architectural structures or features were also generated, which could improve graptolite lifestyle or directly enhance the competitiveness of graptolites in the marine ecosystem. For instance, the development of an unusual manubrium in the proximal ends of some derived glossograptids and primitive diplograptids, would make the tubaria of juvenile stages stronger and reduce the death rate.

Manubrium complex

Cooper and Ni (1986) firstly recognized and showed the complex construction of the manubrium in the proximal end on a number of exquisite Chinese specimens. Maletz et al. (2014) defined the manubrium as 'A complex and prominently shouldered structure on the reverse side of arienigraptid graptolites (Isograptidae), which is formed by the strong downward growth of the initial part of th1[2] and th2[1] and their descendant thecae. It always involves the formation of an arienigraptid suture. The sicula and the early thecae extend downward at least as far as their descendant thecae'. Although the manubrium was initially observed in the isograptids such as *Arienigraptus* in the upper part of the Dapingian in the early Middle Ordovician, it was more commonly recognized in the *Pseudisograptus* of the early Darriwilian (Maletz and Zhang, 2016) and more typically in the *Kalpinograptus* of late Darriwilian and Sandbian (Jiao, 1977). The manubriate *Kalpinograptus* consists of a number of extremely tightly-folded and compacted proximal thecae, which grow parallel downwards along the sicula for a variable length before they bend outwards. All these thecae are strongly elongated and may reach a length of more than 10mm. As the manubrium indeed includes lots of building thecae, Maletz (2017) speculated that this structure was to make the stipe much stronger and more resistant to any potential attacks in the water column.

Elongation of thecae

In a majority of the Ordovician planktic graptolites, the thecae are short or at a reasonable thecal length/width rate. However, in a few forms of graptolites occurring in the Darriwilian, the thecae are unusually elongated, and the thecal apertures develop complex processes. Among the most typical genera with elongated thecae is *Nicholsonograptus*, which develops exceedingly-elongated and compactly-arranged bundle-thecae in the single S-shaped stipe (Fig. 2). There could be up to 14 thecae in the cross section of the stipe at some specific positions (Wang, 1975). It seems likely that the S-shaped stipe probably resulted from the different growth rates of thecae or the prolonged mature stage of zooids in the distal stipe, and to maintain a good equilibrium in the water column. The aperture widths of almost all the thecae in *Nicholsonograptus* are similar, ca. 0.31-0.37mm, but the length of the elongated and slender thecae increase rapidly towards the distal end. At some theca, the thecal length/

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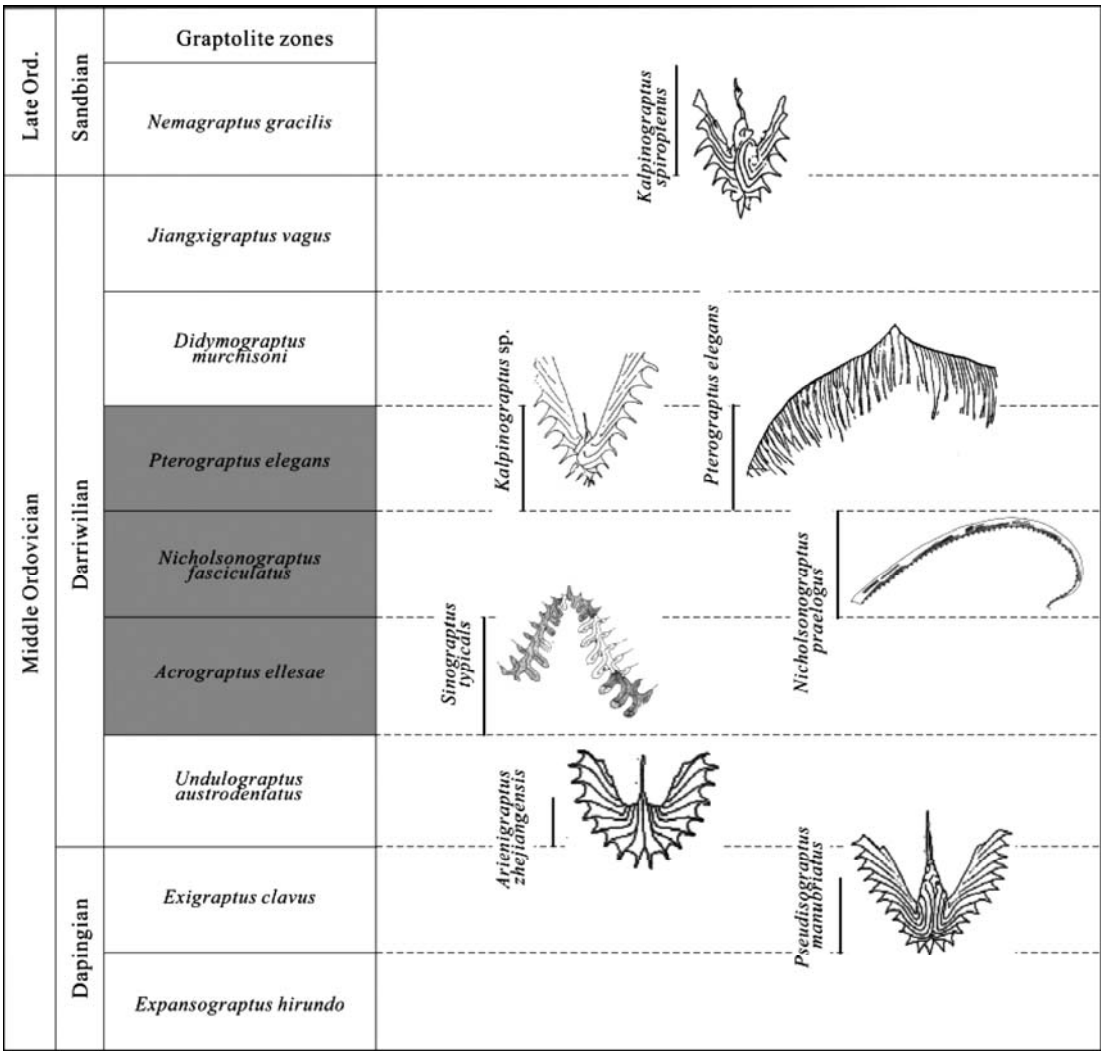

Fig. 1.Graptolites with complex architectures in the Middle Ordovician.
Note: the manubrium complex in *Arienigraptus*, *Pseudisograptus* and *Kalpinograptus*; the elongated thecae in *Nicholsonograptus*; the complexities of thecal apertures in *Sinograptus*.

width rate can be high up to 27 in the distal end, which is rarely observed in the graptolite evolutionary history. The high thecal length/width rate in *Nicholsonograptus* can easily increase the number of thecae across the stipe, and result in the formation of bundle-thecae that are compactly arranged along the single S-shaped stipe, an architecture probably increasing the feeding efficiency of graptolite zooids.

Complexities of thecal apertures

The morphologies of thecal apertures range from 'introverted' through 'perpendicular' to 'everted', and may be further complicated by developing various apertural processes, which have often been taken to distinguish species or genera. The thecae of benthic and early planktic graptolites in the early Ordovician are of simple tubes without apertural modifications. The morphologies of thecal apertures, however, become complex in the Middle Ordovician by developing various processes such as spines, lobes, shelves, hoods, hooks, and selvages. These thecal complexities are well presented in the intricately-folded and modified thecae of *Sinograptus* occurring in the Darriwilian, in which a tongue-shaped genicular apertural hood is developed and the aperture opened dorsally with a very restricted canal -like space between the apertural margin and the overhanging genicular hood (Fig. 1). In addition, remarkable laterally-protruding processes from the dorsal margin of the apertures are developed. These processes together with the overhanging genicular hoods, make a considerable restriction to the apertures (Zhang and Fortey, 2001; Maletz et al., 2018). These complexities of thecal apertures may serve to protect the zooids from potential attacks when they extend out of the apertures to build the tubaria or capture food particles in the water column.

3 Discussions

The development of complex architectures or morphologies in the Ordovician graptolites may be most likely related to a protection mechanism or feeding efficiency. In the general, long-term evolution of graptolites, simplifications of the tubaria are well represented and exampled, e.g. the reduction of stipes in the Ordovician dichograptids and diplograptids, and the simple thecal arrangement in the Silurian and Devonian monograptids. However, these simplifications are accompanied or alternated temporarily with a few examples of morphological complications, as shown above and also in *Nemagraptus*, *Syndyograptus* and *Amphigraptus* of the late Ordovician (Chen et al., 2016), and the *Diversograptus*, *Cyrtograptus* and *Linograptus* of Silurian (e.g. Zhang and Lenz, 1997; Lenz et al.,

Fig. 2. The elongated thecae in *Nicholsonograptus praelongus* Hsü from Anji, Zhejiang Province.
(a) S-shaped tubaria of a single stipe; (b) Close-up showing the extraordinarily-elongated and compactly-arranged bundle-thecae with complex thecal apertures.

2012). The complexities of the Darriwilian graptolites discussed here may be related to a quiet environment with plentiful nutrients, as indicated by the anoxic, deep-water facies in which they are preserved. *Nicholsonograptus*, *Pseudisograptus* and *Kalpinograptus* illustrated here have been recorded only in deep-water depositional settings (Zhang and Chen, 2007), and never in association with other shallow-water faunas. In such habitats, these graptolites can have enough time and space to grow complex constructional structures, either to increase the feeding efficiency or to better protect their feeding space.

Key words: Complexity, graptolite, tubaria, Ordovician, Darriwilian.

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