**Halýsis** Høeg, 1932 — an ancestral tabulate coral from the Ordos Basin, North China

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**Abstract**

The problematic calcareous microfossil **Halýsis** is abundant in the Middle Ordovician Darriwilian Stage of the western edge of the Ordos Basin, North China. The rich and well-preserved specimens of **Halýsis** in this area facilitate detailed studies for its skeletal construction and tube microstructure. **Halýsis** differs from calcified cyanobacteria and calcareous red and green algae in morphology, skeletal construction and microstructure, as well as reproduction mode. **Halýsis** typically consists of multiple juxtaposed parallel tubes arranged in sheets (‘multiple-tube’ type) or is just composed of one tube (‘single-tube’ type). In ‘multiple-tube’ **Halýsis**, tube fission by bifurcation results from the insertion of a microcrystalline wall at the center of a mother tube. This study demonstrates for the first time that the tube walls of **Halýsis** have a laminofibrous (fibronormal) microstructure, composed of fibrous calcite perpendicular to wall surface, and recognizes the ‘single-tube’ type **Halýsis** composed of one tube; in addition, for the first time, this study finds out that ‘multiple-tube’ **Halýsis** develops buds from the conjunction of two tubes and ‘single-tube’ **Halýsis** shows wide-angle Y-shaped branchings. Based on these findings, this study further compares **Halýsis** with tabulate corals. **Halýsis** appears stratigraphically earlier than **Caténipora** and **Aulópora**, and has a smaller tube size. ‘Multiple-tube’ **Halýsis** resembles **Caténipora** and ‘single-tube’ **Halýsis** resembles **Aulópora** in skeletal construction and microstructure, and in their tube walls of laminofibrous microstructure composed of fibrous calcite perpendicular to the tube wall surface. **Caténipora** and **Halýsis** are both characterized by the absence of septal spines. The similarities suggest that **Halýsis** may be the ancestor of **Caténipora-like** and **Aulópora-like** tabulate corals.

**Keywords:** **Halýsis**, Morphology, Taxonomic affinity, Middle Ordovician, Tabulate coral, Wuhaï, Inner Mongolia

1 Introduction

**Halýsis** Høeg 1932 is a problematic calcareous microfossil occurring commonly in Early- to Mid-Paleozoic carbonate rocks (Shen and Neuweiler 2015). It has been reported from shallow marine limestones of the Lower Ordovician to Devonian Systems (Guilbault et al. 1976; Poncet 1986; Mamet and Shalaby 1995; Munnecke et al. 1999, 2001; Frisch et al. 2013) disagreed with the interpretation of a row of parallel tubes or cells and interpreted **Halýsis** as consisting of parallel-juxtaposed, partly-branching tubes. Shen and Neuweiler (2015) confirmed the palisade-like arrangement of tubes in **Halýsis**. In this study, we present evidence that some **Halýsis** samples are composed of single tubes and have ‘single-tube’ skeletal construction.

With regard to the affinity of **Halýsis**, Munnecke et al. (1999, 2001) considered that the skeletal ultrastructure of **Halýsis** strongly resembles those of cyanobacteria,
e.g., *Girvanella*, and proposed that *Halysis* is a morphologically highly variable, palisade-like cyanobacterium. Riding and Braga (2005), however, compared *Halysis* with coralline-like red algae in cell size, cell shape, wall structure and flattening. More recently, Shen and Neuweiler (2015) interpreted *Halysis* as a siphonous green algae, citing similarities in skeletal architecture, growth form and biostratinomy. Although *Halysis* has been studied for nearly one hundred years, its systematic position remains in dispute.

*Halysis* occurs abundantly in a deepening-upward succession of Darriwilian-age limestones in the Ordos Basin, North China. It is present in both the underlying shallow water bioclastic calcarenites and the overlying thin-bedded deeper water marls. It has potential as an indicator of the sedimentary environment. Based on an examination of two hundred thin sections during this study, we found that (1) *Halysis* specimens from the Ordos Basin have a wall microstructure similar to those of tabulate corals, but different from those of cyanobacteria, coralline red algae and green algae; (2) many specimens of *Halysis* are composed of a single tube. Also we studied the mode of branching and tube fission for clues to *Halysis’* affinities.

2 Geological setting
The studied section is geographically located on the Laoshidan Mountain of the northwestern Ordos Basin, southeast of the Hainan district in Wuhai City, Inner Mongolia Autonomous Region, North China (Fig. 1).

Lower and Middle Ordovician strata are widely exposed in the Hainan area; the Upper Ordovician series is also present, but generally has been eroded away (Wang et al. 2016; Zheng et al. 2018). The Ordovician strata in this area are divided into seven formations: Sandaokan Formation, Zhuozishan Formation, Kelimoli Formation, Wulalike Formation, Lashizhong Formation, Gongwusu Formation, and Sheshan Formation (Jing et al. 2015), from base to top. A succession of the Middle Ordovician Zhuozishan and Kelimoli Formations is the focus of this study. The succession is more than 600 m thick and consists of calcarenite, marlstone, dolomitic limestone, dolostone, limestone and shale (Fig. 2).

*Halysis* occurs in the 184.7 m to 304.9 m interval of the studied section, with associated fossils including cyanobacteria (*Girvanella*), gastropods, brachiopods, cephalopods, echinoderms, trilobites, and the calcified cyanobacterium *Fontofilia furculata* Wu et Liu, 2015 (Yang et al. 2015) (Figs. 2 and 3). The presence of the conodont *Histiodella kristinae* in this interval, which has also been recorded in western Newfoundland (Stouge 1984; 2012) and the Tarim Basin (Stouge et al. 2011), indicates a middle Darriwilian age (Wang et al. 2013; Jing et al. 2015; 2016).

3 Material and methods
The Middle Ordovician Zhuozishan and Kelimoli Formations of the Laoshidan section were mainly composed of carbonate rocks of a variety of sedimentary facies, and were measured meter by meter (Fig. 2) in this study. A total of 267 hand specimens were collected at an interval...
by two or three meters, and 267 thin sections were made from these samples. Examination of thin sections revealed the presence of *Halysis* in 24 thin sections from the upper Zhuozishan Formation to the lower Kelimoli Formation (Fig. 2; Members Z3 and K1), particularly from the Member Z3. In addition, we examined 6 thin sections with *Halysis* from the Upper Ordovician Lianglitage Formation of Bachu area in the Tarim Basin (Cai et al. 2008). Lithological and paleontological features of the thin sections were examined using an Olympus BX41 transmitted light microscopy, and thousands of photomicrographs were taken. The microstructure of *Halysis* was observed by Olympus BX 41 transmitted light microscopy and by FEI Quanta 450FEG scanning electron microscopy (SEM) at the PetroChina Research Institute of Petroleum Exploration and Development. The *Halysis* samples were coated with gold and observed under the SEM at 5 kV, 0.4 mA. Morphometric analysis of *Halysis* was performed following the methodology of Munnecke et al. (2001), Frisch et al. (2013) and Shen and Neuweiler (2015).

Comparisons of *Halysis* with calcareous cyanobacteria (*Girvanella*), algae (*Dasycladales, Pernocaculus, Pseudosolenopora filiformis*), and tabulate corals (*Catenipora*...
and Aulopora) were made based on their skeletal microstructure, tube size and mode of reproduction. Dasycladales and Girvanella specimens from the Ordovician of the Ordos Basin, Permocalculus from the Middle Permian of the Lengwu section (in Zhejiang Province), Pseudosolenopora filiformis from the Upper Ordovician of the Tarim Basin, Catenipora from the Upper Ordovician Sanqushan Formation of Yushan area (in Jiangxi Province) were studied, and, Aulopora from the Lower Devonian Sipai Formation of Xiangzhou area (in Guangxi Province) were compared. Where the Halysis tubes are arranged in sheets and present a chain- or bead-like appearance in transverse section, we use ‘$Dp$’ to signify the diameter of tubes measured parallel to the alignment of chains, and ‘$Dn$’ for the diameter of tubes measured normal to their alignment of chains. ‘$Wp$’ signifies the wall thickness measured parallel to the chain alignment, and ‘$Wn$’ is the wall thickness measured normal to the chains.

4 Results

4.1 Morphology of Halysis

In this study, Halysis occurs in thin- to medium-bedded dolomitic limestone and limestone of the upper Zhuoishan Formation and the lower Kelimoli Formation (Z3-K1; Figs. 2 and 4a). In some horizons of the Zhuoishan Formation, it forms the principal grain component of wackestone and packstone (Fig. 4b-d).

In most cases, Halysis consists of multiple juxtaposed parallel tubes arranged in sheets (Fig. 4b, d), and then is termed ‘multiple-tube’ Halysis, in which the number of tubes ranges from 2 to more than 30. Less commonly, Halysis is just composed of one tube (Fig. 4c, d), and termed ‘single-tube’ Halysis. In longitudinal sections, tubes of both types can be of very variable length. The tubes in ‘multiple-tube’ Halysis are parallel to each other (Fig. 4e), and juxtaposed, forming a palisade-like structure. Most tubes are relatively straight to gently curved but occasionally show bending (Fig. 4f). In cross sections, Halysis tubes range from circular to elliptical and even square (Fig. 4g, h). The infilling of the tubes is typically sparry calcitic (arrow in Fig. 4 g) but can also be micritic (Fig. 4h). In oblique sections, Halysis tubes appear ovoid and have varied lengths (arrows in Fig. 4i). When less-well preserved, as in the Upper Ordovician Lianglitage Formation of Bachu area in the Tarim Basin (e.g., Cai et al. 2008), Halysis tubes tend to become sparitic and, when severely affected by diagenesis, can appear as elliptical circles in cross sections, or be destroyed (Fig. 5).

4.2 Microstructure of Halysis

The tube wall of Halysis from the Middle Ordovician Laoshidan section in Northwest Ordos Basin exhibits fibronormal (laminofibrous) microstructure, i.e., it consists of parallel fibrous calcite perpendicular to the wall surface in both cross section (Fig. 6a-d) and longitudinal section (Fig. 6i-j). Under the scanning electron microscope, the tube wall is composed of thin lath-like calcite crystals with thickness of 1.2–2.5 μm, width of 5–10 μm and length of 10–20 μm, arranged in a shingled pattern (Fig. 6e, f); and shows long flakes of calcite perpendicular to tube surface (Fig. 6k, l). The interior of the tube is filled with blocky calcite cement or micrite (Fig. 6g-l).
Micrite fillings indicate that the tubes of *Halysis* were mostly open, since micrite cannot enter a closed tube. In contrast, the tube wall of *Halysis* from the Upper Ordovician Lianglitage Formation of the Tarim Basin exhibits inconspicuous laminofibrous microstructure (Fig. 5), due to recrystallization. Some tubes of *Halysis* show structures resembling the tabulae of tabulate corals (Fig. 6i, j) as very thin and slightly curved in the same direction. These tabula-like structures are not common in the studied samples, probably because they merged with cement.

The tubes of ‘multiple-tube’ *Halysis* are nearly circular in cross section in almost all cases, and appear chain-like in transverse section. The diameter of a *Halysis* tube measured parallel to the chain alignment (Dp) is approximately equal to the diameter measured normal to the chain alignment (Dn) (Fig. 7a). Mean values of Dp and Dn for the ‘multiple-tube’ *Halysis* are 110.6 μm and 111.1 μm, and mean values of Dp and Dn for the ‘single-tube’ *Halysis* are 155.5 μm and 157.5 μm (Table 1), respectively. The wall thickness of a *Halysis* tube measured parallel to the chain alignment (Wp) and that measured normal (Wn) are also roughly equal (Fig. 7b). The mean Wp values of the ‘multiple-tube’ *Halysis* and the ‘single-tube’ *Halysis* are 9.8 μm and 12.5 μm, which are nearly a tenth of their corresponding mean Dp values; the mean Wn values of the ‘multiple-tube’ *Halysis* and the ‘single-tube’ *Halysis* are 10.5 μm and 12.7 μm respectively, which are also nearly a tenth of their corresponding mean Dn values (Table 1; Fig. 7). The mean Dp, Dn, Wp, and Wn values of the ‘single-tube’ *Halysis* is respectively larger than those of the ‘multiple-tube’ *Halysis*, which illustrates that the size of the tube in ‘single-tube’ *Halysis* is basically larger than the mean size of the single tube in ‘multiple-tube’ *Halysis* (Table 1; Fig. 7). The Dp/Dn ratios of ‘multiple-tube’ *Halysis* range from 0.77 to 1.32, and the variation of the Dp/Dn ratios of ‘single-tube’ *Halysis* is from 0.87 to 1.14; the Wp/Wn ratios of ‘multiple-tube’ *Halysis* range from 0.50 to 1.33 and those of ‘single-tube’ *Halysis* vary from 0.77 to 1.29 (Table 1).
The interiors of all tubes, far from the tube ends, are often, although not always, filled with granular calcite cement (Figs. 8, 9), while the tube ends are often filled by micrite. This could indicate that tabulae were present in all tubes before they merged with cement, which prevented the infilling of the interiors by micrite. And, since almost all *Halysis* skeletons were broken, the open ends of the tubes were filled by micrite. In Fig. 9c and e, the broken tubes are short and filled with micrite, without tabulae. In consideration of some previous observations also about the sediment filling of tubes (e.g., Frisch et al. 2013), this study could expect that if no tabula existed in the tubes, the interiors of some of these tubes would be filled with micrite.

### 4.3 Tube reproduction

'Multiple-tube' *Halysis* shows two modes of tube reproduction: fission and budding. Fission is the division of a mother tube into two daughter tubes by insertion of a microcrystalline wall in the center of the mother tube (Fig. 8a, b), and the two daughter tubes are parallel to each other and share a common wall. Budding is where a new branch begins from the contact between two adjacent tube walls. Initially, the new tube does not need too much space (Fig. 8c). As it grows, the space enlarges naturally and the daughter tube grows parallel to the old tubes (Fig. 8k). The first mode, i.e., fission, is more common (Fig. 8) during our observation. The diameters of the daughter tubes are smaller than that of the mother tube at the inception of fission (Fig. 8g-j). The relative frequency of budding, the number of budding sites versus the total tube number, may differ at different growth stages of the *Halysis* tube: in Fig. 8b, almost every tube has a new bud, while in Fig. 8k, budding occurs only locally in two out of fourteen tubes.

Reproduction in 'single-tube' *Halysis* is a process by which a mother tube develops into two daughter tubes, each with an independent wall, and the two new branches grow at an angle of 60°–100°, with a Y-shaped configuration (Fig. 9). The difference between the diameters of the daughter tube and the mother tube is very small. Some of the individual branches have nearly the same diameter as the unbranched tube (Fig. 9a, b, f). The diameters of the tubes range from 112 μm to 220 μm.

Based on observations on *Halysis* from the Middle Ordovician Laoshidan section in thin sections (Fig. 4) and their features of reproductions (Figs. 8 and 9), three types of morphologies are proposed for 'multiple-tube'
In the first type, which is the most common, partly-branching tubes are arranged parallelly (Fig. 10a). In the second and less common type, reproduction occurs as in the first type, with the only difference that the tubes curve at differing degrees (Fig. 10b). In the third and uncommon type, the new bud originates at the junction between two adjacent tube walls (Fig. 10c). And one morphology type for the ‘single-tube’ *Halysis* is that the tube bifurcates, forming two new branches at an angle of less than 100° (Fig. 10d).

**4.4 Taxonomic position of *Halysis* in tabulate corals**

Construction and microstructure are two important features to distinguish skeletal fossils. *Halysis* consists of one tube or a series of tubes in chain-like arrangement (Shen and Neuweiler 2015) and exhibits laminofibrous...
(fibronormal) microstructure instead of micritic microstructure in the tube wall (e.g., Munnecke et al. 2001; Riding and Braga 2005; Feng et al. 2010) under plane-polarized light. The laminofibrous or radiofibrous microstructure is common in the skeletons of Tabulata, rugose corals, stromatoporoids, Ostracoda and some other groups (Hill 1981; Dai 1994). Recognition of laminofibrous microstructure in *Halysis* suggests a possible affinity between *Halysis* and Tabulata.

The Tabulata is a large group of extinct Paleozoic corals characterized by skeletons composed of many tubes with developed or undeveloped tabulate structures. Tabulate corals can be classified into four morphological types: (1) those being reptant and composed of one to several trumpet-shaped tubes; (2) those being phacelloid in form and composed of many side-connected but contactless tubes; (3) those being massive and composed of many side-contact tubes; and, (4) those being dendroid and composed of contiguous tubes that are arranged parallelly like a fence (Hill 1981; Lin and Chi 1988). An Ordovician representative of fence-like tabulate corals is *Catenipora* (Fig. 11a), which is systematically assigned to Suborder *Halsytilina* Sokolov 1947 (Hill 1981) and consists of numerous contiguous tubes parallel to each other.

‘Multiple-tube’ *Halysis* is similar to *Catenipora* in several aspects. Firstly, both are composed of parallel-juxtaposed tubes with a fence-like arrangement (Fig. 11). Secondly, tube walls in both have a laminofibrous microstructure, composed of fibrous calcite perpendicular or slightly oblique to the tube wall surface (Figs. 4, 6, 8 and 11). Third, *Catenipora* is characterized by the absence of septal spines (Wang and Deng 2010), and the same applies to *Halysis*. In addition, *Halysis* and *Catenipora* both occur in marlstone or dolomitic limestone (Fig. 2), which indicates that they both lived in a low energy environment. A possible difference is that *Catenipora* has distinct tabulae, but tabulae may have merged with cement in *Halysis*, though they were present in life (Figs. 8a-d, i-j, Fig. 10 d-e). Another difference is that the tubes in *Catenipora* are arranged into fence-like sheets that have a mesh-like

| Table 1 Tube measurement of the *Halysis* from the Middle Ordovician Zhuozishan and Kelimoli Formations of the Laoshidan section in Northwest Ordos Basin, North China |
|-----------------|----------------|----------------|----------------|----------------|----------------|----------------|
|                 | Dp (μm) | Wp (μm) | Dn (μm) | Wn (μm) | Dp/Dn | Wp/Wn |
| **‘Multiple-tube’ *Halysis*** |         |         |         |         |       |       |
| Mean            | 110.6   | 9.8     | 111.1   | 10.5    | 0.99  | 0.93  |
| Maximum         | 178     | 19      | 165     | 19.2    | 1.32  | 1.33  |
| Minimum         | 60      | 5       | 72      | 7       | 0.77  | 0.50  |
| **‘Single-tube’ *Halysis*** |         |         |         |         |       |       |
| Mean            | 155.5   | 12.5    | 157.5   | 12.7    | 0.99  | 0.98  |
| Maximum         | 220     | 20      | 195     | 20      | 1.14  | 1.29  |
| Minimum         | 112     | 8       | 120     | 9.7     | 0.87  | 0.77  |
appearance in transverse section (Fig. 11b, c), but in Halysis the fence-like sheets do not appear to be mesh-like (Fig. 6). The third difference is that the tubes in Halysis are much smaller than those in Catenipora. Tube diameters of the ‘multiple-tube’ Halysis in this study range from 60 μm to 178 μm (Table 1), and can reach 190–250 μm in previous data (Riding and Braga 2005; Shen and Neuweiler 2015), whereas the tube diameters of Catenipora are much greater (Fig. 11d, e). Despite these three differences, overall similarities in their skeletal construction and tube wall
Microstructure are obvious. Therefore, this study suggests that *Halysis* could have an affinity with *Catenipora*, and might also belong to the Tabulata.

The earliest occurrence of the ‘multiple-tube’ *Halysis* was in the Lower Ordovician (Guilbault et al. 1976), while the *Catenipora*-like corals did not appear until the Middle Ordovician (Hill 1981). Since *Halysis* is much older and smaller than *Catenipora*, we suggest that the ‘multiple-tube’ *Halysis* is a possible ancestor of the fence-like tabulate corals such as *Catenipora*.

*Aulopora* is a genus of the ‘single-tube’ type, composed of small trumpet-like tubes laterally connected at the base (Fig. 11f), and shows close similarities with the ‘single-tube’ *Halysis*. Tabulae may or may not be present in the *Aulopora*; where tabulae are present, they can be sparse or numerous (Fenton 1927; Hill 1981; Scrutton 1990). As noted above, tabulae can be present in the ‘single-tube’ *Halysis* but are not always observed (Fig. 6i-j), and in many cases, tabulae may have merged with cement. For example, the *Halysis* specimens in the Tarim Basin are severely affected by diagenesis and lack tabulae (Fig. 5). Nonetheless, more decisive aspects of our taxonomic assignment are based on the skeletal construction and tube microstructure of *Halysis*.
The tubes of Aulopora and ‘single-tube’ Halysus are both round in cross sections and have thin walls with similar laminofibrous microstructure (Fig. 6a-b, Fig. 11f-g); and, they both exhibit elongate and somewhat quadrate or rectangular shapes (Fig. 6i-j, Fig. 11h-i) in longitudinal sections. Even though there is a difference in the size ranges of these two genera, they have an overlap. The tube diameter of ‘single-tube’ Halysus in this study ranges from 112 μm to 220 μm, and the tube diameter of Halysus described by Shen and Neuweller (2015) can reach 247 μm; while tubes of Aulopora are 150–500 μm in diameter (Fig. 12). Thus the tube-size ranges of Aulopora and Halysus show an overlap (Fig. 12). In addition, the tubes of Aulopora and ‘single-tube’ Halysus both show similar reproduction mode of mainly basal or lateral gemmation (Fenton and Fenton 1937), and of Y-shaped branching (Fig. 9), respectively. Both Aulopora and ‘single-tube’ Halysus first appear during the Early Ordovician Period. The above similarities also support the systematic position of Halysus in tabulate corals.

Halysus tubes are not closed and the opening for the polyps would be at the top (Fig. 10). The sections in Fig. 8j and k could be produced when the tubes were curved like in Fig. 10b. Whether the filling in the tubes is cement or sediment depends on how easily the sediment could enter the tubes. The tops and the ends of the Halysus tubes may be filled with sediment, whereas the interior may be filled with cement due to the presence of tabulae. Frisch et al. (2013) show some examples of tubes filled with sediment.

5 Discussion
Høeg (1932) placed Halysus in incertae sedis because he considered there was insufficient evidence to assign it to any family. Guibault et al. (1976) attributed
Halysis tentatively to the family Codioaceae in terms of the branching mode and the leaf-shaped morphology with a narrow stem fixed on the ground. Munnecke et al. (2001) considered that Halysis is a morphologically highly variable, palisade-like cyanobacterium. Riding and Braga (2005) concluded that the morphology of Halysis is more likely a single planar sheet of laterally adjoining cells and suggested that Halysis could be a coralline red alga. A three-dimensional model of Halysis revealed that the skeletons of Halysis consist of parallel-juxtaposed, partly-branching tubes, and the interpretation of a single sheet of adjoining cells was then rejected by Frisch et al. (2013).

A possible taxonomic affinity between Halysis and siphonous green algae was proposed by Shen and Neuweiler (2015). Controversy about the taxonomic affinity of Halysis continues and we therefore consider comparisons between Halysis and calcareous green algae, calcareous red algae and cyanobacteria based on their microstructure, tube size and reproduction mode.

Benthic fossil calcareous green algae include two main groups, the Dasycladales (Fig. 13a-b) and the Bryopsidales (siphonales) (Fig. 13c-d). Udoteaceae and Codioaceae are two families of the order Bryopsidales (Verbruggen et al. 2009). Calcification in living Udoteaceae is characterized by precipitation of needle-shaped aragonite, a process described as “early micritization” by Macintyre and Reid (1995). Since aragonite is not a stable mineral, it generally transforms to granular calcite in diagenesis, and is preserved as granular calcite in fossils (Mu 1991; Granier 2012). All fossils of Codioaceae are composed of granular calcite. A similar example, based on our own materials, is the Gymnocodiacean Permocalculus sp. from the Middle Permian Lengwu Formation of Tonglu area in Zhejiang Province, East China (Fig. 13c-d). The differences between Halysis and Codioaceae include: (1) Halysis consists of small tubes and Codioaceae are composed of filaments. Though tubes and filaments are roughly similar in shape, the former are more regular and generally straight, while the latter generally are irregularly curved. (2) The tubes in Halysis are parallel, but the filaments in Codioaceae and Udoteaceae are generally irregularly intertwined in bundles. (3) The tubes in Halysis have regular calcareous walls, while the filaments of Codioaceae have not. The tube wall of Halysis has a laminofibrous microstructure, whereas the skeletons in Codioaceae are composed of granular calcite. And, the spaces between filaments are lined by the carbonate precipitate induced by metabolism of the living Codioaceae, which is originally needle-like but changes to granular calcite during diagenesis. In addition, the elements of Udoteaceae are much larger than Halysis. Because of these differences, the likelihood that Halysis belongs to

![Fig. 12 Diameter-measurement comparisons of the Halysis tubes recorded in previous literature (Riding and Braga 2005; Shen and Neuweiler 2015) and studied in this study, together with the Aulopora. Tube diameters recorded as internal diameters in the literature (Munnecke et al. 2001; Frisch et al. 2013) are excluded.](image-url)
Codiaceae and/or Udoteaceae (Bryopsidales; siphonales) is minimal. Distinct difference also exists between calcified cyanobacteria and *Halysis*. Cyanobacteria include filamentous types and non-filamentous types. Only some genera have calcified fossils. The non-filamentous calcified cyanobacteria have no morphological similarity with the *Halysis*. The filamentous sheaths of filamentous calcified cyanobacteria can be preserved as tubes (Riding 1977, 2011; Liu et al. 2011). However, the filaments of cyanobacteria are irregularly curved (e.g., *Girvanella*) (Riding 1991) while the tubes in *Halysis* are generally straight. All tubes in *Halysis* are parallel to each other and arranged like a fence, and possess the laminofibrinous microstructure; whereas filaments in the filamentous calcified cyanobacteria are composed of micrites (Pratt 2001; Liu and Zhang 2012) (Fig. 13e). The size difference between the filaments of calcified cyanobacteria and the tubes of *Halysis* is conspicuous. The diameter of the filaments is generally very small and cannot exceed 50 μm, but the diameter of many known *Halysis* tubes can exceed 150 μm (Fig. 12). The commonest mode of reproduction in the cyanobacteria is vegetative and asexual, either by means of binary or multiple fission in unicellular and colonial forms or by fragmentation and spore formation in filamentous species (Gualtieri and Barsanti 2014), while the reproduction in *Halysis* is budding and branching. Considering these differences, the taxonomic similarity of *Halysis* with calcified cyanobacteria proposed by Munnecke et al. (2001) is not confirmed. *Halysis* differs from calcified red algae. Red algae constitute a very large group, only a few of which have calcified skeletons. The calcified thallus of the genus *Pseudosolenopora*...
filiformis (Nicholson 1888) (Fig. 13f) found from the Upper Ordovician in the Tarim Basin (Yang et al. 2015), is composed of radially-arranged calcified cells with widths of 22–50 μm. The cell walls in radiate direction are calcified better than the concentric walls, and are more distinct. Coralline red algae have two forms: articulate and non-articulate; the former form includes more than ten genera; the latter also called crustose coralline algae (CCA) includes more than twenty genera. The thalli of the articulate forms are composed of radially-arranged calcified cells. The thalli of the non-articulate forms consist of two parts, a basal part composed of radially-arranged calcified cells and a surface part composed of several layers of grid-like calcified cells. Most of the genera, Lithoporella, has a thallus composed of a unistratose hypothallium and a unistratose epithelium (Turner and Woelkerling 1982a; Liu 1990). At first sight, the vertical sections of Lithoporella and Lithophyllum shown by Riding and Braga (2005, their figure 3) were somewhat similar to the cross section of Halysis, and this is probably why an affinity between Halysis and Corallinaceae was proposed. However, there are substantial differences between them. The most important is that Halysis consists of tubes arranged in a fence-like layer, while the thalli in the calcified red algae are composed of radially-arranged cells (Fig. 13f). Another important difference is that the tube walls of Halysis have a laminofibrous microstructure (Fig. 6a-b), while the calcified cell walls in Corallinaceae have two Mg-calcite layers or aragonitic crystals (Basso 2012; Caragnano et al. 2014) which can turn into micrite or granular calcite during diagenesis. Most corallines are dioecious, and the reproduction of coralline red algae is mainly completed by the fertilization of female conceptacles and the vegetative propagation, during which a fragmentary thallus grows into a new coralline (Fott 1971). Lithoporella has gametic conceptacle or carposporophyte and cannot rely on vegetative propagation (Turner and Woelkerling 1982b). This feature is significantly different from that of Halysis. Due to these considerable differences, the affinity between Halysis and the coralline red algae was rejected by Frisch et al. (2013).

3) Halysis differs from calcified cyanobacteria, calcareous green and red algae in skeletal construction and microstructure. In contrast, Halysis resembles tabulate corals, such as Catenipora and Aulopora, in their skeletal construction and microstructure. Thus, the affinity between Halysis and calcified cyanobacteria, and the affinity between Halysis and calcareous green and red algae, proposed by previous researchers are not supported by this study. Furthermore, the similarities both between ‘multiple-tube’ Halysis and Catenipora, and between ‘single-tube’ Halysis and Aulopora, support the taxonomy of Halysis in tabulate corals, as a possible ancestor of the group.

6 Conclusions

1) Halysis Hoeg 1932 is a calcareous microfossil that is common in the Middle Ordovician Darrwilian Stage of the northwestern Ordos Basin, North China, and mainly shows two types of skeletal construction of the ‘multiple-tube’ and the ‘single-tube’.

2) The ‘multiple-tube’ Halysis is more common, and is reproduced by fission and budding; and, the ‘single-tube’ Halysis is reproduced by Y-shaped branching. The tube wall has a laminofibrous microstructure, described for the first time in this study.

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