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贵州中寒武世凯里生物群中宏观藻类化石新材料

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摘要: 贵州省台江县中寒武世凯里生物群含有丰富的非钙质藻类和具有软躯体后生动物化石, 它为布尔吉斯页岩型生物群在世界广泛分布提供了更有力的证据。在生物群的宏观藻类中描述了 5 个属 5 个种, 包括 2 个新属。它们是 *Marpolia spissa* Walcott、*Acinocricus stichus* Conway Morris and Robison、*Udotealga erecta* Yang、*Eosargassum sawata* Yang 和 *Rhizophyton zhaoyuanlongii* Yang, 并且将凯里生物群中的宏观藻类化石组合与加拿大布尔吉斯页岩生物群中的宏观藻类进行了对比, 发现两个生物群不仅具有相似的动物化石组成, 而且宏观藻类化石组成也很相似。

关键词: 贵州; 中寒武世; 凯里生物群; 宏观藻类化石
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New Macroalgal Fossils from Middle Cambrian Kaili Biota in Guizhou Province, China

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Abstract: Abundant and well-preserved remains of noncalcareous algae and soft-bodied metazoans were collected from Middle Cambrian Kaili biota in Taijiang county, Guizhou Province, China. These remains provide further evidence for the wide geographic distribution of many Burgess Shale taxa. Among the algae, 5 genera (including two new genera) and 5 species are described. They are *Marpolia spissa* Walcott, *Acinocricus stichus* Conway Morris and Robison, *Udotealga erecta* Yang, *Eosargassum sawata* Yang, and *Rhizophyton zhaoyuanlongii* Yang. Contrasting the macroalgal fossil assemblage in the Kaili biota with one in the Burgess Shale biota, it is clear that similarity of the Kaili biota and the Burgess Shale biota is reflected by the same content of not only the soft-bodied metazoans, but also the noncalcareous algae.

Key words: Guizhou Province; Middel Cambrian; Kail biota; macroalgae

Evolution insights provided by the Burgess Shale biota from the Middle Cambrian of British Columbia are becoming more widely appreciated, especially as they pertain to be diversification of early metazoans. The discovery in other Cambrian localities of soft-bodied fossils that are directly comparable to those from the Burgess Shale is, therefore, of particular significance in demonstrating the wide distribution of this biota. Up to the present, many sites are now known from the Laurentian craton, South China platform, which during the Cambrian period appears to have occupied an equatorial location isolated from other major Craton[1-4].

Here we report the occurrence of new taxa of algae from Kaili biota that enlarge our knowledge of Cambrian diversity. The Kaili biota extends further the distribution of the Burgess Shale-type biotas. Moreover, on the basis of the similarity of the algal fossils between the Burgess Shale biota and the Kaili biota, the factors controlling the provincialization of Middle Cambrian biogeography will be mentioned in this paper. Some of the wider implications of the continuing discoveries of Burgess Shale-type biotas will be discussed elsewhere, though comment is given here, but among these new discoveries, the Chengjiang biota and the Kaili biota from South China are of special importance given the postulated palaeogeographic separation between the Laurentian and Chinese Yangtzi platform.

The Kaili biota occurs at the middle part of the *Oryctocephalus indicus-Xingrenaspis* zone in the middle part of the Kaili Formation at Balang, Taijiang, Guizhou

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Province[5, 6], the exact age of the Kaili biota is early Middle Cambrian, because the first occurrence of the Kaili biota is coincident with the first occurrence of Middle Cambrian key fossils (such as *Oryctocephalus indicus*, *Pagetia prolata*, *Microryctocara nevadensis*) of Middle Cambrian[7], below the *Oryctocephalus-Xingrenaspis* zone. Moreover, a large number of the Lower Cambrian trilobite *Bathynotus* elements are widely distributed, while other Lower Cambrian trilobite such as *Redlichia*, *Protoryctocephalus* are also collected. Altogether, its age belongs to the early stage of Middle Cambrian.

The Kaili biota includes 12 phyla, which are algae, acritarchs, Poriferia, Coelenterata (including Ctenophora and Cnidaria), "Worms", Tardipolypoda, Medusiform animals, Brachiopoda, Hyolithida, Mollusca, Arthropoda, and Echinodermata. Also present are problematical or enigmatic taxa and trace fossils[4, 7]. Recently, new fossils have been discovered[7], including *Ottoia* Walcott, *Naraoia* Walcott, *Palaeoscolex* Whittard, *Urokodia* Hou *et al*, *Microdictyon* Bengtson *et al*, anomalocarids, fuxianhuids and other taxa. Because, more than 120 genera have been recognized, so far the Kaili biota is among the most diverse Burgess Shale-type biotas following the Burgess Shale and the Chengjiang biotas. The most remarkable fossils in the Kaili biota are non-trilobite arthropoda, echinoderms and medusiform animals. Moreover, abundant and well-preserved macroalgal fossils also appear to be much important part of the biota[8—10].

1　Comparison between the Kaili biota and the Burgess Shale biota

The macroalgal fossils in the Kaili biota, until now, consist of 3 morphological types, 1) branch type, major forms of macroalgal fossils in the Kaili biota, such as *Marpolia* and *Thamnophyton*. 2) Belt type, such as *Bosworthia*, *Eolaminaria*, *Konglingiphyton*, and *Enteromophites*[9, 10]. 3) Silk and thread type, such as *Eoulothrix* and *Palaeospinella*. Moreover, based on the observations of macroalgal fossils in the Kaili biota, two macroalgal assemblages have been established, which are (with an ascending order): *Bosworthia-Eolaminaria* assemblage, and *Marpolia-Thamnophyton* assemblage.

At present, more than 20 macroalgal fossil genera have been recognized, macroalgal fossils of the Kaili biota are among the most diverse Burgess Shale-type biotas (including Burgess Shale biota and Chengjiang biota). The comparative relationship of the macroalgal fossils between the Kaili biota and the Burgess Shale biota is shown in Table 1.

Table 1　The comparative relationship of the macroalgal fossils between the Kaili biota and the Burgess Shale biota

Kaili biota	Burgess Shale biota
Rhodophycophyta	Rhodophycophyta
Palaeocodium yichangiaum	*Waputikia ramosa*
Paraamphiros siniansis	*Dalyia nitens*
Wahpla sp.	*D. racemata*
Dalyia racemata	*Wahpia insolens*
Bosworthia simulans	*W. mimica*
Phaeophycophyta	*W. virgata*
Eolaminia grandis	*Bosworthia simulans*
E. perelegans	*B. gyges*
Eosargassum sawata	Chlorophycophyta and Cyanophycophyta
Konglingiphyton erecta	*Margaretia dorus*
Palaeodictyota dichotoma	*Morania confluens*
Fractibeltia vein	*M. costellifera*
F. formosus	*M. elongata*,
F. typical	*M. fragmeata*
F. fibrillata	*M. frondosa*
Leafiophyton dichuarae	*M. ? globosa*
Wavilaminaria taijiangia	*M. parasitica*
Yuknessia sp.	*M. ? reticulata*
Chlorophycophyta	*Marpolia spissa*
Morania confluens	*M. aequalis*
Marpolia spissa	Phaeophycophyta?
M. aequalis	*Dictyophyton gracilis*
Thamnophton formosus	Uncertain taxa
Eoulothrix fibrillata	*Sphaerocodium cambria*
Enteromophites siniansis	*S. praecursor*
Uncertain taxa	
Palaeospinella typical	
Palmalga glumacea	
Flabelliphyton lantianensis	
Kailiphyton regularum	
K. simulans	
Udotealga erecta	
Sinocylindra yunnanensis	
Doushantuophyton cometa	
Guizhouella ramulosa	

From Table 1, two biotas share the same elements, including *Dalyia nitens*, *Bosworthia simulans*, *B. gyges*, *Morania*, *Marpolia spissa*, *M. aequalis and Wahpia*. Moreover, the morphology (such as branching pattern) of macroalgal fossils in the two biotas also is similar. Among the macroalgal fossils, the distribution of *Marpolia* is widespread, known from China and Canada, from the Middle Cambrian of Utah[4], and the Paseky shale of Czech Republic[11] and Russia[12] as well.

Based on the pattern of biogeographic distribution of the Cambrian macroalgae and the similarities of the algae and metazoan fossils in the Kaili biota to those of the Burgess Shale biota[2, 3, 5, 13, 14], many paleontologists consider that the Laurentian and Chinese Yangtzi platform were close in the middle Cambrian, while isolated by open ocean[15].

We suggest that the factors controlling the provincialization of Cambrian biogeography are mainly palaeolatitude. Because evolutionary level of metazoan is relatively low in the Precambrian-Middle Cambrian, and biotic diversifying energy is low as well. Schopf's model[16] of biogeographical region is not suitable for early metazoan and metaphyla, based on the pattern of geographic distribution of the metazoan in the Precambrian-Cambrian, the new model of the Precambrian-Middle Cambrian biogeographical region established[10], that could express the similarities among the members of the Chengjiang biota, the Kaili biota and the Burgess Shale biota.

The ecologic environment of the Kaili biota may be reconstructed according to the macroalgal fossil and other fossil assemblages, and features of sedimentation in the Kaili Formation. Although the abundant macroalgal and early metazoan fossils always occur together in the Kaili Formation, it turns out that most fossils in the Kaili biota were reworked, suggesting that the mechanism of taphonomy of the Kaili biota is similar to that of the Burgess Shale biota in Canada. Moreover, a comparison of the macroalgal fossils in the Kaili biota with the Precambrian ones[3, 17—19] shows that the evolutionary level of algae in the Cambrian is higher than that of algae in the Precambrian, for example, the thallusos of *Eosargassum sawata* Yang, present jagged pattern with receptacle structure.

2 Fossil Description

Kingdom Prokaryota

Division ?Myxophyceae?

Class, Order, Family uncertain

Genus *Marpolia* Walcott, 1919

Type species: *Marpolia spissa* Walcott 1919

Marpolia spissa Walcott 1919

(Figs. 1, 8, 9, 11, 13—15)

1919 *Marpolia spissa* Walcot[21]: 234, Pl. 52, Figs. 1, 1a-b.

1923 *Marpolia spissa* Walcot, Walcott[21]: 59—61, Pl. 5, Fig. 1.

1966 *Marpolia spissa* Walcott, Johnson[22]: 24—25, Pl. 7, Figs. 1—3.

1981 *Marpolia spissa* Walcott, Gunther and Gunther[23]: Pl. 67B.

1985 *Marpolia* Walcott, Conway Morris and Whittington: Fig. 4.

1985 *Marpolia spissa* Walcott, Whittington: Figs. 4.2.

1988 *Marpolia spissa* Walcott, Conway Morris and Robison[4]: 5—6, Figs. 1—2.

1994 *Marpolia spissa* Walcott, Mao *et al*: 346, Pl. 1, Figs. 1—5, Pl. 2, Fig. 1 (non).

1994 *Marpolia spissa* Walcott, Briggs *et al*[24]: 53, Figs. 1, 2.

1996 *Marpolia spissa* Walcott, Steiner *et al*[25]: 287, Fig. 7.

2001 *Marpolia spissa* Walcott, Yang *et al*[10]: 287, Pl. 2, 3, Figs. 1—8.

Lectotype: Thallus, USNM 35403, illustrated by Walcott, 1919, Pl. 52, Fig. 1; selected here.

Materials: 50 specimens of complete thalli collected by Yang and Zhao from the Kaili Formation, and many dissociated filaments and fragments.

Occurrence: Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China.

Diagnosis: Thallus small; 2—3 cm high, sometimes to about 5 cm in height. Filaments numerous, branching basally at low angles to form a dense tuft. Most filaments are composed of an inner trichome of uniserial cells. Filament range from 20 to 60 μm in width and averages about 40 μm. Rarely, two to four trichomes share a single sheath. Rarely trichomes may be naked. Cells of trichomes discoidal, ranging from 2 to 4 μm in length, and from 2 to 10 μm in width; heterocysts absent. Terminal cells of trichome unknown.

Description: Remains of colonies range from micro- to macrofossils. Bushy to tufted colonies are composed of numerous filaments and irregularly spaced false branches. Filaments commonly bear smooth sheaths and impressions of sediment grains. Trichomes and cell structures are unknown. Sometimes complete thallus is composed of regularly 5 to 6 sheaths, and some complete thalli with "holdfast" present in the Kaili biota (Figs. 1, 13). The complete thalli are scarce in the Burgess Shale biota and Paskey Shale[11, 24, 25]. Their morphology is also similar to Pila bibractensis from Permian of French[26].

Discussion: Fossilized cell remains of filamentous cyanobacteria mainly show clear signs of shrinkage and disaggregation[27]. Therefore, taxonomy of such remains is based on the width of sheath[27]. Filament dimension of *Marpolia spissa* from the Kaili biota represent 9 to 100 μm, this range of dimension of *Marpolia spissa* is coincident with that of *Marpolia spissa* from the Burgess Shale[4, 27] and the Pasekly Shale[11]. The morphological similarities between *Marpolia* and recent *Cladophora scopaeformis* (Ruprecht) Harvey may hint their belonging to the same division.

Despite the broader range of filament width, they belong to *Marpolia spissa*, as this view mentioned by Steiner and Fatka[11].

Most macroalgal fossils of the Kaili biota are composed of *Marpolia* genus, while the morphological form of *Marpolia* is coincident with the recent *Cladophora scopaeformis* (Ruprecht) Harvey. Therefore, we suggest that

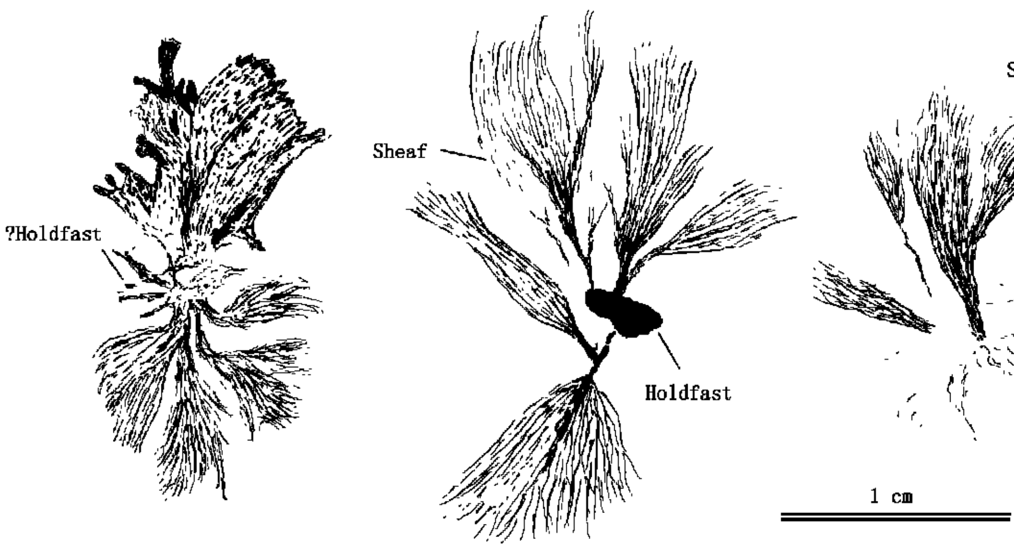

Fig. 1. The map showing typical shape of *Marpolia fossil* in the Early - Middle Cambrian Kaili Fm. of Taijiang country, Guizhou Province, China.

Marpolia lives at tide zone just like recent *Cladophora scopaeformis* (Ruprecht) Harvey[26].

Division Chlorophyta

Class, order, family uncertain

Acinocricus stichus Conway Morris and Robison, 1988

(Plat. I—11, 12)

1981 *Peytoia-like* Gunther and Gunther[23], Pl. 58B.

1982 *Acinocricus stichus* Conway Morris and Robison[4], Pl. 1, Fig. 6, text-Fig. 1G.

1988 *Acinocricus stichus* Conway Morris and Robison[4], 11, Figs. 5—10.

Lectotype: Thallus, KUMIP 204353, illustrated by Conway Morris and Robison, 1988, 11, Figs. 5—10. selected here.

Materials: 8 specimens with complete thalli collected by Yang and Zhao from the Kaili Formation, and many dissociated filaments and fragments.

Occurrence: Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China.

Diagnosis: Thallus is consisted of long axis bearing prominent spinose whorls at more or less regular intervals. Elongate spines on each whorl separated by conspicuously shorter spines; arrangement may be bilaterally symmetrical. Whorls may house short branches with closely spaced spines, probably in whorls. A broad axis bears approximately 10 whorls of spines. Neither end is clearly preserved. Most specimens are detached whorls of spines, but their original arrangement can be seen in specimens with multiple whorls. Holdfast and distal termination unknown.

Description: This taxon has been previously illustrated[4]. Most specimens from the Kaili biota are broken into whorls of spines, without a broad axis bearing some spines (Figs. 10, 12). Because of disturbance of water engine, sometimes specimens are representatively spines on the surface of shale.

Discussion: Conway Morris and Robison[4] considered it is similar to the alga Chaetocladus from the Silurian of Wisconsin. At present, Bian *et al* (unpublished) discovered *Tarimia leei* from Upper Ordovician of Xinjiang Province, China that is 2.8 cm long, with an axis bearing approximately 30 whorls of spines. Bian *et al* (unpublished) propose that the specimen belongs to the Bryophyte. The hypothesis may be right, because Strother *et al*[28] reported a new evidence for land plants from the lower Middle Ordovician of Saudi Arabia, and other new evidence for land plants from the Middle Cambrian of North America[29].

Division Phaeophycophyta

Order Fucales

Family Sargassaceae

Eosargassum gen. nov.

Etymology: A combination of geologic time and alga *Sargassum*.

Type species: *Eosargassum sawata* sp. nov. (specimen no. GTM-9-1-100; Fig. 2)

Description: Thallus is consisted of leaves, para-stem and reproductive branch. Leaves include two types of leaf and capped leaf, with crenulated margin. Holdfast unknown.

Discussion: This new taxon has not been previously illustrated. Its shape is very similar to the living *Sargassum kjellmanianum* Yendo, for the former bears crenulated leaves and capped leaves and reproductive branches.

Eosargassum sawata sp. nov.

(Figs. 2, 6)

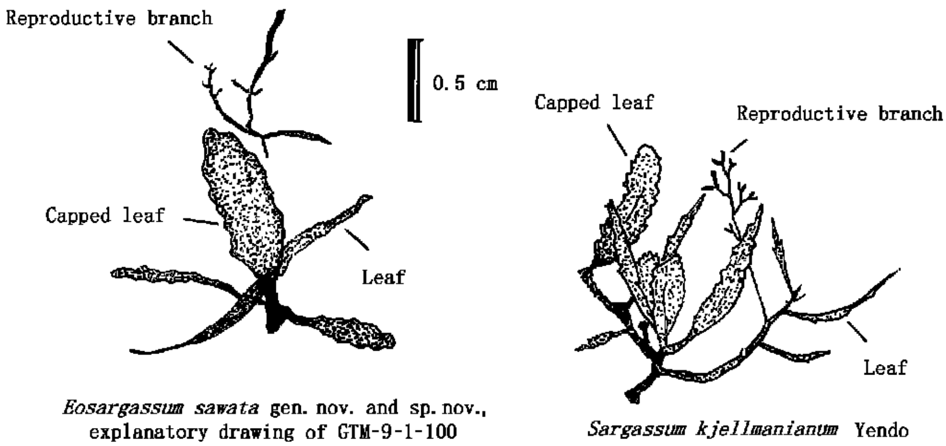

Fig. 2. Comparison between fossil *Eosargassum sawata* and modern *Sargassum kjellmanianum* Yendo.

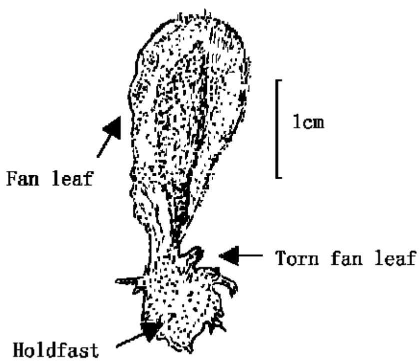

Fig. 3. *Udotealga erecta* gen. nov. and sp. nov., explanatory drawing of holotype, GTM-10-336.

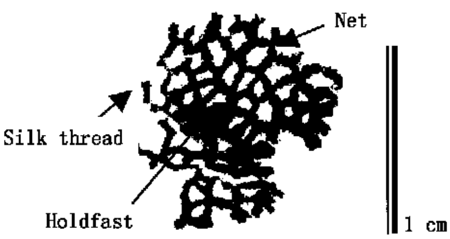

Fig. 4. *Rhizophyton zhaoyuanlongii* gen. nov. and sp. nov., explanatory drawing of holotype, GTM-9-2-97.

Etymology: Greek *sawat*, saw-shape.

Holotype: Incomplete thallus, GTM-9-1-100; Fig. 2, collected by Yang and Zhao from the Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China. The specimen is pale-brown to dark-gray, noncalcareous mudshale.

Occurrence: Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China.

Description: Thallus preserved in shale is incomplete one with only leaves, capped leaves and reproductive branch; capped leaf common 5 mm long, 2 mm wide; leaf 9 mm long, 0.5—1 mm wide; reproductive branch small.

Discussion: The comparison between fossil *Eosargassum sawata* and modern *Sargassum kjellmanianum* Yendo shows that the evolutionary level of algae is higher in Cambrian, and the morphological characteristics of fossil thalli is near to the level of the modern algae. Because the macroalgal fossil shares with capped leaves and reproductive branch, *Eosargassum sawata* probable belongs to Phaeophycophyta.

Division ? Phaeophycophyta

Class, order, family uncertain

Udotealga gen. nov.

Etymology: Ladin *Udote*, leaf-like, fan leaf.

Type species: *Udotealga erecta* sp. nov. (specimen no. GTM-1-10-336; Fig. 3)

Description: Thallus probably consists of some fan leaves, which crowd in the holdfast. Because of incomplete preservation, only a fan leaf and holdfast remain, but at least 3 fan leaves were torn by water current.

Discussion: This new taxon has not been previously illustrated. Its morphology is very similar to modern *Udotea* Lamouroux, but the specimen is noncalcareous,

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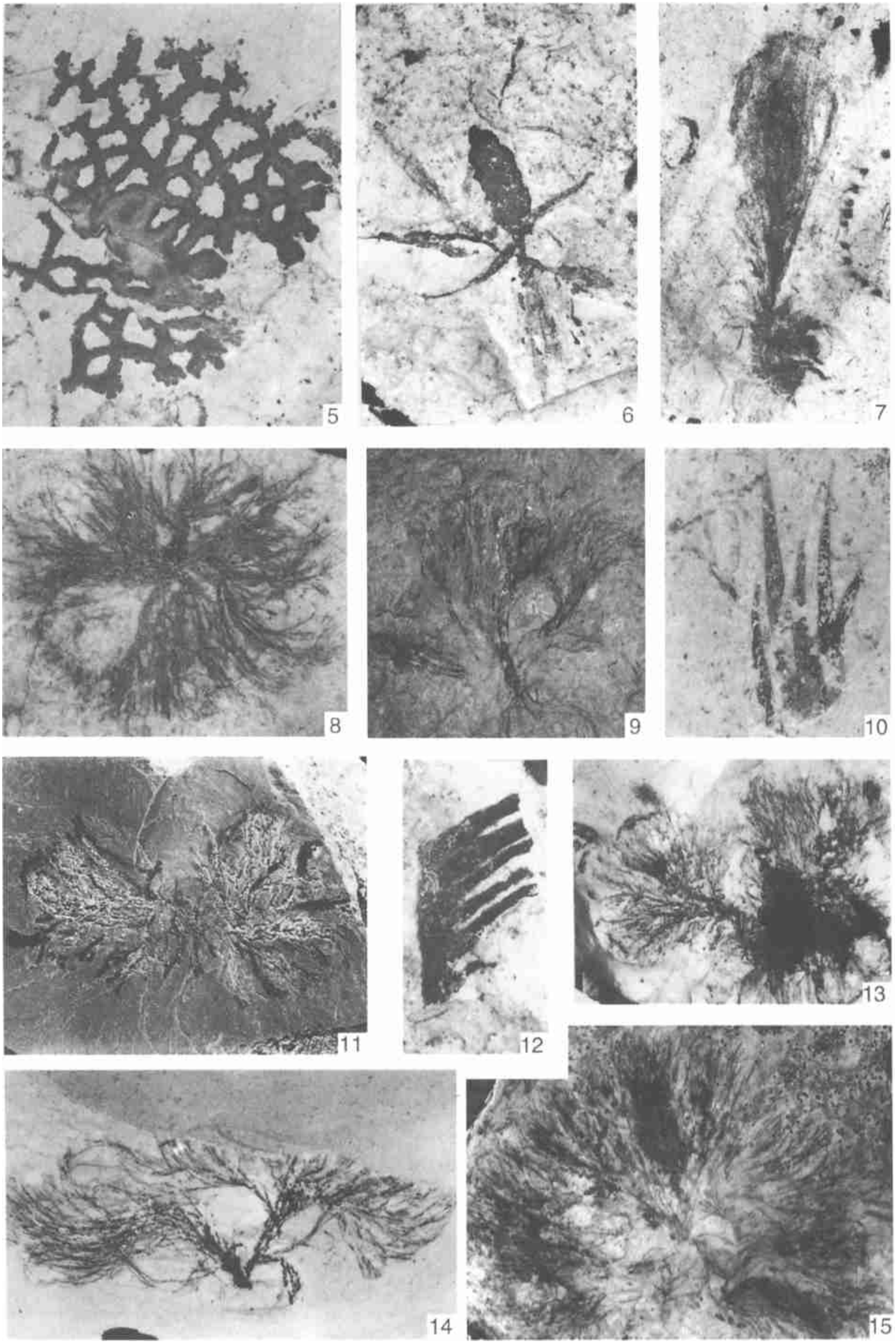
Figs. 5—15. **5.** *Rhizophyton zhaoyuanlongii* gen. nov. and sp. nov., No. GTM-9-2-97. ×4. **6.** *Eosargassum sawata* gen. nov. and sp. nov., No. GTM-9-1-100, ×3. **7.** *Udotealga erecta* gen. nov. and sp. nov., No. GTM-10-336, ×4. **8.** *Marpolia spissa*, Walcott, No. GTM-9-1-444, ×3. **9.** *Marpolia spissa*, Walcott, No. GTM-9-1-200, ×3. **10.** *Acinocricus stichus* Conway Morris and Robison, No. GTM-9-3-1320, ×3. **11.** *Marpolia spissa*, Walcott, No. GTM-8-5-1100, ×3. **12.** *Acinocricus stichus* Conway Morris and Robison, No. GTM-9-2-320, ×4. **13.** *Marpolia spissa*, Walcott, No. GTM-8-5-946, ×3. **14.** *Marpolia spissa*, Walcott, No. GTM-8-4-117, ×3. **15.** *Marpolia spissa*, Walcott, No. GTM-8-5-888, ×3.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possibly suggesting the nonevident biomineralization later.

Udotealga erecta sp. nov.

(Figs. 3, 7)

Etymology: Latin *erecta*, erect.

Holotype: Incomplete thallus, GTM-1-10-336; Fig. 3, collected by Yang and Zhao from the Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China. The specimen is pale-brown to dark-gray, noncalcareous.

Occurrence: Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China.

Description: Thallus is preserved in shale, incomplete, with only one fan leaf and holdfast. Holdfast large, 8—9 mm in width, 30 mm in length, with "rhizoid", at least 3 fan leaves torn (Figs. 3, 7). A fan leaf 30 mm long, 9 mm wide, without stipe.

Discussion: The specimen *Udotealga erecta* from the Kaili formation is rare, and only an incomplete thallus is found. Based on the morphology of thallus, it probably belongs to Phaeophycophyta. The morphological form of the algal fossil is similar to *Flabelliphyton* Yuan[17] (*Huizhouella* Yan, Xing et Xu) from Lantian Formation of Upper Sinian of Anhui Province[14], but *Udotealga erecta* is different from *Flabelliphyton* (*Huizhouella* Yan, Xing et Xu) composed of numerous oblate cells, and from *Cometiphyton* Ding, from Duoshantou Formation of Upper Sinian of Hubei Province[17]. In addition, the abovementioned algal fossils from Upper Sinian, only consisted of an single folium, while *Udotealga erecta* is composed of at least three foliums.

Division Chlorophycophyta

Class Chlorophyceae

Order ? Cladophorales

Family ? Cladophora

Rhizophyton gen. nov.

Etymology: Ladin *Rhizo*, plant root-like, reticulate.

Type species: *Rhizophyton zhaoyuanlongii*, sp. nov. (specimen no. GTM-1-10-336; Fig. 4)

Description: Thallus is consisted of some silk threads, silk threads intertwin and form reticulates or nets. Single net is tetragonal. There are about 20 reticulates or nets in the specimen.

Discussion: This new taxon has not been previously illustrated. The morphology is very similar to modern *Rhizoclonium* Kutzing, but the specimen is noncalcareous.

Rhizophyton zhaoyuanlongii sp. nov.

(Figs. 4, 5)

Etymology: Latin *zhaoyuanlongii*, indicating hearty congratulation to Prof. Zhao Yuan-Long who discovered the Kaili biota.

Holotype: Incomplete thallus, GTM-9-2-97; Fig. 4, collected by Yang and Zhao from the Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China. The specimen is pale-brown to dark-gray, and noncalcareous.

Occurrence: Middle Cambrian Kaili Formation of Taijiang, Guizhou Province, China.

Description: Thallus preserved in shale, is a complete algal fossil, which is consisted of a big holdfast and intercrossed silk thread. Silk thread is 1 mm in diameter. There are at least 20 nets, whose area of single tetragonal net is about 4 mm^2.

Discussion: The specimen *Rhizophyton zhaoyuanlongii* from the Kaili Formation is a complete thallus preserved. The morphological character of thallus is similar to modern *Hydrodictyon* Roth, therefore, it probably belongs to Chlorophyta. But the fossil thread is not consisted of some single cells as that of modern *Hydrodictyon* Roth. Additionally, the fossil algae bear a big holdfast that is absent for modern *Hydrodictyon* Roth. Until now, no other reports of algal fossil do suggest any useful information.

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