Progress and significance in research on the early Middle Cambrian Kaili Biota, Guizhou Province, China*

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Abstract Important progress in research on the Kaili Biota has been made recently. Many interesting components from Chengjiang Biota and Burgess Shale Biota have been discovered, e. g. *Microdictyon* of lobopodia; *Ottoia*, *Palaeoscolex* of worms; *Naraoia*, *Marrella* of Trilobitioidea, *Mollisonia*, anamalocarids and other non-trilobite arthropods; and new sorts of echinoder-mas, macroalage fossils and so on. Recent work on the Kaili Biota has resulted in the following developments: (i) an increase in the number of animal genera, up to more than 100 genera in total, so that the Kaili Biota has become the third most diverse of the Burgess Shale-type Biota after the Burgess Shale and Chengjiang Biotas; and (ii) the most noteworthy fossils in the Kaili Biota are echinoderms, non-trilobite arthropods and soft-bodied medusiform fossils, especially the most diverse echinoderms. The progress provides envidence for the biodiversity of marine organisms presented after the "Cambrian Explosion" and serves as a link between the earlist Cambrian Chengjiang Biota and late early Middle Cambrian Burgess Shale Biota. It is of great significance in the reconstruction of the Cambrian palaeoplate, palaeongeography and in research on taphonomy.

Keywords: Kaili Biota, three biotas, biodiversity.

The earliest Middle Cambrian Kaili Biota is one of the very important Burgess Shale-type biotas in the world after discovery of Chengjiang Biota in eastern Yunnan and of significance for the evolutionary study of metazoa. This biota was first reported in 1994[1~6] and attracted much attention from palaeontologists[7~11]. But the composition of the biota is characterized by a few soft-bodied animal fossils and non-trilobite arthropods as well as very abundant trilobites[1,12] (Fig. 1). Thanks to the discovery of new material in different places since 1998, research on the Kaili Biota is progressing well. Some important components belonging to both the Burgess Shale Biota and the Chengjiang Biota have been found, including *Naraoia*, *Ottoia*, *Palaeoscolex*, *Marrella*, *Isoxys*, *Mollisonia* and Anomalocarids[13] (Fig. 2). The Kaili Biota presents a completely new appearance.

1 Composition changes of the Kaili Biota

(i) The phylum of Lobopodia has been found. The representatives of lobopodia are *Paucipodia* and *Microdictyon* (Fig. 2(g)), of which the latter is very important and ranges from the Chengjiang Biota[14,15] to the Kaili Biota[9,14,15].

(ii) The number of genera of non-trilobite Arthropods has increased from three genera[1,12] up to eighteen genera, of which *Marrella* (Fig. 2(b)), *Mollisonia* (Fig. 2(e)) were known only from the Burgess Shale Biota[16,17], while *Naraoia* (Fig. 2 (g)) and *Tuzoia* are widely distributed in the Chengjiang Biota and the Burgess Shale Biota[9,10,17~19]. The discovery of the front organs and mouth apparatus of Anomalocarids (Fig. 2(c)) shows a rather abundant non-trilobite Arthropods in the Kaili Biota.

(iii) Echinoderms are the most noteworthy member of the Kaili Biota, and show one of the characteristic features differentiated from that of the Chengjiang Biota and Burgess Shale Biota[1,3,12,13]. With exception of Eocrinoidea (Crinozoa) and Homoiostelea (Homalozoa), Edrioasteroidea and Holothuroidea (Echinozoa) have recently been found in the Kaili Biota. More than 1500 specimens of

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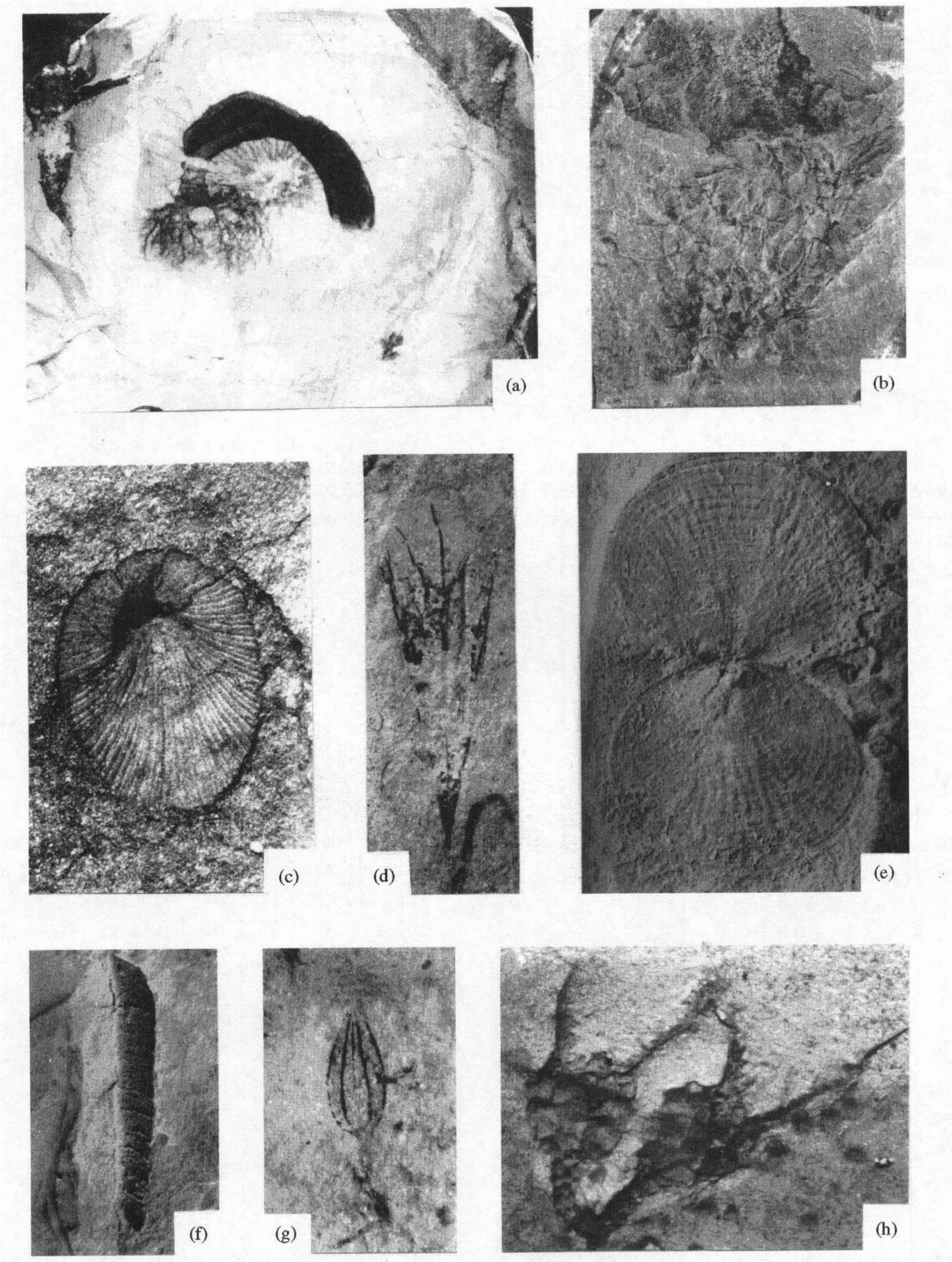

Fig. 1. Major members of Kaili biota before 1999.

(a) *Pararotadiscus guizhouens* (Zhao et Zhu), seeing clear tentacles. ×1, GTBj-13-3-220; (b) Chancellorids, ×3, GTBM-9-5-493; (c) *Scenella radians* (Babcock et Robison), top layer of disc. ×15, GTB-20-2-2b; (d) *Haplophrentis*? *carinatus* (Mathew), ventroinner view, seeing guts trace, ×7, GTB-22-1-47; (e) *Glyptacrothe bohemica* (Barrande), dorsal and ventral valve connected with each other. ×6, GTBM-21-346; (f) Echiurids, complete body of warm, ×3, GI-6-42; (g) *Wiwaxia taijiangensis* (Zhao, Qian and Li), lateral sclerite with root, ×18, GTBM-20-1400a; (h) *Sinoecrinus ninus* (Zhao, Huang et Gong), two individuals connected with each other with its end of stem. GTB stands for Wuliu-Zengiayiyany section, GTBM stands for Miaobanpo section and GTBj stands for Jinyinshan section, all of them located in Balang village, Taijiang county, Guizhou Province of China. The specimens were collected from 1982 to 1998. All the specimens are preserved in the Institute of Paleontology and Bio-mineralization, School of Resource and Environment, Guizhou University of Technology.

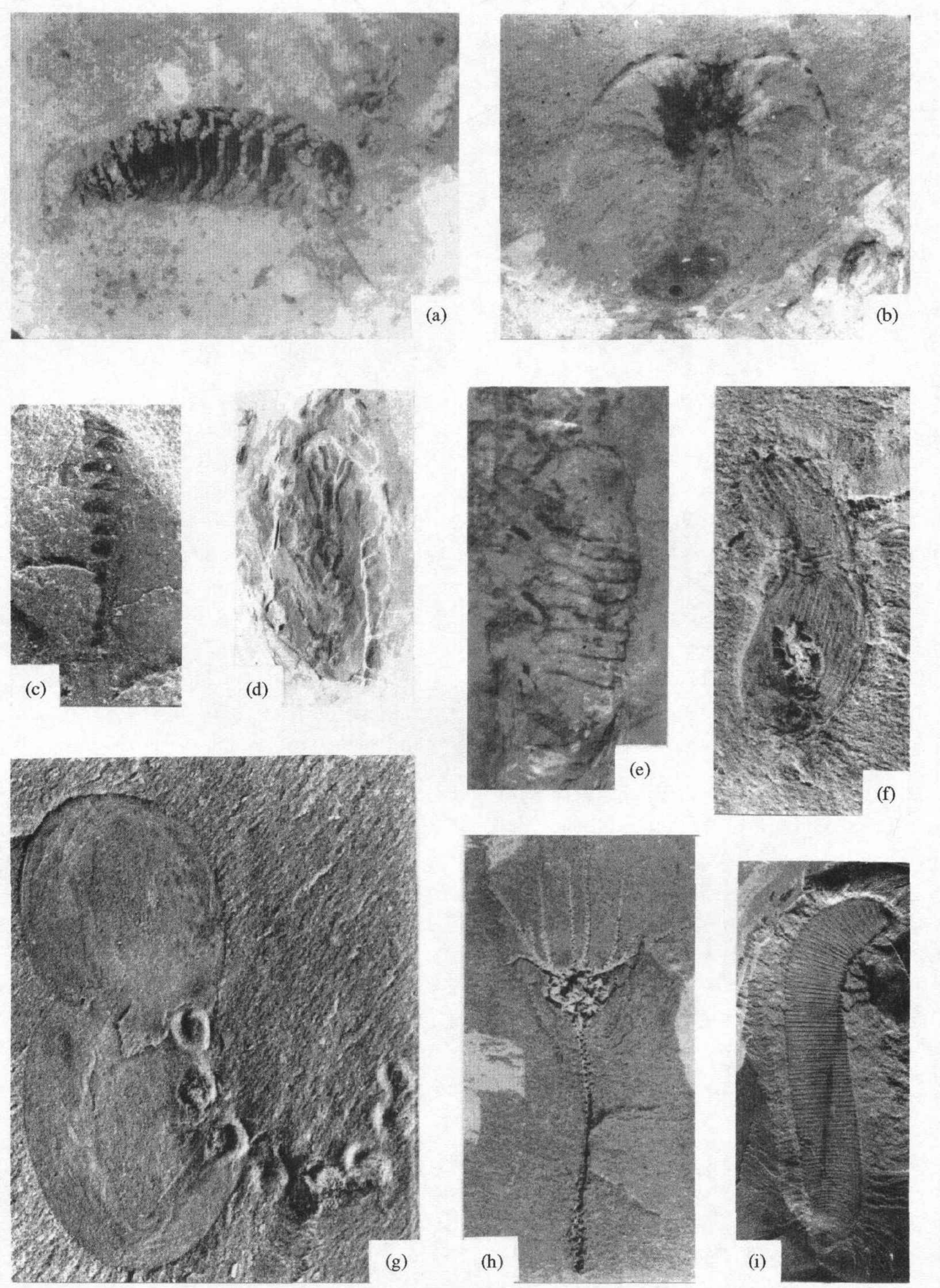

Fig. 2. New members of Kaili Biota after 1999.

(a) *Leanchoilia illecebrosus* (Hou), ×8, GTBM-9-1-556; (b) *Marrella* sp., ventral view, seeing gills and appendages, ×4, GTBM-9-5-1075; (c) Anomalocarids tooth, ×4, GTB-21-16; (d) *Pollingeria* sp., ×3.5, GTBM-9-5-3271; (e) *Mollisonia* sp., ×4, GTBM-9-2-1156; (f) *Palaeopriapulites* sp., ×1.5, GTBj-13-3-232; (g) *Naraoia* cf. *compacta* (Walcott), associated with *Microdictyon* sp., ×6, GTBM-9-3-318b; (h) *Crinozoa* gen. et sp., nov. theca little, stem tiny, special branch, ×4, GTBM-9-1-526a; (i) *Ottoia* sp., seeing black alimentary canal, ×1.5, GTBj-13-2-231. GTB stands for Wuliu-Zengiayiyany section, GTBM stands for Miaobanpo section and GTBj stands for Jinyinshan section, all of them located in Balang village, Taijiang county, Guizhou Province of China. The specimens were collected from 1999 to 2001. All the specimens are preserved in the Institute of Paleontology and Bio-mineralization, School of Resource and Environment, Guizhou University of Technology.

Sinoeocrinus globosus belonging to Eocrinoidea, preserving the holdfast have been collected. The fossils of Echinoderms in the Kaili Biota are the most abundant in the Burgess Shale-type biotas.

(iv) The number of soft-bodied fossils has increased. Except "Worms", e.g. *Ottoia* (Fig.2(i)), *Palaeopriapulites* (Fig.2(f)), *Palaeoscolex*, *Maotianshania*, *Selkirkia* sp., *Cricocosmia*?[20], there are a lot of specimens belonging to Medusiform metazoan interpreted as Lophophorata, *Pararotadiscus guizhouensis* Fig. 1(a))[13], to Hyolithids, *Haplophrentis*? *carinatus*, showing muscle insertion areas[1,13](Fig. 1(d)), and to Arthropods, *Naraoia* preserving appendages.

(v) The Macroalgae fossils are very abundant in the Kaili Biota. More than twenty genera of the Macroalgae fossils have been recorded including Brown Algae, Red Algae, Green Algae and Corallina Algae, especially the report on the Corallina Algae *Paramphiroa sinensis* Yang in early Middle Cambrian Kaili Biota is of great significance, its known occurrence in Cretaceous period can be traced back to the early Middle Cambrian time[22].

To date, the Kaili Biota contains representatives of 11 phyla, namely Porifera (Spongia), Brachiopoda, Cnidaria, Priapulida (Worms), Lophophorata (Medusiform fossils), Lobopodian, Mollusca, Arthropoda, Echinodermata, Algae and Acritarchs, including a total of over 130 genera, of which more than 100 genera are animals and the Kaili Biota has become one of the three largest Cambrian Burgess Shale-type biotas in the world. The core of the Kaili Biota is made up of non-trilobite Arthropods, Echinoderms and soft-bodied preserved animals.

2 Significance of research on the Kaili Biota

The discovery and present progress in the Kaili Biota provides not only global paleontological information but also very useful evidence for the evolution of the earliest metazoan, biodiversity of marine organisms and variety of marine environments after the "Cambrian Explosion", correct reconstruction of the Cambrian palaeoplate, palaeongeography, and for the research on taphonomy.

2.1 The significance of research on biodiversity of marine organisms and variety of marine environments

The first evidence of the early "Cambrian Explosion" is the world-wide distributed small shelly fossils which occurred in the basal Lower Cambrian[25,26]. The small shelly fauna from the Meishucun stage of Yunnan comprises important representatives of about 10 phyla, including over 60 genera[25~27]. The second evidence is the well-known Chengjiang Biota which preserves soft-bodied fossils. These evidences demonstrate marine organisms[9,10,18,25,26].

The third evidence of the "Cambrian Explosion" is the earliest Middle Cambrian Kaili Biota[25]. In comparison with the Chengjiang Biota, although the collecting of and research on the Kaili Biota are still limited, all groups preseved in the Chengjiang Biota have been found in the Kaili Biota except Vertebrata, and very abundant Echinoderms and higher diversity of Brachiopoda[13] show the number of phyla of marine organisms is higher than that of the Chengjiang Biota. Arthropods, especially trilobites clearly dominate in the Kaili Biota, both in number of specimens and in generic and specific diversity, showing again marine biodiversity. The Kaili Biota occurs in the middle-upper parts of the Kaili Formation and the latest Early Cambrian Taijiang Biota occurs in the lower part of the Kaili Formation. Between the Kaili Biota and the Taijiang Biota there exists an international Lower-Middle Cambrian boundary.

There are 62 trilobite genera (subgenera)1) in the Kaili Formation. Of which 38 genera including 18 families occur in the Taijiang Biota, the other 44 genera (subgenera) including 22 families are found in the Kaili Biota, of which 20 genera (subgenera) including 15 families are across the Lower-Middle Cambrian boundary. In China there are 210 trilobite genera in Lower Cambrian, meanwhile up to 573 genera occurring in Middle and Upper Cambrian including neritic and pelagic forms[28]. The early Cambrian Burgess Shale-type biotas, for example the Chengjiang Biota[9,10,18,25], Big Gully fauna[29,30], and other Burgess Shale-type biotas[29], shallow water environments, but most of the Middle Cambrian Burgess Shale-type biotas including the Kaili Biota[30,31], were formed in a shelf in deeper water environments[19,29,32]. We believe that the Burgess Shale-type biota originated from the shallow water environ-

1) Yuan, J. L. et al. Trilobite fauna of the Kaili Formation from southeastern Guizhou, South China (in press).

ments[32]. Nevertheless, the Middle Cambrian Burgess Shale-type biota, may have inhabited various water environments, for example, Wheeler biota[19] may have inhabited shallow water environments, while the Kaili Biota and Marjum Biota[19] in deeper water environment[30,31]. The reason and mode of taphonomy for the Burgess Shale-type biotas are quite different in various biotas, the animals of the Burgess Shale Biota have been rapidly entombed by soft mud resulting from storms under generally reducing conditions[9,17,32], while the animals of the Kaili Biota have been rapidly buried by the suspension mud in a slightly oxidizing environment[30,31]. The animals of the Wheeler biota may be entombed due to rapid burial in fine, smothering sediment, probably during storm events[19].

2.2 In the early evolution of metazoa, the Kaili Biota forms a connecting link between the preceding and the following

There are more than forty locations where the Burgess Shale-type biota[29] produced, consisting of ten or twelve biotas[33]. The early Cambrian Chengjiang Biota and the early Middle Cambrian Kaili Biota and Burgess Shale Biota are on a large scale of the Burgess Shale-type biota[13]. The Kaili Biota is younger than the Chengjiang Biota, but older than the Burgess Shale Biota in two polymerid trilobite zones[1,9,12,13,34], so that it inherits the past and ushers in the future. Some components of the Kaili Biota, e.g. *Maotianshania*, *Microdictyon*, and anomalocarids, originated from the Chengjiang Biota[13~15,35]; the others of the Burgess Shale-type biota, for example, *Marrella*, *Pollingeria* (Fig.2(d)), *Mollisonia*, *Wiwaxia* (Fig.1(g)) and so on, might derive from the Kaili Biota[1,4,12,13,36] or evolve from the latest Early Cambrian Taijiang Biota[4,36], then extending to the Burgess Shale biota[4,7,9,16,17]. Therefore, the Kaili Biota provides very useful information on the origin, radiation, migration and extinction of the early metazoa of the Cambrian.

The Kaili Biota is located about 600 km east of Kunming or Chengjiang. The components of the two biotas are quite similar, both containing more than twenty congenera. The Kaili Biota might derive from the Chengjiang Biota by migrating from eastern Yunnan to southeastern Guizhou in order to adapt to the new environment. The first stop of the Chengjiang Biota had inhabited Malong of eastern Yunnan, forming the late Early Cambrian Malong Biota[27], which coincides with the Conway Morris' theory that the Burgess Shale-type biota developed from the shallow water environment to deeper water environment[32].

2.3 Research on reconstruction of paleoplate and paleogeography

The report on the Chengjiang Biota was brought to many astonished paleontologists and geologists[38,39]. In 1987, Conway Morris reported of the Lower Cambrian Sirius Passet Biota, and he noticed a certain relation between the South China plate containing the Chengjiang Biota and the Laurentia plate bearing the Burgess Shale Biota and Sirius Passet Biota. He believed that there existed a Pacific channel between the two plates, through which the biotas could easily migrate towards each other[40]. Later on, he suggested that there existed a palaeopacific ocean between the two plates[9]. However, on the paleogeographical map the South China plate is far from the Laurentia. Between the South China plate and Laurentia plate there may exist a Siberian plate, an Indian plate and an Australian plate[17,41]. In South China and Laurentia most of the Burgess Shale-type biotas occurred in Lower and Middle Cambrian. Although these biotas differ from each other, they have many common genera, families and phyla, very similar models of taphonomy. Only trilobites of Corynexochidae clearly dominate in various biotas of both regions, for example, *Oryctocephalus*, *Microryctocara*, *Bonnia*, *Oryctocephalites*, *Oryctocephalina*, *Arthricocephalus*, *Goldfieldia*, *Kootenia*, *Olenoides*, *Dorypyge* and so on, and similar genera in Ptychopariida are quite familiar. This cannot be attributed only to the fact that the two regions are at the same latitude. Actually the two plates are not so far apart as is believed by some geologists.

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