Hydrozoan-like Ediacaran fossils from South China
华南伊迪卡拉纪类水母化石新发现

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Abstract: An abundant and diversified assemblage of benthic fossils from the Ediacaran Doushantuo black shales in the Wenghui section of Guizhou Province contains two discoidal carbonaceous forms, *Kullingia* rotadiscopsis sp. nov. and Eoaequorea xingi gen. & sp. nov. The fossils have well-preserved concentric rings and radiating lines, and resemble many circular casts and moulds in Ediacaran clastic and carbonate rocks in the world, such as *Aspidella*, *Ediacaria*, *Cyclomedusa*, *Eoporpita*, *Ovatoscutum*, *Spriggia* and *Kullingia*. The Doushantuo carbonaceous macrofossils help us to inquire into the current functional identifications of circular disks as the holdfasts of unknown organism or scratch circles. Although there is not sufficient correspondence in morphology to warrant reinterpreting all previously described *Kullingia* and *Aspidella* form-genus-type structures, these carbonaceous compressions are prone to be the ancestor of pelagic jellyfish-like organisms with medusoid hydrozoan affinity.
Key words: Ediacara; discoidal macrofossils; South China; medusoid organisms

摘要:华南黔东北地区伊迪卡拉系陡山沱组黑色页岩中产出丰富多样的海相底栖宏体化石组合,其中包含2个新属种*Kullingia rotadiscopsis* sp. nov. 和 *Eoaequorea xingi gen.* & sp. nov.。新类别具有保存清晰的碳质同心环纹和辐射状纹饰,形态上相似于国外广泛分布在碎屑岩和碳酸盐岩中的伊迪卡拉纪典型的圆盘状化石,例如*Aspidella, Ediacaria, Cyclomedusa, Eoporpita, Ovatoscutum, Spriggia, Kullingia*等。上述化石在国外几乎都保存为印痕,近年来多被解释为不明亲缘底栖生物的圆形固着痕迹或抓痕、圆环状扫痕等,华南陡山沱组碳质压膜保存的圆盘状宏体化石显然不支持该解释。目前,还没有充分的证据表明华南新发现的碳膜化石与国外形态类似的印痕化石如*Kullingia*和*Aspidella*具有相同的亲缘关系,但支持将华南化石归属为可能最早的浮游型水螅水母。
关键词:伊迪卡拉纪;圆盘状宏体化石;华南;似水母生物
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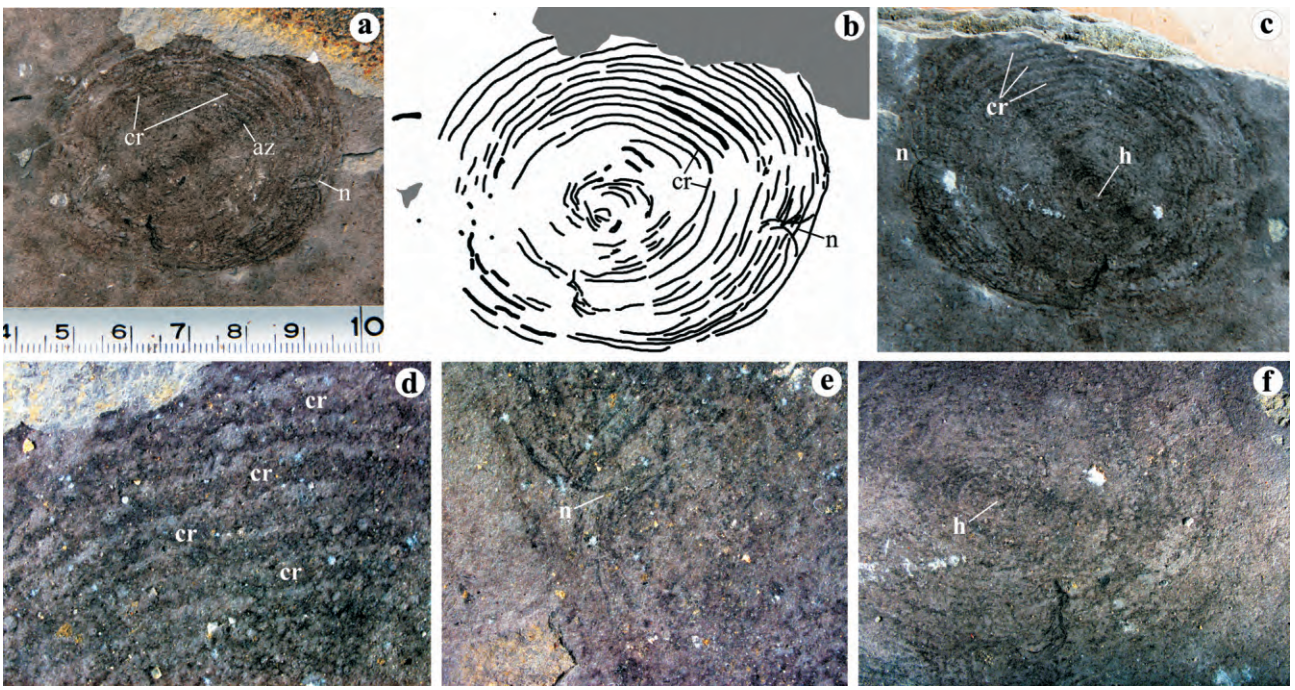
1 Introduction

Discoidal carbonaceous compressions are comparatively rare in the black shales of the Ediacaran/Sinian Doushantuo Formation, South China, with the exception of the mass-buried *Beltanelliformis*[1] reported previously[2]. They are, however, abundant in many Ediacara deposits in Newfoundland, England, Australia, Canada, Russia, India and other European areas-discoidal imprint macrofossils occur rather frequently as moulds and casts in coarse siliclastic and carbonate sediments. The wide distribution and diversity of these forms has led to different views and interpretations of their phylogeny and ecology[3-7]. Their concentric and radial grooves and ridges originally resulted in allocation to planktonic medusoid cnidarians[8-9], but later many palaeontologists[3,10-16] interpreted them as attachment structures of benthic frondose organisms because of the preservation of a holdfast-stalk continuum or some discoidal fossils with typical Ediacaran fronds, such as *Charniodiscus* with Charnia. They have even been interpreted as marine fungi or microbial mats[17-18], as well as trace fossils[19-20]. Disk-like concentric grooves and ridges have rather been explained as tool marks or scratch circles formed by current rotation of benthic pennatulids or tube-forming animals (e.g., sabelliditids)[21].

This paper reports carbonaceous compressions with well-preserved concentric and radial structures (Plate Ⅰ, Ⅱ) from the Late Ediacaran Doushantuo shales in Southern China. The compressions show close resemblance to the discoidal Ediacaran imprint fossils. The fossils are interpreted at least in part to possibly represent free-swimming soft-bodied marine animals with discoidal or medusoidal outlines. The identical fossiliferous beds in the Doushantuo Formation also bear abundant tentacle-like carbonaceous compressions (Fig.1- a,b), which implies the previous proposals of medusoid affinity of the Ediacaran discoidal macrofossils.

Plate Ⅰ



a. holotype of *Kullingia rotadiscopsis*, M; b. sketching image of a; c. counterpart of a, ZMNH M10072 ; d~f. close up of a and c, noted the perfect concentric ribbons (d) in the upper part of a, the uncertain neckline structures (e) in the right part of a and the central part of c (f). The minimum scale is 1mm.

cr—carbonaceous ring; az—axis-like zone; n—notch; h—hollow

2 Results

2.1 Systematic palaeontology

Phylum Cnidaria

Class Hydrozoa

Order and **Family** ? uncertain

Genus *Kullingia* Glaessner, 1974

New species *Kullingia rotadiscopsis* sp. nov.

(Plate Ⅰ-a~f)

Etymology: The specific name derives from rota, wheel, *discus* disk, and *-opsis*, like. The name alludes directly to the similarity with the Cambrian Chengjiang genus *Rotadiscus* Sun and Hou[22], 1987.

Material: One nearly complete disc in part and counterpart. Specimen number: ZMNH M10072 (Zhejiang Museum of Natural History, Hangzhou, China).

Holotype Plate I-a, c.

Horizon and locality: Ediacaran, Doushantuo Formation, layer 13; Wenghui, Jiangkou, Guizhou, China.

Diagnostic: Disc large, radially symmetric, without radial canals or striations, and with concentric carbonaceous ribbon-like rings.

Description: Circular to ovoid in shape, about 5.3 cm in maximum diameter; up to 25 concentric carbonaceous rings from centre to fringe; showing decentralized slightly on outer part and ca.1.7-2.0 mm between each circle(Plate Ⅰ-d), whereas on the central part relatively dense(Plate Ⅰ-f). Rounded shape interrupted by a small uncertain neckline-like notch on one outer side showing about 3 ribbons sinuous and closed (Plate Ⅰ-a,b,e). A black, not readily apparent axis-like zone about 2 mm wide extends through the center on the surface of the disc possibly due to every concentric ribbons thicken.

Phylum Cnidaria

Class Hydrozoa

Order and family uncertain

New genus and species *Eoaequorea xingi* gen. and sp. nov.

(Plate Ⅱ-a~e)

Etymology: The generic name derives from *eos*, dawn, and *Aequorea*, a modern genus of hydrozoan medusae. The specific name is dedicated to Professor Yusheng Xing, Feng Tang's Ph.D. teacher in CAGS (Chinese Academy of Geological Sciences, Beijing).

Material: Two separate specimens in part and counterpart, one nearly complete disc and the other with the central area abraded away. Specimen numbers: ZMNH M10073, M10074.

Type species: *Eoaequorea xingi* sp. nov.

Generic diagnosis: Disc flat, circular to sub-circular, with numerous straight, simple and unbranched radial striations from center to fringe, distinct concentric rings and finer annular lines.

Holotype Plate Ⅱ- b, c; Number: **ZMNH M10074**.

Horizon and locality: Ediacaran, Doushantuo Formation, layer 13; Wenghui, Jiangkou, Guizhou, China.

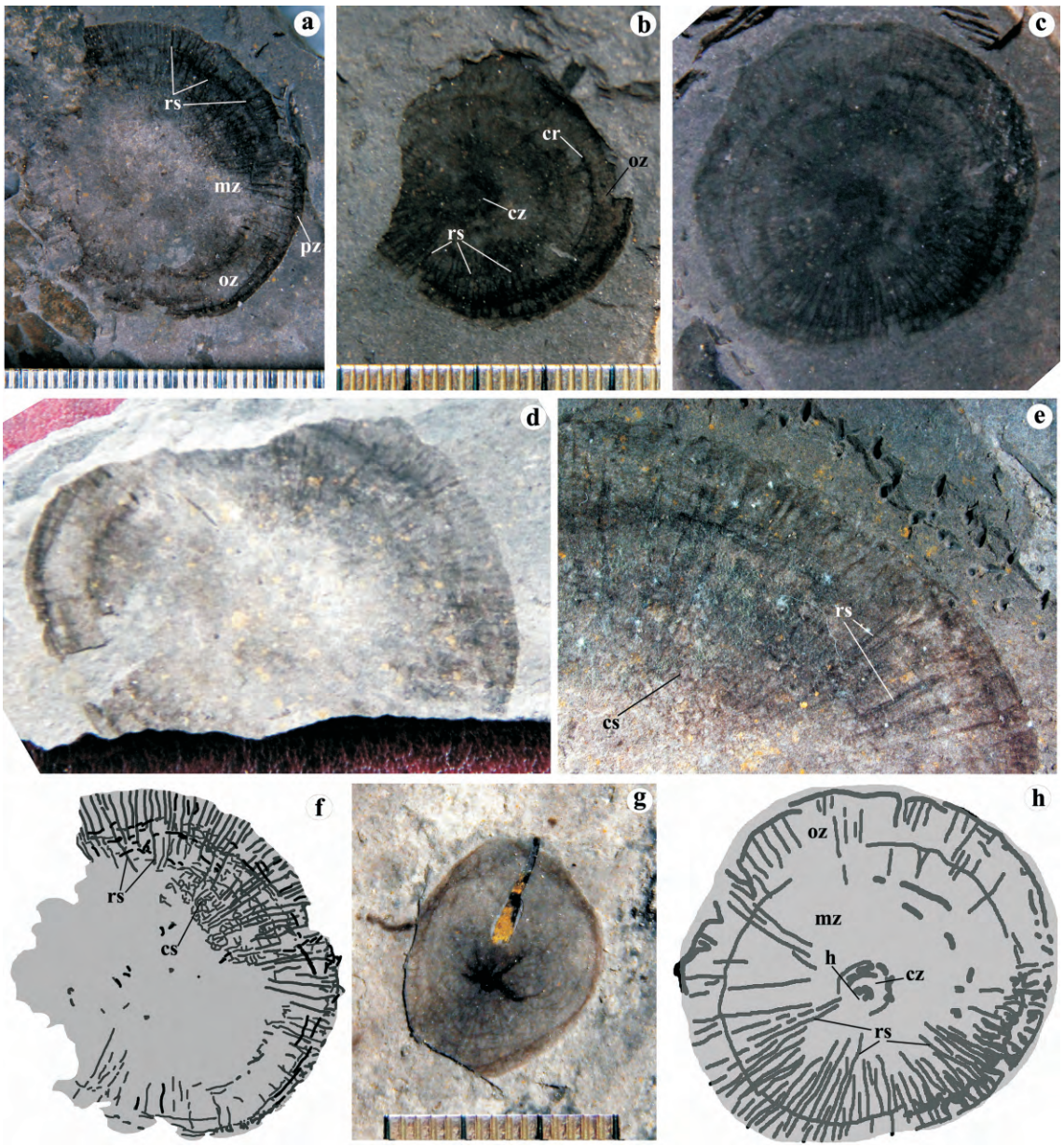
Description: Disc flat, circular to sub- circular, about 2-3 cm in diameter; carbonaceous radial striations, numerous, straight and unbranched, from center to fringe, spaced at most 1.3 mm in the outmost part but often much closer together in peripheral zone (Plate Ⅱ-a,b); 3-6 carbonaceous concentric ringscontained respectively in three zones(Plate Ⅱ- b,h) or wrinkles, irregular and incomplete in the outer part, darker on peripheral margins; inconspicuous and fine annular lines in the inner half showing partially cobweb-like structure(Plate Ⅱ-a,e,f) together with circular and radial striations; black carbonaceous ring about 1-1.6 mm wide in center of disc with a 1.2 mm hollow(Plate Ⅱ-h) lacking carbonaceous film.

2.2 Comparison with other taxa

(1) Kullingia rotadiscopsis

Kullingia is a circular imprint disk with sets of concentric rings from Late Ediacaran to Early Cambrian of South Australia, Newfoundland, Ukraine and northern Sweden. It was initially interpreted as a chondrophorine hydrozoan[23], but is currently thought to be a scratch circle, possibly of an anchored, tubular organism[21]. Regular and dense concentric lines, and

Plate Ⅱ



a. paratype of *Eoaequorea Xingi*, ZMNH M10073, noted the black central ring with some abrasion; b. field photograph of c; c. holotype of *Eoaequorea Xingi*, ZMNH M10074; d. counterpart of a; e. right-upper close up of a; f,h. sketching images of a and c; g. holdfast of macroscopic algae fossils, ZMNH M10075. The minimum scale is 1mm. rs—radial striation; oz—outer zone; mz—middle zone; pz—peripheral zone; cr—carbonaceous ring; cz—central zone; h—hollow; cs—cobweb-like structure

lack of radial ones, can be seen on the rounded carbonaceous film described here as *K. rotadiscopsis*. It is similar to *Kullingia* with the diagnostic concentric rings and lines, but different from *Cyclomedusa* (*C. delicata*), which has a conical central part, larger size and broader concentric ridges[3], as well as *Kaisalia*, which apparently has three concentric zones[13,24]. *Ovatoscutum* in the Rawnsley Quartzite, Australia, is another Ediacaran impression of a slightly irregular rounded disc with a central suture-like pseudo-axis interrupting its rounded shape and most of the concentric ridges, connecting to a triangular notch[9,25]. Although *K.*

rotadiscopis also has a V-shaped notch-like structure and an axis-like zone throughout the entire disc, it is apparent different from *Ovatoscutum* as above description(Plate Ⅰ-a,c,e).

Rotadiscus, perhaps a synonym of *Kullingia*, is another possible chondrophore genus from the early Cambrian Chengjiang biota and middle Cambrian Kaili biota in South China[21,26]. However, the fine radial lines on *Rotadiscus* are regarded as compression features of the ventral surface upward of a jellyfish bell, and the carbonaceous concentric rings are much narrower than those analogues of the specimen at Wenghui. *Spriggia*, probably another name of Ediacaran *Aspidella* in South Australia[13], is also another flat disc similar to *Kullingia* with dense concentric ridges and grooves, differing only in possession of fine radial lines extending from specimen margin[3,6].

Although some paleontologists argue that *Kullingia* are not the fossil impressions of hydrozoans or other animals, instead are scratch circles—a series of concentric grooves cut in sand or mud by the action of current- perturbed (current- swivelled) objects anchored to the benthos at one end[21], the *Kullingia*-type carbonaceous compression at Wenghui calls in question the popular hypothesis. Scratch marks of an anchored organism would leave no organic compression on the sea bottom. The burial and preservation in *situ* of the macroalgae fossils with intact holdfasts[27] (Fig.1-c,d) also argue against a high-energic environment to yield remarkable wave and current in this site, instead few planktons including the pelagic cnidarian *Kullingia* and ctenophoran *Eoandromeda*[28] occasionally to be delivered here.

In addition, two modern free-floating hydrozoans that live on the surface of the open ocean, *Porpita* and *Velella* both consist of two main parts: the float and the hydroid colony[29]. The hard float is round, about one inch wide or smaller, almost flat, and resembles the Wenghui Kullingia with series of regular concentric rings (but Porpita has radiating ridges). The neckline-like notch (Plate Ⅰ-e) of the *Kullingia* is very similar to the fold of limbus of *Porpita porpita*[29].

(2) *Eoaequorea xing*

This species is similar to other Ediacaran forms, such as *Aspidella*, *Ediacaria*, *Eoporpita* and *Cyclomedusa*, preserved in convex hyporelief at the bedding plane. Most of them have concentric rings and radial grooves, but remain different from the Wenghui specimens. The widely distributed *Aspidella* in most cases has a round invaginated disc with radial ribs extending from center to margin[3,6]. *Ediacaria*, numerous in South Australia and White Sea, is preserved as flat to low-relief imprints of a three-zonal attachment surface separated by a deep concentric groove, and has irregular and sparse radial grooves mainly confined to outer zone[13,25]. *Eoporpita* is common in Russia as rounded or ovate discs with an apparently raised central disc or cone surrounded by well- proportioned concentric rings, fine radiating striations in a generally smooth and slender outer zone[13,29]. Although *Cyclomedusa radiata* is most similar in shape to the Wenghui *Eoaequorea xingi*, the concentrically structured central dome without radial grooves is quite unlike that of the latter one[6,13].

Living Aequorea is a kind of bioluminescent pelagic hydromedusa with radial canals regularly arranged, concentric chitinous septa and organic-rich velums, calcareous bioluminescent albumen, strong muscles and wandering crimp-hair-like tentacles[30]. *Aequorea*-like organisms after being buried, dehydrated, compressed and carbonization may possibly form fossil compressions such as seen at Wenghui. In addition, if their slender, easily- detached tentacles were floated into the euphotic zone and well-preserved alongside with the benthic algae megafossils, they would be much similar to the coiled, thread-like carbonaceous specimens excavated from the Doushantuo shales in the Wenghui section (Fig.1-a,b), in spite of lacking direct association between the thread- like features and the discoidal fossils. Hence, the new findings are named as *Eoaequorea*.

3 Discussions and Implications

Both of the above-described carbonaceous com-

pressions occurred in soft substrate such as silty shales, have exceptionally preserved structures resembling the concentric and radial grooves and ridges in Ediacaran impressions. This discovery implies that the concentric and radial grooves/ribbons in Ediacaran impressions/compressions might partly be body fossils of some ancient soft-bodied organisms, which contain dense or strong organic-rich tissue (e.g. rigid radial canal and chitinous septa or float in some hydromedusae) resisting physical degradation and chemical decomposition during the taphonomic stage. However, a current interpretation implies that most discoidal Ediacaran fossils are not stranded jellyfishes, but buried holdfasts of frond-like organisms or clusters of sea anemones living between fair-weather and storm wave base[31-32], and many concentrically ornamented discs of Ediacarian and Cambrian age are gas escape marks, load structures, or biological tool marks, formed by tethered tubular fossils[31]. Although several exceptionally preserved specimens from South Australia and Newfoundland demonstrate the integrated association of holdfast and frond, the discoidal compressions, especially regular in South China would be interpreted as multicellular Hydrozoan-like eukaryotes, rather than the attachment disc in the above-mentioned prevalent suggestions, let alone the microbial colonies and the scratch marks by uncertain benthic organisms. All previously described "discoidal" structures will also be awaiting for more deliberation.

The South-China analogs in morphology especially as carbonaceous compressions contrast of Ediacara-type discoidal impressions preserved as casts and moulds elsewhere worldwide, should be adverse evidence for the functional interpretations of the anchoring and scratching structures of sessile frondose or tubular Ediacara organisms, and the phylogenetic interpretation of microbial colonies or marine fungi; but might be propitious macrofossil record to revive the traditional medusozoan or hydrozoan hypothesis on the deep evolutionary relationships of animal, at least to present an alternative reinterpretion. The Doushantuo compressions make it clear that these soft-bodied organisms had thin, organic external wall and stiff internal trellis (i.e. concentric or radial structures) resisting gradual corrosion in shale and mudstone; whereas the Ediacaran casts and moulds in sandstone and siltstone require that the original organisms had sufficiently mechanical integrity to retain their three-dimensional shape when inundated by sand and quickly followed the fossiliferous diagenesis[2]. The carbonaceous remains in South China clarify some of the similar casts and moulds in morphology probably yet to be body forms of buried jellyfishes, not to be holdfasts or scratch circles of the frond-like benthic organisms.

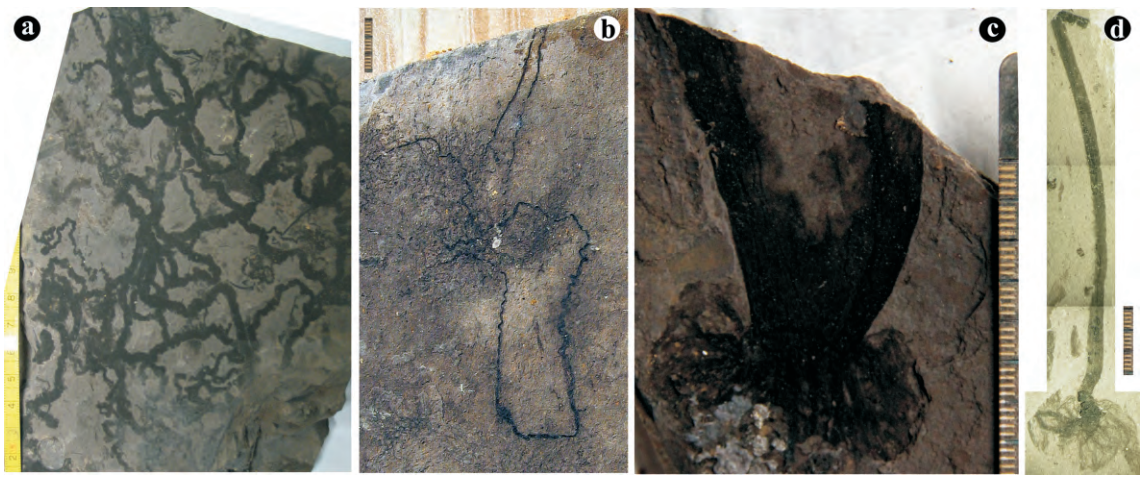


Fig.1 Meandering tentacle-like carbonaceous compressions(a, b), ZMNH M10076(a), M10077(b), and almost complete rhizoid holdfasts of two macroalgae fossils(c, d) ZMNH M10078(c), M10079(d). The minimum scale is 1mm.

The rounded holdfasts of multicellular algae fossils in the equivalent horizons almost have indistinct, disorder or fragmentary carbonaceous ornamented rhizoids (Plate Ⅱ－g, Fig.1－c,d), in reversely, the new Wenghui discs are characterized by regular, rigid and legible carbonaceous concentric ribbons and radial striations. This indicates that they at least are not macroalgal holdfasts and relatively had a recalcitrant organic integument or internal trellis. The Doushantuo silty shales of somewhat deoxidized, lower－energy sedi-

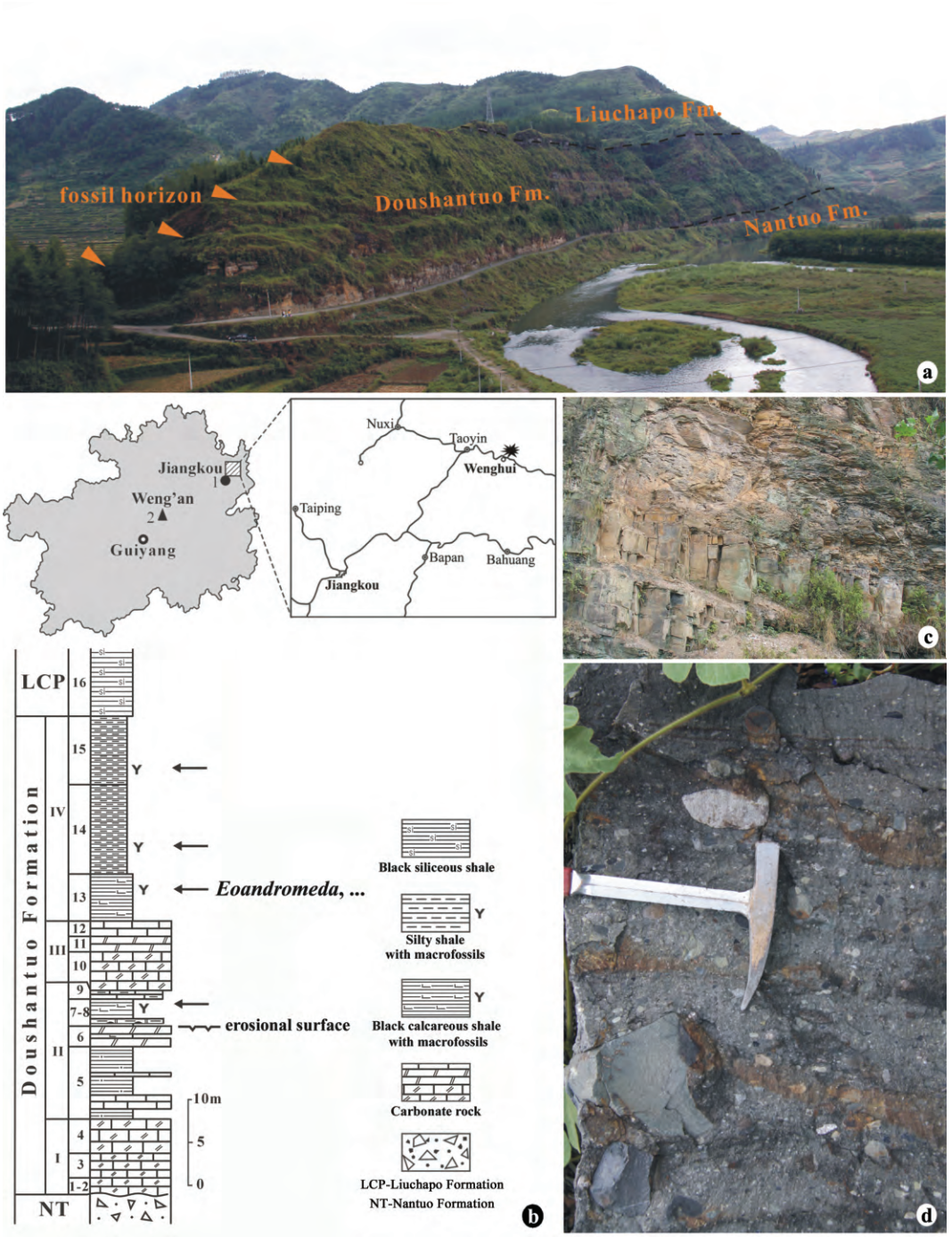


Fig. 2　Field section at Wenghui village, Jiangkou, Guizhou, South China (a), location and column of Wenghui section (b), photograph showing the horizon of the Eoandromeda and discoidal macrofossils (c), and the diamictites of Nantuo Formation(d)

mentary environment provide more possibility to assign the discs to the easier- preserved hydromedusa with the stiff radial canals and annular chitin floating chambers, rather than other cnidarian affinities, let alone the functional classifications (holdfasts or scratch circles).

4 Methods

We recently discovered a new Ediacaran lagerstätten preserved as carbonaceous compression macrofossils in the Doushantuo black shales covering the glacial diamictite of Nantuo Formation at Wenghui, Guizhou Province, South China[27-28] (Fig.2-a~d), which contains a diverse benthonic algal biota, exceptionally occurring two new discoidal macrofossils above- mentioned, *Kullingia rotadiscopsis* and *Eoaequorea xingi* sharing the features of concentric rings and radial lines with the impressions (casts and moulds) reported previously in the Ediacara assemblages worldwide. Herein they are firstly confirmed to be some diploblastic- grade adult animals, instead holdfasts or scratch circles of unknown soft-bodied organisms. Supplementary information show the locality and rock unit (stratigraphic setting) (Fig.2- b) of these carbonaceous compressions and almost complete holdfasts of macrofossil algae from the same quarry at Wenghui[27](Fig.1).

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