



<https://doi.org/10.11646/palaeoentomology.1.1.11>

<http://zoobank.org/urn:lsid:zoobank.org:pub:4DED29EB-5517-473D-A11A-90BCF2B1B787>

## Various amberground marine animals on Burmese amber with discussions on its age

YINGYAN MAO<sup>1,2,3</sup>, KUN LIANG<sup>1,3</sup>, YITONG SU<sup>2,4</sup>, JIANGUO LI<sup>3,5</sup>, XIN RAO<sup>3,5</sup>, HUA ZHANG<sup>3,4</sup>, FANGYUAN XIA<sup>6</sup>, YANZHE FU<sup>4,7</sup>, CHENYANG CAI<sup>1,3,8</sup> & DIYING HUANG<sup>3,4,\*</sup>

<sup>1</sup> CAS Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

<sup>2</sup> University of Chinese Academy of Science, Beijing 100049, China.

<sup>3</sup> Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China.

<sup>4</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

<sup>5</sup> Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

<sup>6</sup> Lingpoge Amber Museum, Shanghai, China

<sup>7</sup> University of Science and Technology of China, Hefei 230026, China.

<sup>8</sup> School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, UK.

\* Corresponding author. E-mail: [dyhuang@nigpas.ac.cn](mailto:dyhuang@nigpas.ac.cn)

### Abstract

Burmese amber represents the world's most diverse biota in the Mesozoic. Previous studies have focused on the biodiversity of its inclusions, as well as pholadid borings. Here we report a variety of marine animals symbiotic with or adhere to Burmese amber or the amber deposits, including crinoid columns, corals and oysters. We propose that there is no distinct evidence indicating the secondary transportation of Burmese amber over long distances. The ancient sedimentary environment was likely located in the coastal area. The hardening time of the resin was not long after secretion. The resin has been mixed with fragments of marine organisms in the ancient sediments, and has been deposited for a long time. The zircon age in the sediments surrounding amber approximately represents the age of Burmese amber, but due to limits of the method, the current zircon U-Pb SIMS age may be younger. Therefore, as far as the situation is concerned, the age of Burmese amber may be close to the boundary between the Albian and Cenomanian, or even late Albian. We suggest that it is plausible to generally refer to the age of Burmese amber as mid-Cretaceous, and a precise age requires further biostratigraphic and chronological studies.

**Keyword:** Burmese amber, mid-Cretaceous, marine, iso-crinid crinoids

### Introduction

Burmese amber has yielded numerous bioinclusions, such as diverse insects (including unpublished Mantophasmatodea, only two parasitic orders, Phthiraptera and Siphonaptera, not documented), all extant orders of

arachnids (Selden & Ren, 2017), crustaceans, polypedes, velvet worms, gastropods, multiple vertebrates, plants, fungi, and bacteria. Ross (2018) published a list of bioinclusions in Burmese amber, comprises 38 classes (or similar rank), 102 orders (or similar rank), 525 families, 777 genera and 1013 species, excluding those preserved in the upper Late Cretaceous Tilin amber from Myanmar or copal. Most of the inclusions are arthropods, including 714 genera and 941 species placed in 65 orders (480 families).

The age of Burmese amber has been controversial over the past century. Noetling (1892, 1893) first conducted a geological survey of the amber-yielding area in northern Myanmar. Based on the similarity between the lithology of the producing area and the Cenozoic strata, the age of Burmese amber and the relevant strata was suggested as Miocene. According to the insects preserved in Burmese amber, Cockerell (1917) indicated that its age of the captured biota was probably older than that of the surrounding rocks, probably Cretaceous, but this hypothesis was not widely accepted. Stuart (1923) found Cenozoic foraminiferans, *Nummulites biarritzensis*, from upper strata overlying the amber-producing layers. He believed that this layer was of an Eocene age, similar to the age of Burmese amber. Chhibber (1934) also reported *Nummulites* foraminifera near the amber mine, supporting Stuart's (1923) view; however, in actually, the association between the production horizon of these foraminiferans and the amber-producing layers remains elusive (Grimaldi *et al.*, 2002; Cruckshank & Ko, 2003). Sahni & Sastri (1957) reported another foraminiferan, *Orbitolina hukawngensis*, from the amber mine and suggested an

Albian to Cenomanian age. However, they believed that the foraminiferans came from older strata, and the age of Burmese amber was still considered as Eocene. In the 1990s, palaeontologists discovered many families and subfamilies of insects that comparable to those from the Cretaceous or older deposits (Rasnitsyn, 1996), which rekindled the idea that the Burmese amber is probably Late Cretaceous in age. Zherikhin & Ross (2000) reported the discovery of Cretaceous gravel-containing ammonite in the amber mine area and the transported foraminiferans-containing clastic. Together with the erosion of the amber surface, which indicates post-transportation, the insect assemblage from the Burmese amber specified a Cretaceous age. Davies E.H. reported the flagellates, algae, ferns and moss fossils in Burmese amber and its surrounding rocks, and palynological studies showed its similarities to those from the Albian of southern Songhua River in northeastern China at 2001 (Yu *et al.*, 1983), but the work was not published (Cruckshank & Ko, 2003). Grimaldi *et al.* (2002) compared the Burmese amber fauna with other ambers, arguing that its age was between those of the Spanish amber and the New Jersey amber, and indicated a probable Turonian-Cenomanian age of this material (90–100 Ma). Cruickshank & Ko (2003) conducted a field investigation of the mining area in Neije Bum, and found the Cretaceous *in-situ* buried ammonite *Mortoniceras* in the amber-producing layers, indicating a middle to late Albian age (Wright *et al.*, 1996). The zircon U-Pb dating of volcanic siltstones in the amber-producing layer indicated an age of  $98.79 \pm 0.62$  Ma (Shi *et al.*, 2012). Based on the bivalve borings on the surface of Burmese amber, Ross (2015) suggested that the Burmese amber was buried after a period of consolidation. The age of Burmese amber should be earlier than the surrounding rock age and combined with the insect appearance of Burmese amber. The age is more likely to be Albian. However, Smith & Ross (2017) found boring bivalves completely encapsulated in Burmese amber, and it is believed that some amber had not yet solidified when the bivalves were captured. The burial time of the Burmese amber is close to the age of the amber inclusions, which now regarded as the earliest Cenomanian.

## Material and methods

All the studied specimens were derived from amber deposits in the Hukawng Valley of Kachin Province, northern Myanmar. The mining is done at a hill named Noiye Bum, near Tanai. Grimaldi *et al.* (2002) provided an overview of the amber deposit and its geological settings. U-Pb zircon dating by Shi *et al.* (2012) constrained the Burmese amber to a maximum age of  $98.79 \pm 0.62$  Ma (equivalent to the Late Cretaceous, earliest Cenomanian).

Photographs were taken using a Zeiss Discovery V20 stereo microscope with a digital camera attached. Extended depth of field images were then digitally compiled using Helicon Focus 3.10 software, and arranged in Adobe Photoshop CS5. The line drawings were prepared by CorelDraw X7. Terminologies of a typical isocrinid symplectical articular facet (Fig. 1a), ligaments between nodal and internodals (Fig. 1b), and different types of articulation between columnals (Fig. 1c) are shown in Figure 1. All material studied in the present paper is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS) except the amber with oysters, which is housed in Shanghai Lingpoge Amber Museum.

## Systematic palaeontology

Phylum Echinodermata Bruguière, 1791 [*ex* Klein, 1734]  
 Class Crinoidea Miller, 1821  
 Subclass Articulata von Zittel, 1879  
 Order Isocrinida Sieverts-Doreck, 1952  
 Suborder Isocrinina Sieverts-Doreck, 1952  
 Family Isocrinidae Gislén, 1924  
 Genus *Isocrinus* von Meyer *in* L. Agassiz, 1836

**Type species.** *Isocrinites pendulus* von Meyer, 1836.

**Diagnosis.** For column: column rounded, sub-pentagonal to pentalobate, proximal columnals pentalobate, alternating in size, and with radial pores in sutures. Internodes generally rather short, about 5 to 10 internodals. Nodals with 5 large, elliptical cirrus sockets, almost as high as nodal, facing outward. Articulation of columnals with elliptical petals and a gradual continuation of marginal and adradial crenulae reaching greatest length in radial marginal areas, there forming an oblique angle with radial axis, and diminishing toward the interradian point and toward center of articular face (after Rasmussen, 1978).

### *Isocrinus* sp.

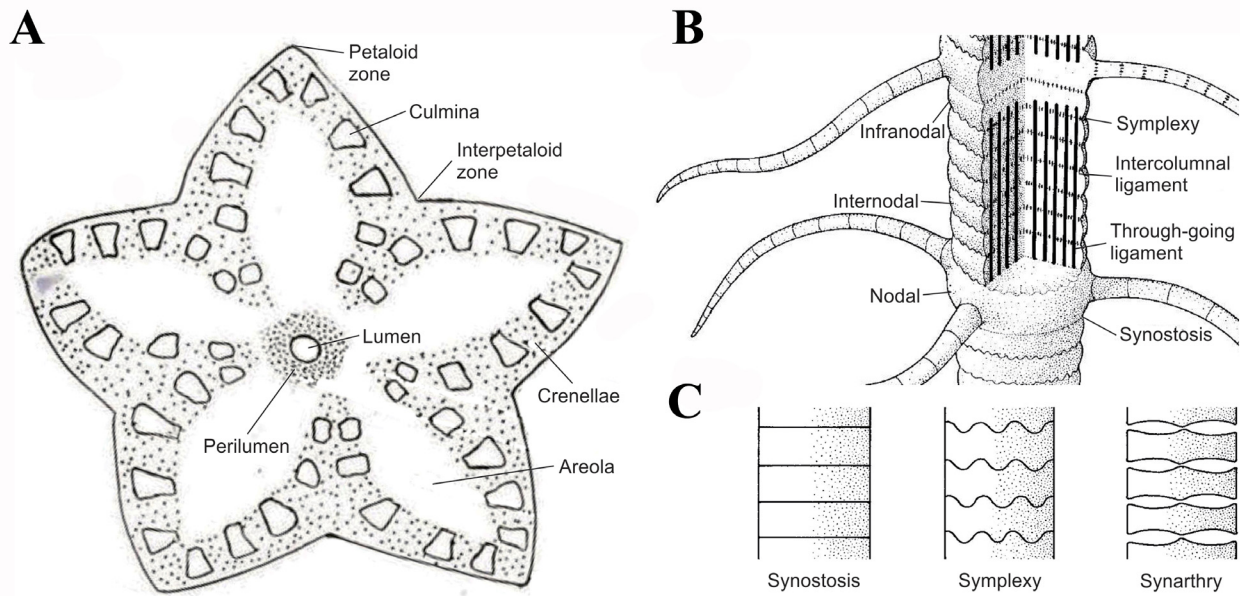
Figs. 2–4

2001 *Isocrinus*; Donovan, p. 186.

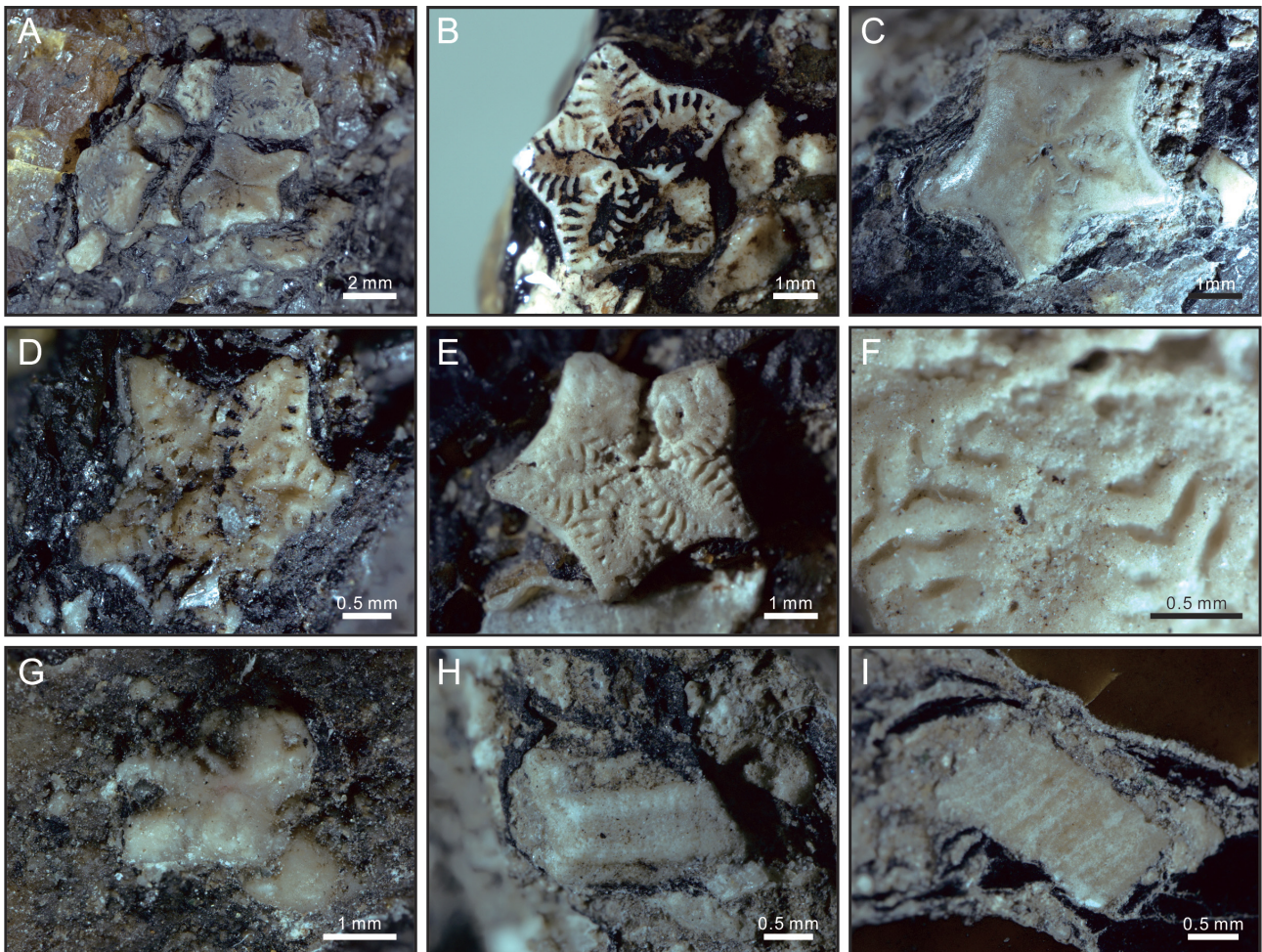
2001 *Isocrinus* sp.; Donovan & Veltkamp, p. 725.

2005 *Isocrinus* sp.; Donovan *et al.*, p. 98.

**Material.** 12 amber pieces illustrated here, NIGP169604–169615. More than 30 single columnals including nodals and internodals; other fragments such as pluricolumnals, dimension, and possible brachial.



**FIGURE 1.** A, Terminologies of a typical isocrinid symplectical articular facet. B, Ligaments between nodal and internodals. C, Different types of articulation between columnals. (Adapted from Kalita, 2015 and Hess *et al.*, 2003)



**FIGURE 2.** Morphology of *Isocrinus* sp. A-E, Single internodals or nodals (NIGP169604–169608). F, Enlargement of E, single petal with alternate culmina and crenellae, areola with pores. G, A possible brachial. H-I, Pluricolumnal fragment.

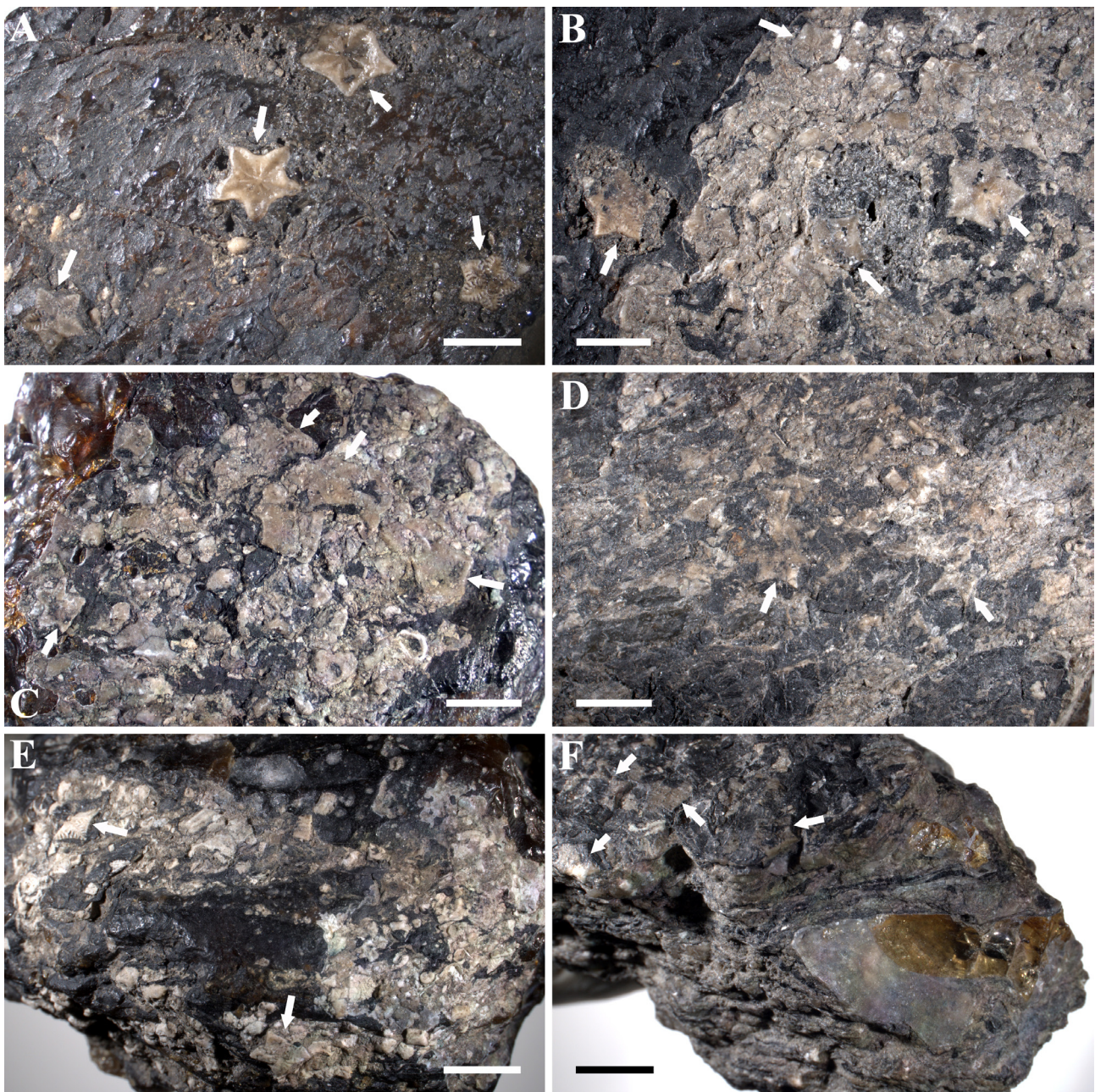
**Locality and Horizon.** Hukawng Valley, Kachin Province, Myanmar; mid-Cretaceous.

**Description.** Columns pentagonal or slightly stellate in section. Symplectial articular columnal facet petaloid, with narrow, lanceolate areolae surrounded by regularly arranged culmina and crenellae, petaloid edge distinctly pointed. Adradial crenulae of adjacent petals confluent, with number of crenulae per petal much high (15 to 17). Crenulae and culmina dense and long, most straight with little bit curve, vary in length between adradial and marginal areas, greatest length in radial marginal areas, diminishing towards marginal and lumen areas. Central petal areas surrounded by larger ligamental pores along the areolae (Fig. 2 F). Centre of columnals pierced

by small and rounded lumen, surrounded by smooth perilumen area (Fig. 2 C). Internodal plates ca. 0.8 mm in height. One cirri composed with six ossicles (Fig. 2 D). One possible divided brachial with faint pinnule.

Two pluricolumnal fragment, one composed of seven columnals (Fig. 2 H), while the other composed of more than ten columnals (Fig. 2 I). Suture forms crenulate line due to symplectial articulation (Fig. 2 H, I). Diameter of nodals and internodals similar. Articulation between nodal and infranodal synostosal, rarely weakly cryptosymplectial, with weak crenulae, and areolae may somewhat sunken (Fig. 2 A, C).

**Remarks.** The isocrinid crinoids first appeared in the Triassic of SW China, Europe, Afghanistan, Siberia



**FIGURE 3.** General habitus of amber pieces with several individuals (with white arrows) of *Isocrinus* sp. (NIGP169609–169614). A–E, Columns of *Isocrinus* sp. on amber surface with other fragments of marine animals. F, White arrow indicating the columns of *Isocrinus* sp. in bedding plane of sediment and ambers pieces in longitudinal section. (Scale bars represent 5 mm.)

and Peru (Mu & Wu, 1974; Hagdorn, 1982, 1983, 1986, 1996, 1999; Simms, 1989, 1994, 1999; Baumiller & Hagdorn, 1995; Twitchett & Oji, 2005; Hagdorn, 2011; Stiller, 2011), and radiated rapidly worldwide in Jurassic, Cretaceous and Cenozoic deposits (Oji, 1985; Hess, 1972; Milner, 1989; Eagle & Hikuroa, 2003; Salamon, 2008; Hunter & Zonneveld, 2008; Hunter & Underwood, 2009; Hunter *et al.*, 2011; Kalita, 2015). Isocrinids have since become the dominant stalked crinoid group in modern oceans (Hunter & Underwood, 2009).

Isocrinid remains are typically preserved mostly as columns (Hunter & Zonneveld, 2008; Hunter & Clark, 2009) and pluricolumnal. The columnals have a distinctive stellate arrangement of articular facets, and the crenarium has radial infoldings that greatly increase its effective length compared with that of circular columnals (Hess *et al.*, 2003).

Many isocrinids have been assigned generic names on the basis of stem elements (Rasmussen, 1961), mainly because of the lack of a diagnostic calyx or cup elements in recovered material (Milner, 1989). Considering the wide range of morphological variation in columnals of isocrinids, some may represent synonyms. Rasmussen (1978) pointed out that “Fossil columnals of Isocrinidae, with articulation similar to *Isocrinus* are generally

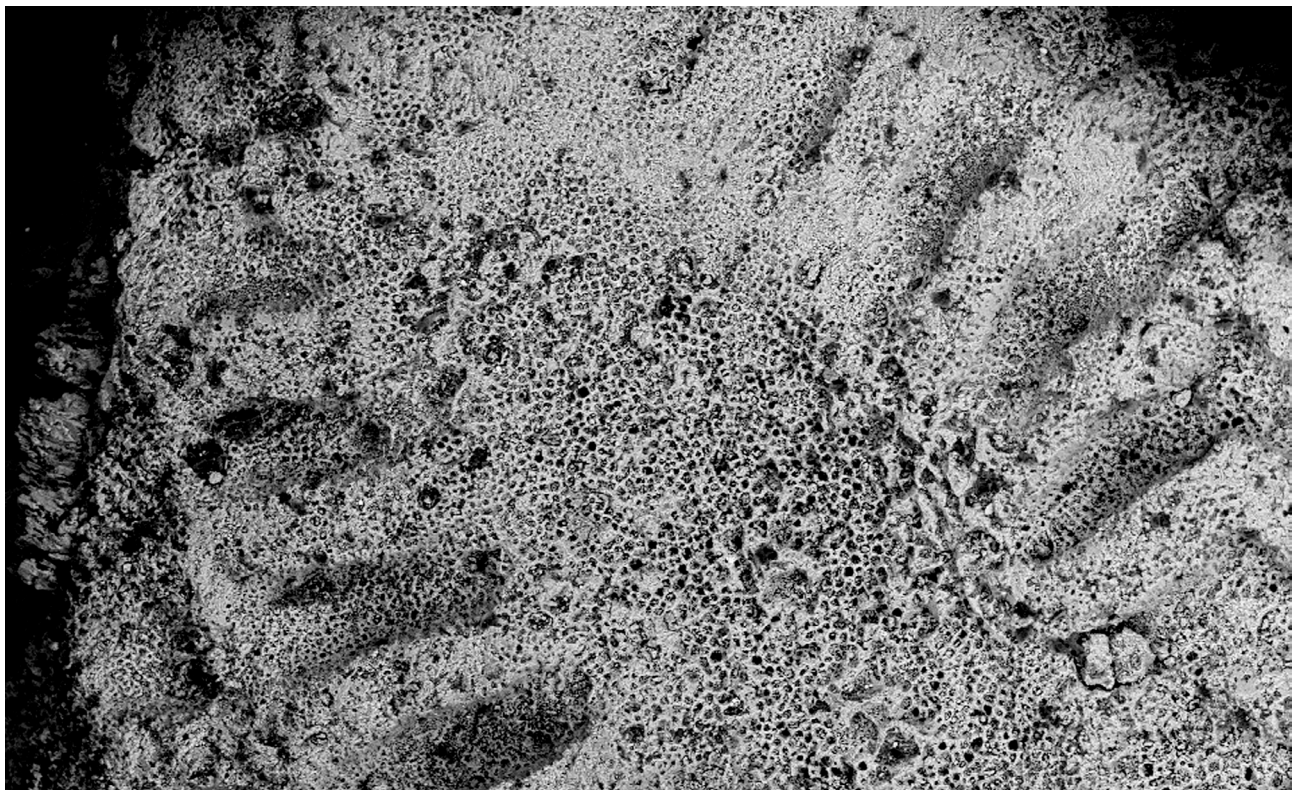
referred to that genus, although such columnals may be found within several genera of this family.”

The difference between *Isocrinus* and *Pentacrinites* in the articular face of the columnals is that *Pentacrinites* has very narrow petals surrounded by a slightly crenulate edge or ridge, and separated by large radial areas. *Isocrinus* differs from other three similar genera (*Chladocrinus*, *Metacrinus* and *Nielsenicrinus*) in having articular face of the columnals with less internodals, longer crenellae, and nodals equal to internodals respectively.

These columnals with typical *Isocrinus* articular facets (symplectial) sculpture consisting of drop- to lancet-like petal floors almost completely surrounded by distinct crenulae oriented radially to peripherally, so they are assigned to *Isocrinus*. In addition, they show greatest similarity with *Isocrinus* sp. (Donovan *et al.*, 2005) in the angular to pointed outline of the columnals, low internodal, confluent crenulae, and the high number of crenulae per petal.

## Discussion

There are more amberground marine animals found recently excluding the above described *Isocrinus* sp. Here we briefly discuss the discovery of fossil coral columnals



100 µm  
|——|

Mag = 54 X

EHT = 20.00 kV

WD = 10.4 mm

Signal A = RBSD

Photo No. = 5679

Date :29 May 2018

Time :14:55:31

FIGURE 4. SEM picture showing surface characters on *Isocrinus* sp.

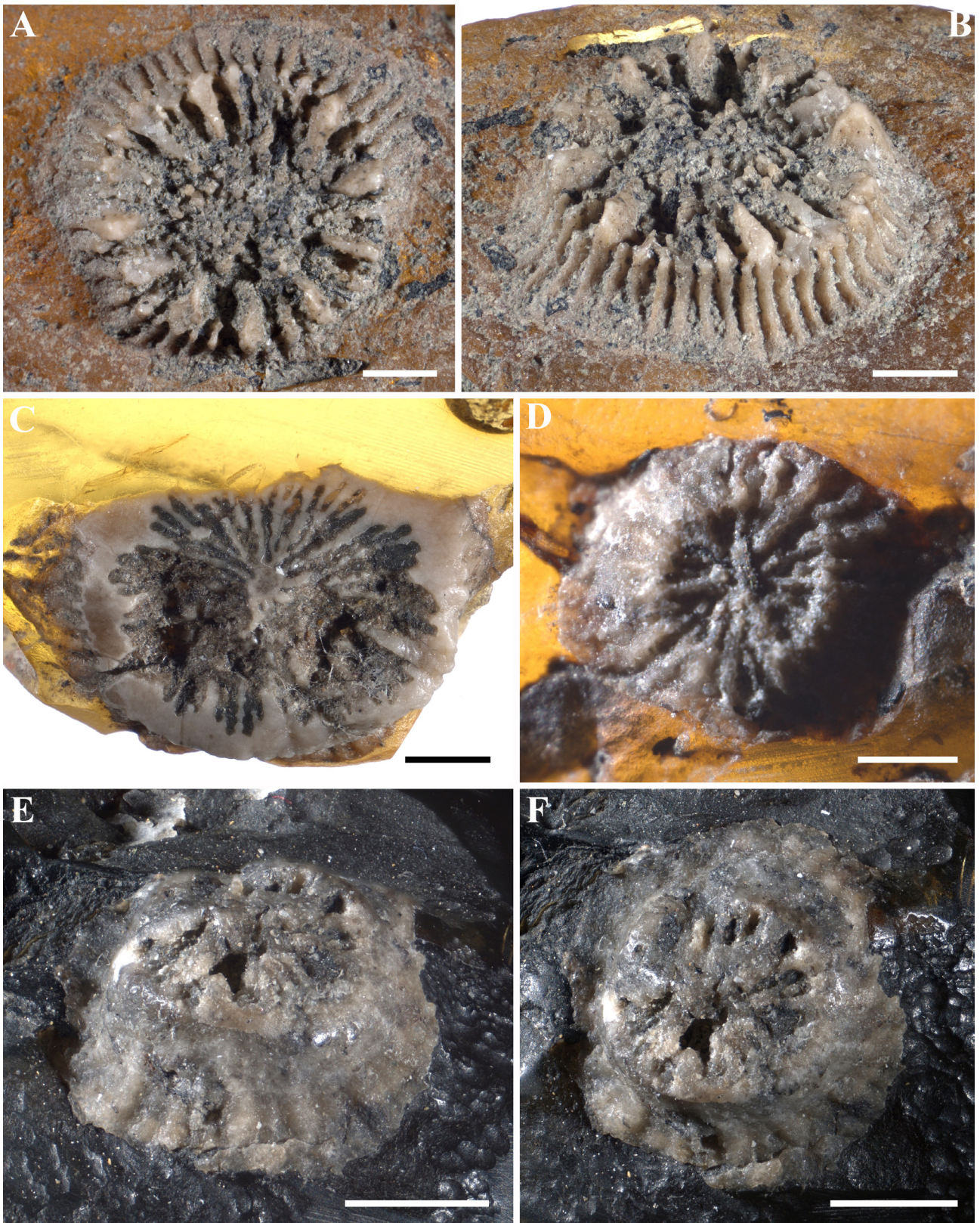
on the surface of Burmese amber or the surface of sediment surrounding the amber (Fig. 5). Scleractinians are a group of calcified anthozoan corals, many of which populate shallow-water tropical to subtropical reefs (Stanley, 2003). They appeared during the Middle Triassic (Vermeij, 1977) and diversified in the tropical Tethys from Jurassic through Cretaceous time (Stanley, 2003). Rare solitary Scleractinia *Epistreptophyllum?* and *Tiarasmilia?*, representing both hermatypic and ahermatypic corals, are found to grow directly on amber. Their settlement suggests a preference for hard substrata. It is noteworthy that all the four specimens are very short, indicating that their life span was relatively short. It could be speculated that the corals were near the seashore where ambers could be transported in shallow-water environments.

Fossil oysters are found on the surface of some Burmese amber (Fig. 6), although their precise taxonomic identity remain unknown. There are three left valves of oyster individuals attached the amber specimen by their natural outer shell surfaces, so that only the inner feature of these oysters are clearly visible. Some oysters were inserted into the amber during their growth, indicating that the amber was not completely hardened. The left valves are small (7 to 13 mm high, and 7 to 10 mm long), moderate convex, with a nearly orbicular outline. Umbo spirally curved, forming an umbonal cavity under the hinge area. The imprint of adductor muscle suited at about the central of the inner face of the valves. In the two relative small valves, chomata is slender and well developed, distributed along all periphery of the valves; while in the larger central valve, chomata is only preserved near the hinge on the commissural shelves.

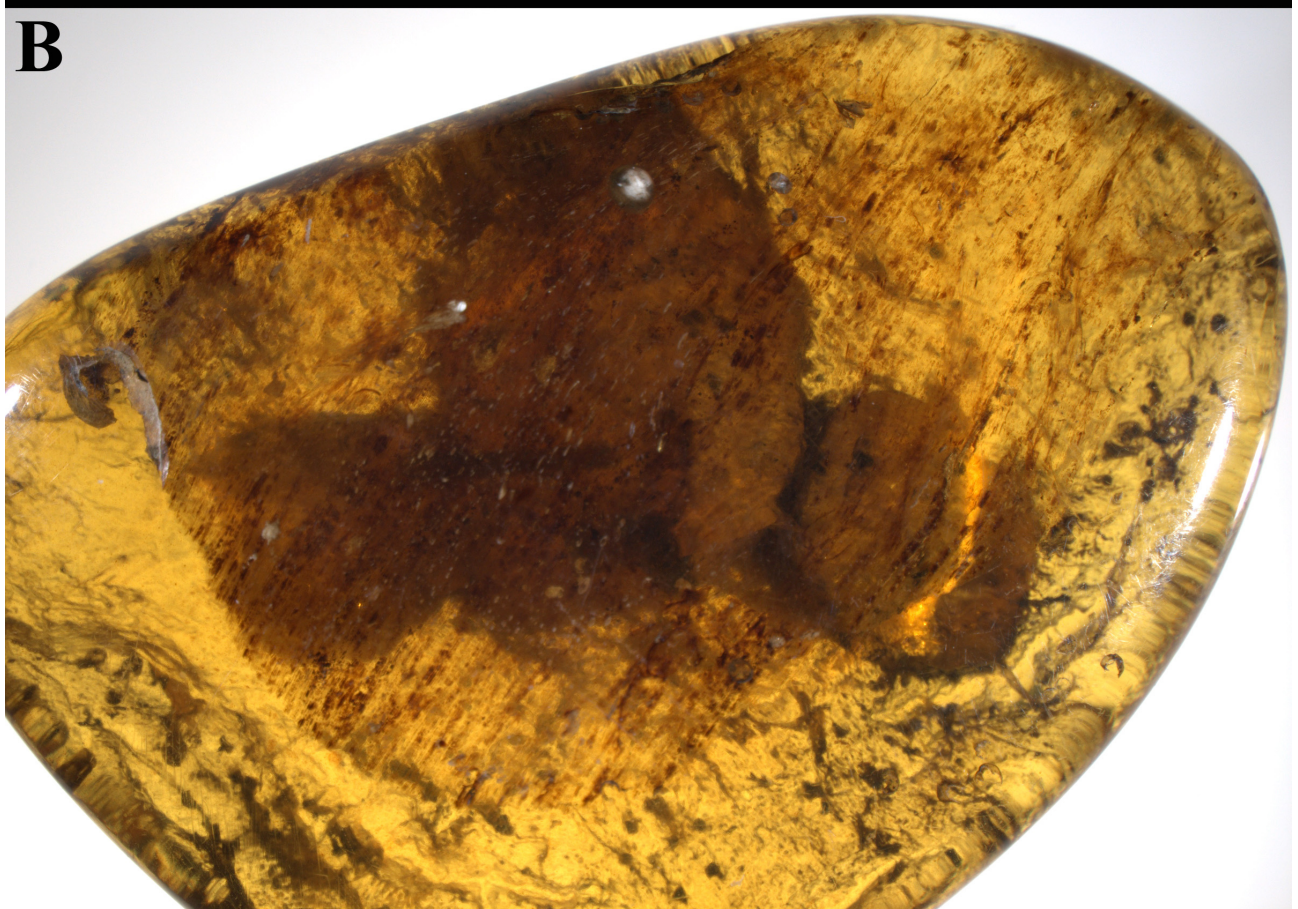
Previous unpublished works indicate that the palynological assemblage of Burmese amber is similar to that of the Albian of southern Songhua River in northeastern China. Recent studies have also revealed two forms of insects from Burmese amber closely associated with pollen-feeding: one is a boganiid beetle as a probable pollinator of cycads (Cai *et al.*, 2018), and the other is Permopsocida (Huang *et al.*, 2017). In the abdomen of a species of Permopsocida in Burmese amber, a large number of pollen grains of *Nyssapollenites* was found (Huang *et al.*, 2016; the original figure 1f scale should be 5  $\mu\text{m}$ , the original text is 50  $\mu\text{m}$ ), which bears important biostratigraphic significance. These pollen grains are tricolporate and highly uniform in morphology (Fig. 7; also see Huang *et al.*, 2016). They are almost always preserved in equatorial view. The outline is triangular with slightly convex sides. The size is small, with an even range between 13 and 15  $\mu\text{m}$ . The ornamentation is very weak, which makes the pollen grain looks psilate under transparent light microscope. Apertures are equatorially situated, with wide and large pores and short and wide colpi. The latter are slightly thickened at the margin.

All of these features, except the relatively small size, are identical to *Nyssapollenites*, a genus with relation to modern plant *Nyssa* (Nyssaceae). This *Nyssa*-like pollen is typical in the Cenomanian angiosperm palynofloras in North America (Norris *et al.*, 1975). It has not been encountered in strata older than Cenomanian although a latest Albian probability was presumed by Singh (1975). Palynological studies of the amber's surrounding rocks in Myanmar clearly needs further study, and it is crucial for the biostratigraphic study of the amber-producing strata in Myanmar.

At present, the more reliable isotope geochronology evidence for Burmese amber comes from Shi *et al.* (2012). Their sample came from more than 10 kg of amber pieces with attached sediments surrounding each piece. They obtained two sets of isotopic ages by SIMS dating, among which younger set of 25 zircon SIMS U-Pbs is  $98.79 \pm 0.62$  Ma. They believe that the age of formation of Burmese amber is not too old for the age of sediment containing these zircons. Therefore, the age of Burmese amber should be the earliest Cenomanian (Shi *et al.*, 2012). If the formation time of these volcanic zircons is the same as that of Burmese amber, and as described above and other data studies reveal that Burmese amber has not undergone significant handling and a long consolidation process, then  $98.79 \pm 0.62$  Ma currently representing the actual age of Burmese amber formation is still uncertain. Recent studies have shown that zircon SIMS or SHRIMP U-Pb dating will be younger than actual age if not treated by chemical abrasion (CA) (Kryza *et al.*, 2012; Metcalfe *et al.*, 2015). Moreover, some authors analyzed the isotope age of the Kuhfeng Formation ash beds and some interesting results based on the comparison of LA-ICPMS, SIMS, and CA-ID-TIMS three common dating methods (Wu *et al.*, 2016). For example, from ash bed A, the age of  $272.0 \pm 5.5$  Ma is obtained by LA-ICPMS method,  $269.0 \pm 104$  Ma by SIMS method, and  $272.95 \pm 0.11$  Ma by CA-ID-TIMS method, and from ash bed C, the age of  $271.5 \pm 3.3$  Ma was obtained by LA-ICPMS method,  $266.3 \pm 2.2$  Ma was obtained by SIMS method, and  $271.038 \pm 0.097$  Ma by CA-ID-TIMS method. It follows that the zircon U-Pb SIMS age is sometimes distinctly younger. However, it has also been shown that the zircon U-Pb SIMS age is consistent with the age measured by the CA-ID-TIMS method in some samples (Wang *et al.*, 2013; Chu *et al.*, 2016). The above instruments for the analysis of zircon by the SIMS method are the same as those for measuring the age of the amber in Myanmar. Therefore, it cannot be ruled out that the zircon age in the amber sediments measured by Shi *et al.* (2012) is more than 1% younger than the actual age.

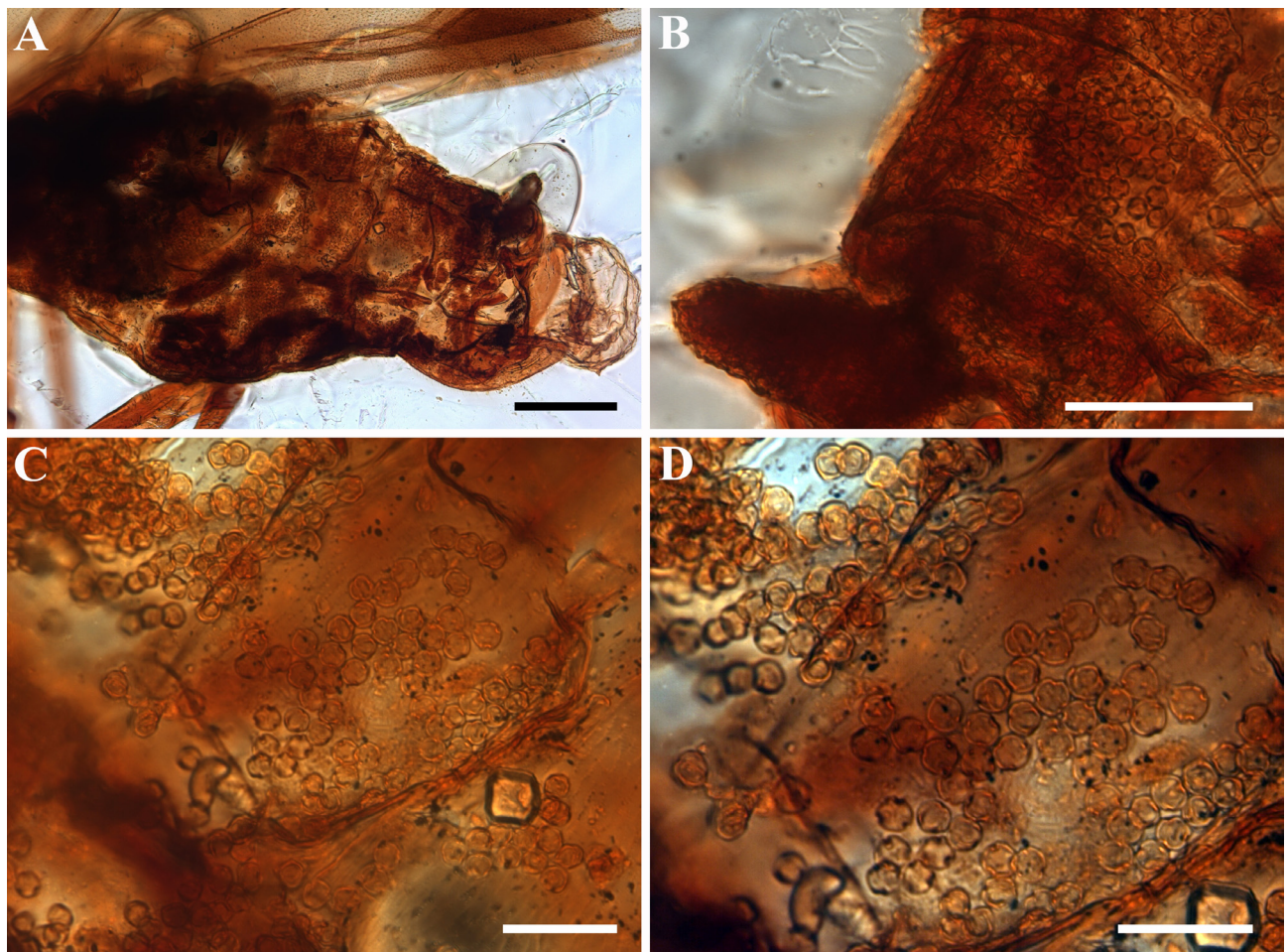


**FIGURE 5.** Corals growth on Burmese amber surfaces (NIGP169615–169618). **A** and **B**, *Tiarasmilia?* in vertical view and vertical-lateral view. **C**, *Epistreptophyllum?* **D–F**, Unidentified coral individuals. (Scale bars represent 1 mm in **D**, 2 mm in others.)



**FIGURE 6.** Oysters growth on the Burmese amber surface (FXBA10102). **A**, Inner surface. **B**, Outer surface. (Scale bars represent 5 mm.)





**FIGURE 7.** The angiosperm pollen *Nyssapollenites* filling the abdomen of an individual of Permopsocida. (Scale bars represent 0.2 mm in A, 0.1 mm in B, 0.05 mm in C and D.)

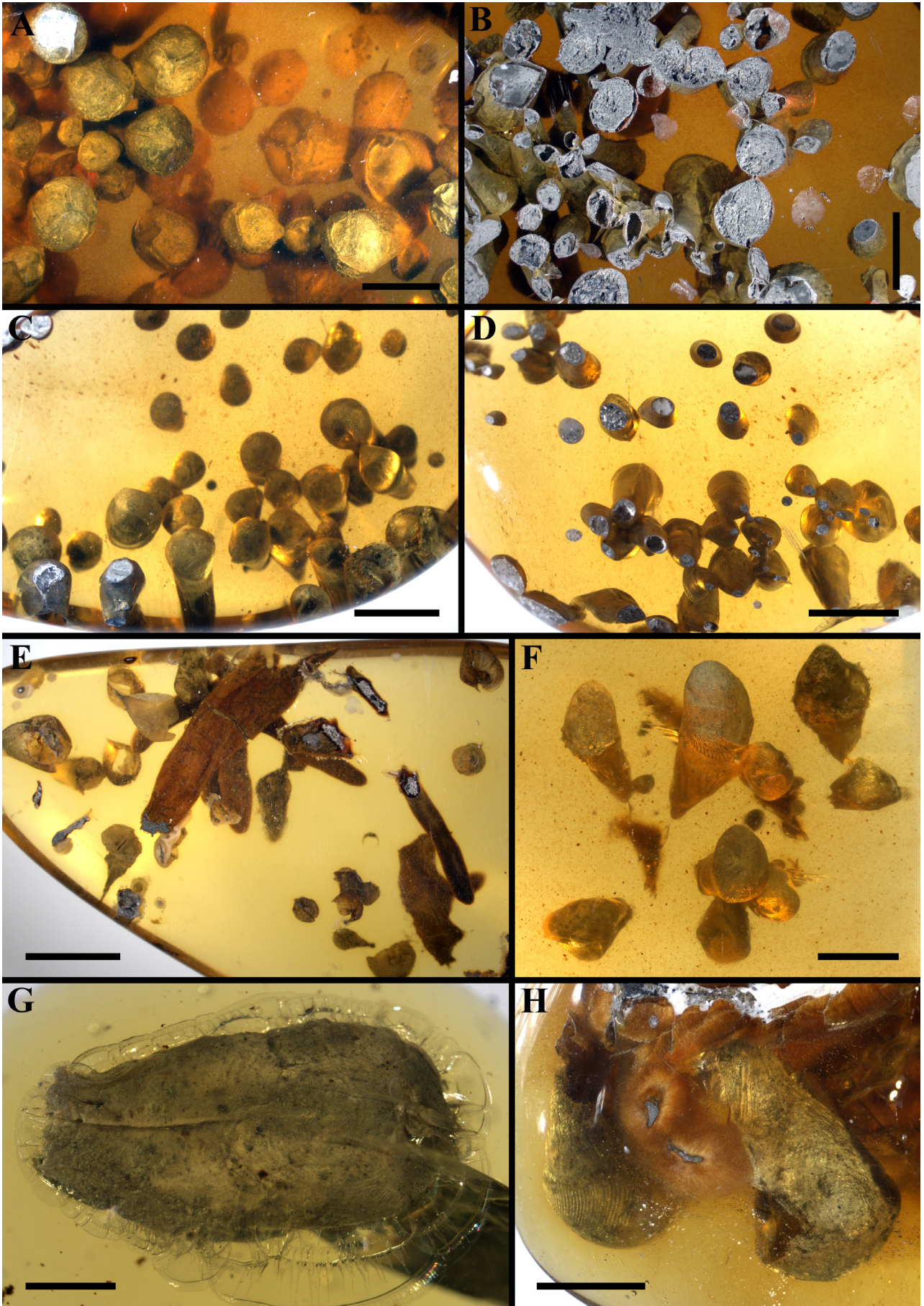
## Conclusion

Burmese amber harbors diverse inclusions, as well as pholadid borings (Smith & Ross, 2017; also see Fig. 8), some shelly marine animals, corals and oysters on the surface of the amber, and a variety of animals adhere to the amber deposits, including isocrinid crinoid columns and other marine animals. Although these fossils provide little information about the age of the amber material on which they are found, their presence sheds light on the palaeoenvironment. The shape of the amber suggests that it has not been transported over long distances, and the amber-producing plants are not far from the beach or just by the sea. After amber is produced and deposited with debris from marine organisms, some pholadid bivalves can bore into its surface during a relatively short exposure time, and sessile organisms such as corals and oysters can grow on the surface of amber. These pholadid bivalve borings are particularly common and indicate a character of coastal situation of amber-secreting trees (Smith & Ross, 2017). These ambers may or may not be completely hardened, and their exposure time of several years or tens of thousands of years does not have a significant impact

on the definition of the Burmese amber era. At present, the zircon U-Pb SIMS age of Burmese amber is closer to the actual age (Shi *et al.*, 2012), but the current zircon U-Pb SIMS age may be younger. Therefore, the age of Burmese amber may be close to the boundary between the Albian and Cenomanian, or even the Late Albian. We suggest that it is plausible to generally refer to the age of Burmese amber as mid-Cretaceous, and a precise age requires further biostratigraphic and chronological studies.

## Acknowledgements

This work was supported by the Strategic Priority Research Programme of the Chinese Academy of Sciences (grant numbers XDB26000000 and XDB18000000), National Natural Science Foundation of China (grant number 41688103), and the Second Tibetan Plateau Scientific Expedition (STEP) program to DYH, the National Science Foundation of China (grant number 41402013) to KL.



**FIGURE 8.** Amberground pholadid (NIGP169619–169624) bivalve borings. A–F, Pholadid bivalve borings. G and H, Pholadid bivalves with the borings; G, a large individual. (Scale bars represent 5 mm in A–E, 2 mm in F–H.)

## References

- Agassiz, L. (1836) Prodrome d'une monographie des radières ou échinodermes. *Mémoires de la Société Neuchâtoise des Sciences Naturelles*, 1, 168–199.
- Baumiller, T.K. & Hagdorn, H. (1995) Taphonomy as a guide to functional morphology of *Holocrinus*, the first post-Paleozoic crinoid. *Lethaia*, 28, 221–228.
- Cai, C.Y., Escalona, H.E., Li, L.Q., Yin, Z.W., Huang, D.Y. & Engel, M.S. (2018) Beetle Pollination of Cycads in the Mesozoic. *Current Biology*, 28 (17), 2806–2812. <https://doi.org/10.1016/j.cub.2018.06.036>
- Chhibber, H.L. (1934) *The mineral resources of Burma*. London, Macmillan, 320 pp.
- Chu, Z.Y., He, H.Y., Ramezani, J., Bowring, S.A., Hu, D.Y., Zhang, L.J., Zheng, S.L., Wang, X.L., Zhou, Z.H., Deng, C.L. & Guo, J.H. (2016) High-precision U-Pb geochronology of the Jurassic Yanliao Biota from Jianchang (western Liaoning Province, China): Age constraints on the rise of feathered dinosaurs and eutherian mammals. *Geochemistry Geophysics Geosystems*, 17, 3983–3992. <https://doi.org/10.1002/2016GC006529>
- Cockerell, T.D.A. (1917) Insects in Burmese amber. *Annals of the Entomological Society of America*, 10, 323–329.
- Cruikshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, 215, 441–455. [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)
- Donovan, S.K. (2001) Evolution of Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166, 177–192. [https://doi.org/10.1016/S0031-0182\(00\)00208-X](https://doi.org/10.1016/S0031-0182(00)00208-X)
- Donovan, S.K., Portell, R.W., & Veltkamp, C.J. (2005) Lower Miocene echinoderms of Jamaica, West Indies. *Scripta Geologica*, 129, 91–135. <https://doi.org/10.2307/4067933>
- Eagle, M.K. & Hikuroa, D. (2003) *Chariocrinus* (Crinoidea: Articulata) from the Latady Formation, Behrendt and Hauberg Mountains, Ellsworth Land, Antarctica. *New Zealand Journal of Geology and Geophysics*, 46, 529–537. <https://doi.org/10.1080/00288306.2003.9515027>
- Gislén, T. (1924) Echinoderm studies. *Zoologiska Bidrag från Uppsala*, 9, 316 pp.
- Grimaldi, D.A., Engel, M.S. & Nascimbene, P.C. (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, 3361, 1–71.
- Hagdorn, H. (1982) Untersuchungen an Muschelkalk-Crinoiden, I: Zur Funktionsmorphologie des Stiels triassischer Isocrinida. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 164, 134–136.
- Hagdorn, H. (1983) *Holocrinus doreckae* n. sp. aus dem Oberen Muschelkalk und die Entwicklung von Sollbruchstellen im Stiel der Isocrinida. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 345–368.
- Hagdorn, H. (1986) *Isocrinus?* dubius (Goldfuss, 1831) aus dem Unteren Muschelkalk (Trias, Anis). *Zeitschrift für Geologische Wissenschaften*, 14, 705–727.
- Hagdorn, H. (1993) *Holocrinus dubius* (Goldfuss, 1831) aus dem Unteren Muschelkalk von Rüdersdorf (Brandenburg). In: Hagdorn, H. & Seilacher, A. (Eds.), *Muschelkalk, Schöntaler Symposium 1991. (Sonderbände der Gesellschaft für Naturkunde in Württemberg, 2)*. Goldschneck-Verlag, Stuttgart, Korb, pp. 213.
- Hagdorn, H. (1996) Trias-Seelilien. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 21, 1–17.
- Hagdorn, H. (1999) Triassic Muschelkalk of Central Europe. In: Hess, H., Ausich, W.I., Brett, C.E. & Simms, M.J. (Eds.), *Fossil crinoids*. Cambridge University Press, Cambridge, pp. 164–176.
- Hagdorn, H. (2011) Triassic: the crucial period of post-Palaeozoic crinoid diversification. *Swiss Journal of Palaeontology*, 130, 91–112. <https://doi.org/10.1007/s13358-010-0009-9>
- Hess, H., Ausich, W.I., Brett, C.E. & Simms, M.J. (2003) *Fossil crinoids*. In: Hess, H., Ausich, W.I., Brett, C.E. & Simms, M.J. (Eds), Cambridge University Press, Cambridge, pp. 3–22.
- Hess, H. (1972) *Chariocrinus* n. gen. für *Isocrinus andreae* Desor aus dem unteren Hauptrogenstein (Bajocian) des Basler Juras. *Eclogae Geologicae Helveticae*, 65, 197–210.
- Huang, D.Y., Bechly, G., Nel, P., Engel, M.S., Prokop, J., Azar, D., Cai, C.Y., van de Kamp, T., Staniczek, A., Garrouste, R., Krogmann, L., dos Santos Rolo, T., Baumbach, T., Ohlhoff, R., Shmakov, A.S., Bourgoin, T. & Nel, A. (2016) New fossil insect order Permopsocida elucidates major radiation and evolution of suction feeding in hemimetabolous insects (Hexapoda: Acercaria). *Scientific Reports*, 6, 23004.
- Hunter, A.W. & Clark, N.D.L. (2009) The palaeoecology of two Scottish encrinites: Jurassic crinoid assemblages from the Trotternish Peninsula, Isle of Skye, Scotland. *Scottish Journal of Geology*, 45, 169–176. <https://doi.org/10.1144/0036-9276/01-366>
- Hunter, A.W. & Underwood, C.J. (2009) Palaeoenvironmental control on distribution of crinoids in the Bathonian (Middle Jurassic) of England and France. *Acta Palaeontologica Polonica*, 54, 77–98. <https://doi.org/10.4202/app.2009.0109>
- Hunter, A.W. & Zonnerveld, J.P. (2008) Palaeoecology of Jurassic encrinites: Reconstructing crinoid communities from the Western Interior Seaway of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 263, 58–70. <https://doi.org/10.1016/j.palaeo.2008.01.027>

- Hunter, A.W., Oji, T., Ewin, T.A.M. & Kitazawa, K. (2011) New species of isocrinid crinoids *Chariocrinus japonicas* (Articulata, Echinodermata) from the Lower Cretaceous Mitarai Formation (Tetori Group) of Takayama district, central Japan. *Bulletin of the Mizunami Fossil Museum*, 37, 115–121.
- Kalita, K.D. (2015) New report of Isocrinid crinoid *Chariocrinus* from the Jurassic of Jaisalmer, Rajasthan, India. *Journal of the Geological Society of India*, 86, 597–604. <https://doi.org/10.1007/s12594-015-0350-0>
- Kryza, R., Crowley, Q.G., Larionov, A., Pin, C., Oberc-Dziedzic, T. & Mochnacka, K. (2012) Chemical abrasion applied to SHRIMP zircon geochronology: An example from the Variscan Karkonosze Granite (Sudetes, SW Poland). *Gondwana Research*, 21, 757–767. <https://doi.org/10.1016/j.gr.2011.07.007>
- Metcalf, I., Crowley, J.L., Nicoll, R.S. & Schmitz, M. (2015) High-precision U-Pb CA-TIMS calibration of Middle Permian to Lower Triassic sequences, mass extinction and extreme climate-change in eastern Australian Gondwana. *Gondwana Research*, 28, 61–81. <https://doi.org/10.1016/j.gr.2014.09.002>
- Miller, J.S. (1821) *A Natural History of the Crinoidea or Lily-shaped Animals, with Observations on the Genera Asteria, Euryale, Comatula and Marsupites*. Bryan and Co., Bristol, 150 pp.
- Milner, G.J. (1989) The first record of an isocrinid crinoid from the Tertiary of Australia. *Records of Western Australian Museum*, 14, 385–389.
- Mu, A.T. & Wu, Y.R. (1974) Triassic crinoids. In: Nanjing Institute of Geology and Palaeontology of Chinese Academy of Sciences (Ed.), *A Handbook of the Stratigraphy and Palaeontology of Southwest China*. Science Press, Beijing, pp. 353–354. [in Chinese]
- Noetling, F. (1892) Preliminary report on the economic resources of the amber and jade mine areas in Upper Burma. *Records of the Geological Survey of India*, 25, 130–135.
- Noetling, F. (1893) On the occurrence of Burmite, a new fossil resin from Upper Burma. *Records of the Geological Survey of India*, 26, 31–40.
- Norris, G., Jarzen, D.M. & Awai-Thorne, B.V. (1975) Evolution of the Cretaceous terrestrial palynoflora in western Canada. *The Geological Association of Canada Special Paper*, 13, 333–364.
- Oji, T. (1985) Early Cretaceous *Isocrinus* from northeast Japan. *Palaeontology*, 28, 629–642.
- Rasmussen, H.W. (1961) A monograph on Cretaceous crinoidea. *Biologiske Skrifter Kgl Dansk Videnskabernes Selskab Kobenhavn*, 12 (I), 428 pp.
- Rasmussen, H.W. (1978) Articulata. In: Moore, R.C. & Teichert, C. (Eds.), *Treatise on Invertebrate Paleontology*, Part T, Echinodermata 2 (3). Geological Society of America, Boulder, Colorado and University of Kansas, Lawrence, Kansas, pp. T813–T928.
- Rasnitsyn, A.P. (1996) Burmese amber at the Natural History Museum. *Inclusion*, 23, 19–21.
- Ross A.J. (2015) Insects in Burmese amber. *Entomologentagung 02.–05.03.2015 Frankfurt am Main, Programm und Abstracts*, 72.
- Ross, A.J. (2018) Burmese (Myanmar) amber taxa, on-line checklist v.2018.2. Available from: <http://www.nms.ac.uk/explore/stories/natural-world/burmese-amber/> (Accessed 28 Dec. 2018)
- Sahni, M.R. & Sastri, V.V. (1957) A monograph of the orbitolines found in the Indian continent (Chitral, Gilgit, Kashmir), Tibet and Burma, with observations on the age of the associated volcanic series. *Palaeontologia Indica*, 33 (3), 50.
- Salamon, M.A. (2008) The Callovian (Middle Jurassic) crinoids from the black clays of the Lukow area, eastern Poland. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 247, 133–146. <https://doi.org/10.1127/0077-7749/2008/0247-0133>
- Selden, P.A. & Ren, D. (2017) A review of Burmese amber arachnids. *Journal of Arachnology*, 45 (3), 324–343. <https://doi.org/10.1636/JoA-S-17-029>
- Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L. & Li, X.H. (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research*, 37, 155–163.
- Sieverts-Doreck, H. (1952) ‘Orders of the Articulata’. 614. In: Moore, R.C., Lalicker, C.G. & Fischer, A.G. (Eds.), *Invertebrate fossils*. McGraw-Hill, New York, 766 pp.
- Simms, M.J. (1989) British Lower Jurassic crinoids. *Monographs of the Palaeontographical Society London*, 581, 1–103.
- Simms, M.J. (1994) Crinoids from the Chambara Formation, Pucará Group, central Peru. *Palaeontographica, Abteilung A*, 233, 169–175.
- Simms, M.J. (1999) Systematics, phylogeny and evolutionary history. In: Hess, H., Ausich, W.I., Brett, C.E. & Simms, M.J. (Eds.), *Fossil crinoids*. Cambridge University Press, Cambridge, pp. 31–40.
- Singh, C. (1975) Stratigraphic significance of early angiosperm pollen in the mid-Cretaceous strata of Alberta. *The Geological Association of Canada Special Paper*, 13, 365–389.
- Smith, R.D. & Ross, A.J. (2017) Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish waters, and the age of the amber. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 107, 239–247. <https://doi.org/10.1017/S1755691017000287>
- Stuart, M. (1923) Geological traverses from Assam to Myitkyina, through the Hukong Valley; Myitkyina to northern Putao; and Myitkyina to the Chinese frontier. *Records of the Geological Survey of India*, 54, 398–411.
- Stanley, Jr., G.D. (2003) The evolution of modern corals and

- their early history. *Earth-Science Reviews*, 60, 195–225.  
[https://doi.org/10.1016/S0012-8252\(02\)00104-6](https://doi.org/10.1016/S0012-8252(02)00104-6)
- Stiller, F. (2011) An early isocrinid sea lily from the middle to late Anisian boundary (Middle Triassic) of south west China—evidence for a far east Tethyan origin of the family Isocrinidae. *Palaeontology*, 54, 1415–1433.  
<https://doi.org/10.1111/j.1475-4983.2011.01101.x>
- Twitchett, R.J. & Oji, T. (2005) Early Triassic recovery of echinoderms. *Comptes Rendus Palevol*, 4, 531–542.  
<https://doi.org/10.1016/j.crpv.2005.02.006>
- Vermeij, G.J. (1977) The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, 2, 245–258.
- Wang, L.L., Hu, D.Y., Zhang, L.J., Zheng, S.L., He, H.Y., Deng, C.L., Wang, X.L., Zhou, Z.H. & Zhu, R.X. (2013) SIMS U-Pb zircon age of Jurassic sediments in Linglongta, Jianchang, western Liaoning, Constraint on the age of oldest feathered dinosaurs. *Chinese Science Bulletin*, 58 (14), 1346–1353. [in Chinese]
- Wright, C.W., Calloman, J.H. & Howarth, M.K. (1996) Cretaceous Ammonoidea, *Treatise on Invertebrate Paleontology, Part L Mollusca 4 Revised, vol. 36*. The Geological Society of America and the University of Kansas, Boulder, Colorado, Lawrence, 362 pp.
- Wu, Q., Ramezani, J., Zhang, H., Wang, T.T., Yuan, D.X., Mu, L., Zhang, Y.C., Li, X.H. & Shen, S.Z. (2016) Calibrating the Guadalupian Series (Middle Permian) of South China. *Palaeogeography Palaeoclimatology Palaeoecology*, 466, 361–372.  
<https://doi.org/10.1016/j.palaeo.2016.11.011>
- Yu, J.X., Guo, Z.Y. & Mao, S.Z. (1983) Cretaceous palynological assemblages from the district south of the Songhua River. *Professional Papers of Stratigraphy and Palaeontology*, 10, 1–86. [in Chinese with English summary]
- Zherikhin, V.V. & Ross, A.J. (2000) A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum (Geology Series)*, 561, 3–10.
- Zittel, K.A. von. (1879) *Handbuch der Paläontologie*. I. Protozoa, Coelenterata, Echinodermata und Molluscoidea. München & Leipzig, 765 pp.