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High-fidelity preservation of the Scarabaeoidea (Insecta) exoskeletons from the Miocene of Shanwang

LIANG HU[1,2], HUAYING XIANG[4], CHENYANG CAI[1], TAO ZHAO[3], DIYING HUANG[3] & YANHONG PAN[1*]
[1]*CAS Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 210008 Nanjing, China*
[2]*University of Chinese Academy of Sciences, Beijing 100049, China*
[3]*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China*
[4]*Northwest A&F University, Yangling, Shaanxi 712100, China*
**Corresponding author. E-mail: yhpan@nigpas.ac.cn*

Abstract

The Shanwang Fauna has been one of the well-known Miocene Konservat-Lagerstätten for a long time, but the high-fidelity preservation of the fossils has been often ignored. This paper illustrates the exceptional preservation displayed by some fossil insects from the Shanwang Formation. The microstructures of the preserved exoskeletons were analyzed using a scanning electron microscope and a transmission electron microscope. The epicuticle, procuticle, and some fine details such as cuticular scales could be recognized from the structural remains. These details could enable the identification of valued taxonomic and phylogenetic features and contribute to understanding the diagenetic environment.

Keywords: Miocene, Shanwang Formation, insect exoskeleton, microstructure

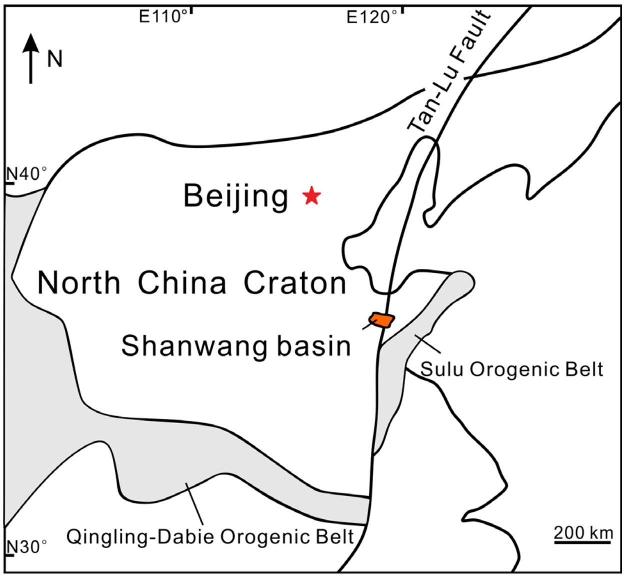

FIGURE 1. Location of the Shanwang Basin (after He *et al.*, 2011).

Introduction

The Shanwang Basin is a small area (< 1 km^2), located about 22 km northeast of Linqu County in Shandong Province, eastern China (36°54' N, 118°20' E) (Fig. 1). It has yielded an extraordinarily well-preserved fossil assemblage, namely the Shanwang Biota (Yang & Yang, 1994; Guo *et al.*, 2007; Chen, 2000; Liang, 1998; Tian, 2015). It constitutes one of the most diversified Miocene biotas in the world where over hundreds of species have been so far described from its diatomaceous lacustrine shales, including fungi, diatoms, plants, crustaceans, insects, fishes, amphibians, reptiles, birds, mammals, etc. (Sun, 1961; Yeh, 1977; Liang, 1998; Hou, 2000; Liu *et al.*, 2002; Storch, 2004; Qiu, 2005; Wang *et al.*, 2005; Roček *et al.*, 2011). The most abundant among all fossil groups, however, are insects and plants, e.g. over 400 formally named insect species have been described to date (Hong, 1983, 1985; Zhang, 1986, 1989, 1990; Zhang *et al.*, 1994). The Shanwang Formation has long been considered as a Miocene Konservat-Lagerstätte (Yang & Yang, 1994). The fossil insects of this biota are especially well preserved. Some even display original colors when they are freshly excavated (Yang & Yang, 1994), but unexpectedly change into black within several days after excavation (Zhang, 1986). Despite this, little is known about the process of preservation, and the high-quality preservation of Shanwang insects is often ignored in the original species descriptions.

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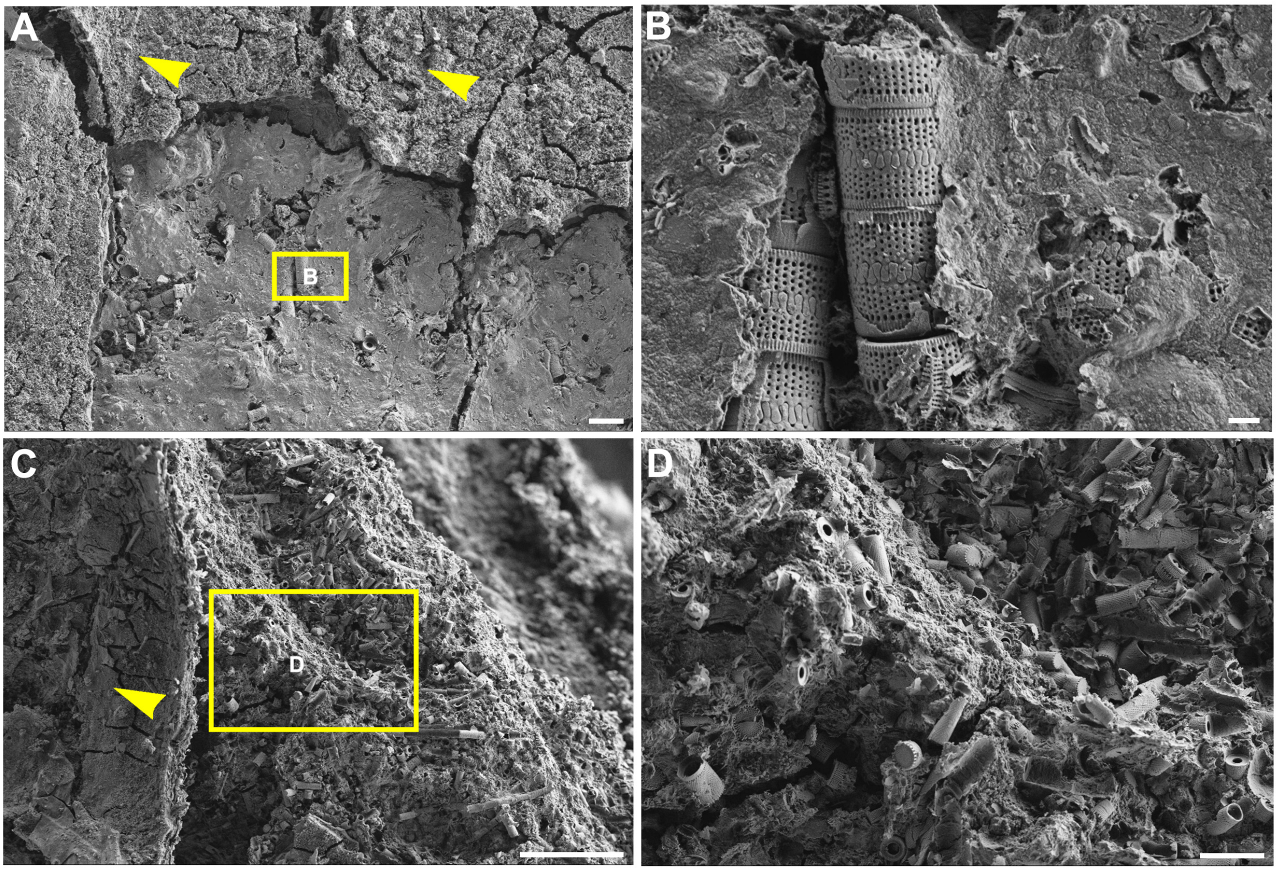

FIGURE 2. SEM images of the diatomite surrounding the beetle. **A**, **C**, The upper layer is the cuticle, blow is the diatomite, noticed in the images; **B**, **D**, Diatoms, enlarged from A, C, respectively. (Scale bar = 100 μm in C; 20 μm in A, D; 2 μm in D).

Current knowledge of the taphonomic significance of the Shanwang Fauna is very limited (Yang & Yang, 1994), and only a few works have discussed volcanism and resulting ash as a possible contribution to the mass mortalities and a contributing factor in the preservation of the Shanwang fossils (Chen, 2000; Guo *et al.*, 2007; Tian, 2015). Guo *et al.* (2007) proposed that the volatile-rich basaltic volcanism changed the environment and altered the lake chemistry, which could have resulted in mass mortality, The resulting falling volcanic ash would then have covered and buried the dead animals and plants, and allowing for exceptionally preserved fossils. In any case, all hypotheses attributed the high concentration and fine preservation of Shanwang fossils to volcanism and sedimentation of fine-grained volcanic ash in the palaeolake (Chen, 2000; Guo *et al.*, 2007; Tian, 2015). Although the volcanism was probably a contributing factor in fossil preservation, the microbial organisms in the lake were even more important contributors to the process of fossilization (O'Brien *et al.*, 2002). The diatomite accumulation often reflects a favorable sedimentary environment for exceptionally preserved fossils, such as fossils from the diatomites of Miocene deposits of Saint-Bausil, southern France, Oligocene Florissant lake beds in United States, and the Miocene/Pliocene Pisco Formation, southern Peru (Riou, 1995; Harding & Chant, 2000; Esperante *et al.*, 2015; Metais & Sen, 2018). The Shanwang fossils are also preserved in diatomites, so their effects should be considered during the fossilization process. Herein we illustrate the exceptional quality of preservation displayed by the Shanwang Formation insects, describe the preservation fabrics, and suggest possible mechanisms that may result in such preservation.

Material and methods

The Tertiary strata of the Shanwang Basin is divided into three formations in ascending order: the Niushan Formation, the Shanwang Formation, and the Yaoshan Formation (Deng, 2003). The Niushan Formation is a set of olivine tholeiite, resting above Precambrian metamorphic rocks or Cretaceous pyroclastic rocks. The Yaoshan Formation is another set of alkali olivine basalt, lying on the top of the Shanwang Formation. The Shanwang Formation consists of clastic sedimentary rocks and diatomaceous shale, interbedded with volcanic ash and basalt. The Shanwang fossils were collected from

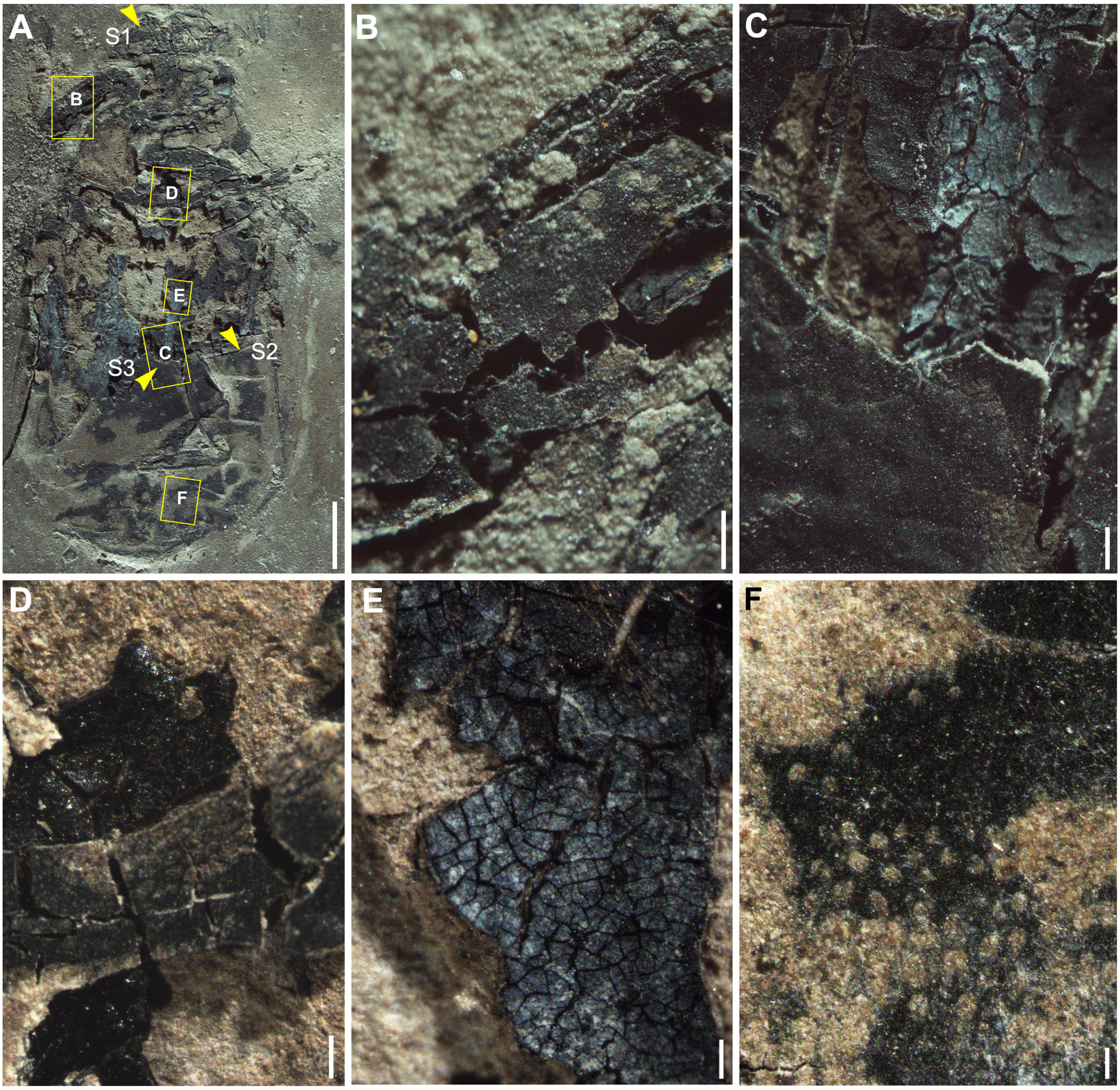

FIGURE 3. Studied specimen under binocular microscope. **A**, General view of the articulated specimen with head, antenna, prothorax, thorax foot, and the elytra in-situ. **B-E**, Enlarged from different parts noticed in A, showing remarkable desiccation cracks. **F**, The posterior of the elytra enlarged from A, showing patterns of the cuticular scales. (Scale bar = 1 mm in A; 0.2 mm in C, D; 0.1 mm in B, E, F).

the diatomaceous shale (about 30 m in thickness) of the Shanwang Formation (Yang & Yang, 1994). For a long time, the age of this formation was generally considered as middle Miocene in age (~15.2–17 Ma) (Li, 1982; Liu & Shi, 1989; Yang & Yang, 1994). However, an early Miocene age (~17–18 Ma) is given to the Shanwang Basin, based on recent advances of the biostratigraphic and radiometric evidences (Deng, 2003; He *et al.*, 2011).

The material discussed in this paper is from the diatomite of the Shanwang Formation in Linqu County, collected by one of us (DYH) and identified as an unknown species belonging to the beetle superfamily Scarabaeoidea (Insecta: Coleoptera). The diatomite is dominated by the genus *Melosira* (Fig. 2, siliceous frustules of centric diatoms), and some species of *Cymbella*, *Fragilaria*, and *Navicula* (Shi, 1990; Li *et al.*, 2010). The modern forms of the majority of this diatom assemblage are living in shallow, normal salinity, nutrient-rich, and still water bodies under warm temperate climates (Shi, 1990; Li *et al.*, 2010).

The fossil was first documented by binocular microscope. Images were taken using a Leica M250A microscope with camera and digital sight attachment in Nanjing Institute of Geology and Palaeontology

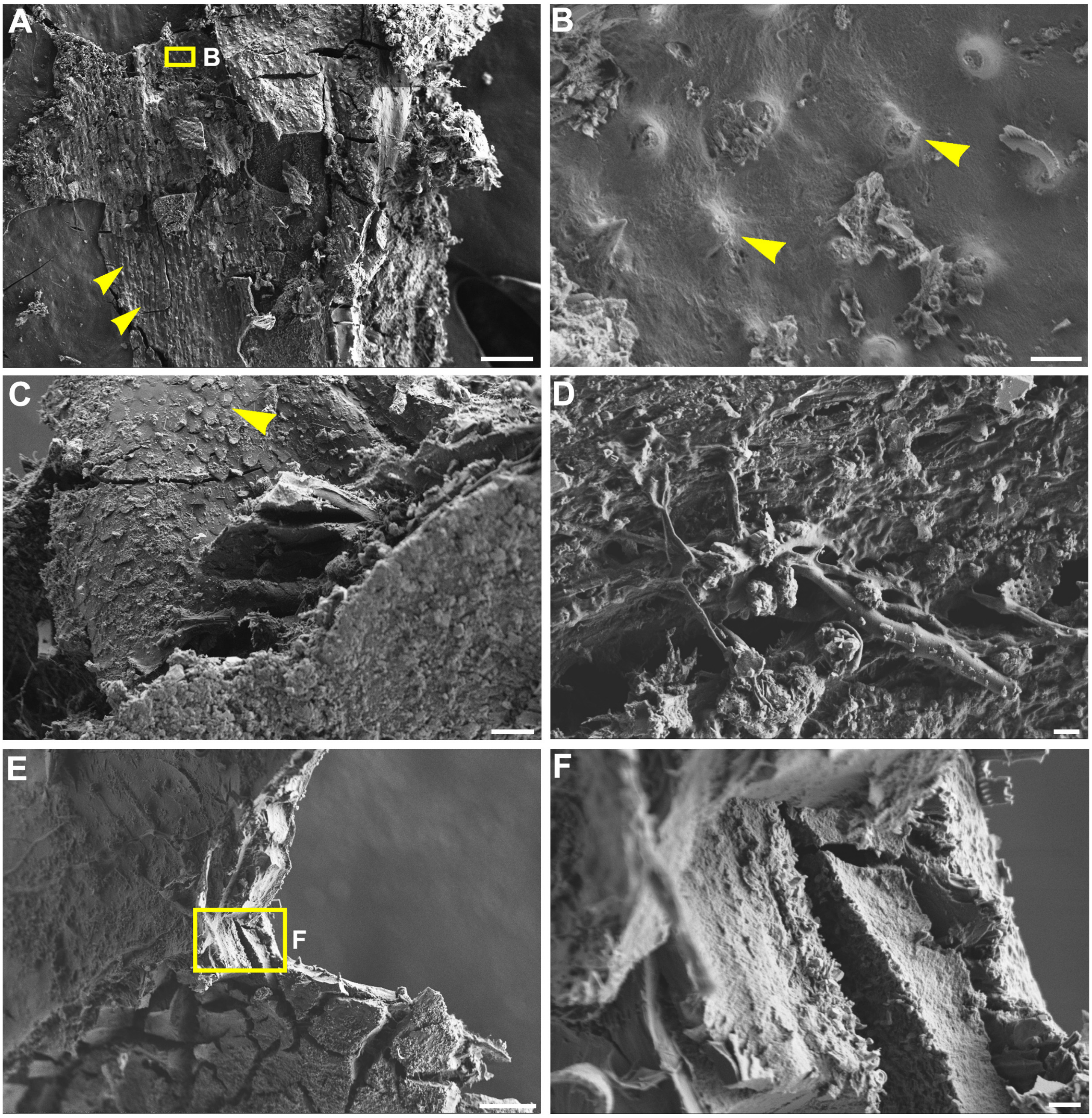

FIGURE 4. SEM images of the preserved microstructure in the surface and cross section of the studied specimen. **A–B**, Enlarged details of the head from S1 in fig. 3A, showing furrow strip structure (with arrows in A) and concave-convex structures (with arrows in B), B is enlarged from A. **C**, Enlarged details of the elytra from S2 in fig. 3A, showing cuticular scales, noticed by arrows. **D–F**, sampled from S3 in fig. 3A; D, Showing the algae or fungi on the surface; **E–F**, Cross section of the exoskeleton, showing two distinct layers, F is enlarged from E. (Scale bar = 50 µm in A; 20 µm in E; 10 µm in C; 3 µm in B; 2 µm in D, F).

(NIGPAS). Then, small samples were taken from different part of the specimen, and mounted on aluminium stubs with a carbon pad for scanning electron microscopy (SEM) documentation. The uncoated samples were examined under Leo 1530 in NIGPAS with variable pressure environment, in high vacuum mode, and a secondary ion detector is used. After SEM examination, the sample was prepared for transmission electron microscopy (TEM) study. The preparing method follows (Pan *et al.*, 2016). The ultra-thin sections (the thickness is 90 nm) were examined with a JEM-2100 in Advanced Analysis Test Center of Nanjing Forestry University.

Results

Macrostructure preservation

The studied specimen appears to be flattened on the bedding plane (Fig. 3A). The black specimen is articulated,

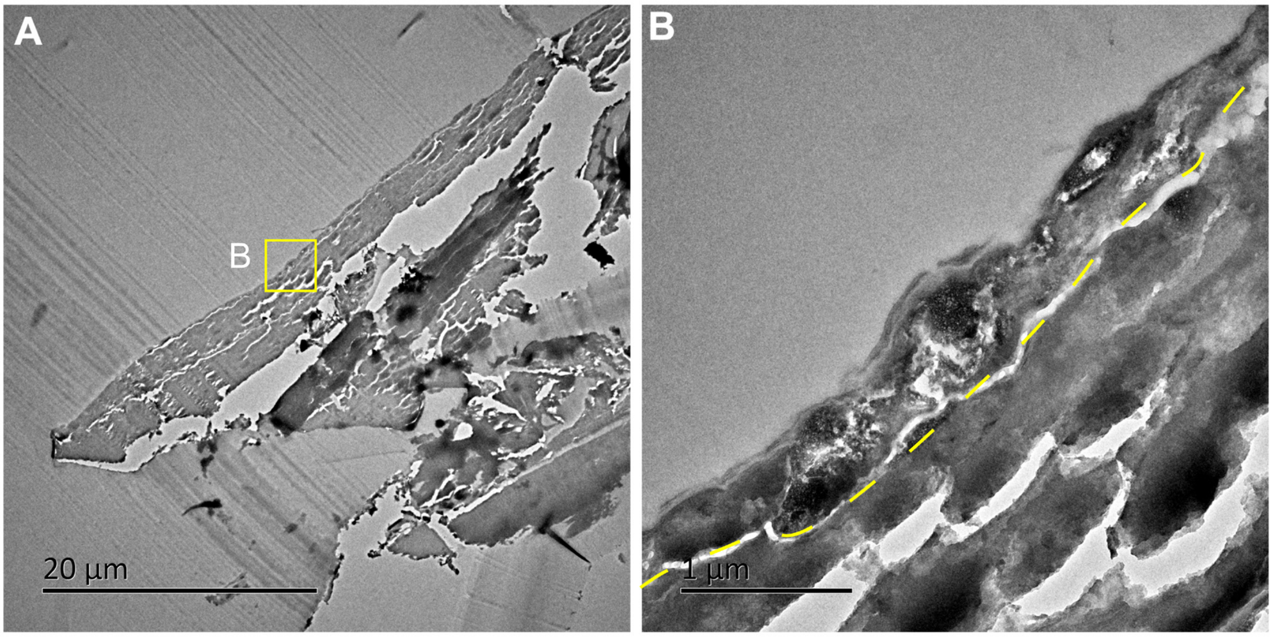

FIGURE 5. TEM images of an elytron. A, Ultrathin cross section. B, Enlarged from A, showing two layering structure, indicated by yellow dashed line.

with head, antenna, prothorax, thorax foot, and the elytra *in-situ* (Fig. 3A). The meso-, metathorax and abdomen are covered by the elytra. The whole specimen is preserved as a thin black carbonaceous compression exhibiting three-dimensionality to some extent within the diatomite lamina, and desiccation cracks are remarkable (Fig. 3B–E). Except for the posterior of the elytra, no desiccation crack is observed but the patterns of the cuticular scales are preserved intact (Fig. 3F).

Microstructure preservation

Surface textures

Here we illustrate the surface textures visible under scanning electron microscopy (SEM). Under the light microscopy, the head of the specimen seemed to be compressed into a mess (Fig. 3A). When it is zoomed in with SEM, there are two observed patterns of surface textures. One is a kind of concave-convex structure, the other is composed of furrow strips (marked with arrows in Fig. 4A–B). For the elytra, in microscopic view, the surface is covered by cuticular scales (Fig. 4C), which is also not seen under the binocular microscope (Fig. 3B–E).

Besides the fine textures, algae or fungi are observed on the surface of the specimen (Fig. 4D), which were most likely growing during the weathering process.

Microstructure of the cross section

The broken edge of the cuticle of the Shanwang fossils were examined under SEM (Fig. 4E–F). Two distinct layers of the cuticle are recognized (Fig. 4F). The ultrathin section of the elytra was examined under TEM. Similar layering structures are also recognized (Fig. 5). An outer thin layer (the thickness is less than 1 micron) and an inner relative thick layer (the thickness is more than 10 microns). In contrast to the outer thin layer, the inner thick layer is much more solid (Figs. 4, 5). Similar structures have been documented in the cuticle of insect fossils from the Bembridge Marls in the Isle of Wight, United Kingdom (Duncan, 1997), which was also preserved as a thin layer of organic material, consisting of two layers. In their specimen, the thickness of the outer layer is 3.0 to 0.1 µm, and is comparable to the outer epicuticle, while the thickness of the inner layer is 10 µm to 0.5 mm thick, and is comparable to the inner procuticle.

The integument of the living insect consists of two units, the epidermis and the cuticle (Hepburn, 1985; Hadley, 1986; Binnington & Retnakaran, 1991; Binnington, 1993). The epidermis is a single layer of cells, which is usually not preserved in the cross section of the fossil integument. In the living insect, the cuticle itself contain an inner portion termed the procuticle primarily composed of chitinous microfibrils in a proteinaceous matrix and a small amount of lipids, and an outmost set of layers termed the epicuticle which lack of chitin (Evans, 1984). In general, the procuticle consists of endocuticle and exocuticle (Neville, 1975). In most beetles, the regions of procuticle are confluent, and do not always have a distinct or sharp boundary between exocuticle and endocuticle (Singh *et al.*, 2016), it could be species associated. The elytra from 14 species of modern

Curculionoidea and 26 species representing 23 families of other beetles were examined by SEM, and all of them show clearly distinguished exocuticle and endocuticle (van de Kamp *et al.*, 2016). Morphologically, the studied specimen is identified as an unknown species of Scarabaeoidea. Microstructural textures of the procuticle exhibited a sharp boundary between the exocuticle and the endocuticle (Fig. 5B, noticed by dashed line) as in modern beetles.

Discussion

Fossil arthropods, especially insects, are abundantly preserved as cuticular remains (Briggs, 1999). Numerous taphonomic experiments have demonstrated that the exoskeleton of arthropods is more decay-resistant than other portions of the animals (Duncan, 1997; Stankiewicz *et al.*, 1998; Gupta *et al.*, 2006). The special structure of cuticle must contribute to its higher potential to be preserved than other tissues (Briggs, 1999; Gupta & Briggs, 2011). The living insect cuticle consists of an outer waxy epicuticle lack of chitin and a procuticle composed of chitin fibers embedded in a protein matrix, cross-linked by catechol, aspartate and histidyl moieties (Evans, 1984; Schaefer *et al.*, 1987, Gupta *et al.*, 2006). According to the decaying experiments (Duncan, 1997; Stankiewicz *et al.*, 1998; Gupta *et al.*, 2006), significant chemical and structural decay of the arthropod cuticle is evident after two to fifteen weeks, and the time is specifically dependent. From the structural level, the proteinaceous matrix decayed first, then chitinous microfibrils, whereas the epicuticle did not show any traces of structural breakdown, in spite of the decaying procuticle (Duncan, 1997). From the molecular level, the proteins decayed first, then the chitin, and the lipids forming the epicuticle changed last (Stankiewicz *et al.*, 1998; Gupta *et al.*, 2006). In our case, the structural remains of the fossil cuticle included both the epicuticle and procuticle, which has not been revealed by the Shanwang insect yet. However, whether the Shanwang insect fossils have preserved any macromolecules requires more specimens to be extensively studied, which may provide additional information about the fossilization of cuticles and possible macromolecules.

The case study of this single Shanwang specimen displays the exquisite preservation quality allowing fine details to be preserved and visible at higher magnification. The fine details of the insect can enable the identification of features for further taxonomic and phylogenetic studies although these details have been largely been ignored by systematics works on Shanwang insects.

Conclusion

There remains considerable work to be undertaken to fully understand the diagenetic environment in which the Shanwang insects were preserved, yet the exquisite preservation is clearly a combination of early diagenetic, microbially induced mineralization, and later *in situ* weathering. Nevertheless, the fine detail can enable the identification of features for taxonomic and phylogenetic studies.

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