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Termite coprolites (Blattodea: Isoptera) from the Early Cretaceous of eastern Inner Mongolia, Northeast China

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Abstract

Well-preserved coprolites (fossil faecal pellets) were found from lignite seams of the Lower Cretaceous Huolinhe Formation at the Huolinhe Basin in eastern Inner Mongolia, Northeast China. These coprolites provide a combination of following features: oval to cylindrical shaped with six longitudinal ridges, hexagonal to elliptical cross-sections, and one blunt end and the other pointed end. According to these distinct features and their size range, the producers of these coprolites are attributed to termites. Termites were estimated to have originated in the earliest Cretaceous with an evolutionary radiation in the Early Cretaceous. The presence of wood debris in the coprolites indicate that the Early Cretaceous termites from the Huolinhe Basin had wood-feeding habits; and anatomical features displaying on the wood debris further suggest their feeding preference was coniferous wood. Besides, the results of a *k*-means clustering analysis performed for these coprolites indicate that three clusters with different proportion were present, suggesting the division of labor in termites' sociality existed as early as the Early Cretaceous.

Keywords: Insecta, coprolites, termites, Early Cretaceous, Huolinhe Formation

Introduction

Termites (Blattodea: Isoptera) represent one of the few lineages of eusocial insects, characterised by cooperative brood care, reproductive division of labor and multiple generations of adults within a colony (Korbon & Thorne, 2017). Modern termites are a relatively small clade, however, they are one of the most important group of insects in modern terrestrial ecosystems acting as recyclers of organic matter essential for feeding on degrading the

fixed carbon in woods, while regulating the soil properties and structure (Eggleton, 2011; Bignell, 2019). The closest living relative of termites is believed to be wood-feeding cockroaches *Cryptocercus*, based on morphological (e.g., Klass & Meier, 2006; Klass *et al.*, 2008) and molecular evidence (e.g., Lo *et al.*, 2000; Terry & Whiting, 2005; Kjer *et al.*, 2006; Pellens *et al.*, 2007; Inward *et al.*, 2007; Wipfler *et al.*, 2019). Thus, termites are assigned to Blattodea as a monophyletic group. Termites have been divided historically into informal sections of the “lower termites” and the “higher termites” based on the presence or absence of flagellate protistan taxa in their hindguts (Engel & Delclòs, 2010). The “lower termites” comprise the families Kalotermitidae, Rhinotermitidae, Mastotermitidae, Hodotermitidae, Termopsidae, and Serritermitidae, while the “higher termites” only include the derived family Termitidae.

An estimated age of the termite origin is at least the earliest Lower Cretaceous based on phylogenetic analysis (Thorne *et al.*, 2000; Engel *et al.*, 2009; Korb, 2010; Bourguignon *et al.*, 2015; Jouault *et al.*, 2021), however, their earliest recorded fossils date back to just the Early Cretaceous (Engel & Delclòs, 2010; Vršanský & Aristov, 2014). So far, the earliest known fossil termites were believed to be the wings of *Valditermes brenanae* from the Hauterivian of England (Jarzembski, 1981) and the body fossils of *Meiatermes bertrani* found from the Barremian of Spain (Lacasa-Ruiz & Martínez-Delclòs, 1986). Two fossil termites, *Melqartitermes myrrheus* and *Lebanotermes veltzae*, were described (however with other unnamed termites) from two Early Cretaceous outcrops of amber from Lebanon (Engel *et al.*, 2007, 2011). Lebanese amber was initially attributed to the Early Aptian (Engel *et al.*, 2011), but nowadays this material is ascribed to the lower Barremian (Maksoud *et al.*, 2017), suggesting that

the Lebanese amber termites represent ones of the oldest termites so far known. Besides, termite coprolites in a wood-boring reported from the Berriasian of Brazil (Pires & Sommer, 2009) could represent the earliest termites in the trace fossil record. Numerous 'basal' termites reported by recent fossil studies, especially those from amber deposits, suggest that an important evolutionary radiation of termites occurred during the Cretaceous (e.g., Engel *et al.*, 2007; Grimaldi *et al.*, 2008; Zhao *et al.*, 2020a, b; Jouault *et al.*, 2021). Both body and trace fossils of termites are known from the Cretaceous around the world (Colin *et al.*, 2011), but the record reported from the Cretaceous of China were just body fossils and mainly distributed in Beijing region (Ren *et al.*, 1995).

Herein we provide fossil evidence of termite coprolites from lignite seams of the Lower Cretaceous Huolinhe Formation (late Barremian to early Aptian) in the eastern Inner Mongolia, Northeast China. Although coprolites of termites are known from the Early Cretaceous to the Holocene over the world (e.g., Rogers, 1938; Rohr, 1986; Rozefelds & De Baar, 1991; Colin *et al.*, 2011; Moreau *et al.*, 2019; Zhao *et al.*, 2020a, b), this study consists of the first evidence of termites' coprolites in China. Coprolites studied here generally provide combinatorial features, including oval to cylindrical shaped with six longitudinal ridges and hexagonal to elliptical cross-sections, which are usually typical characteristics of termites' faecal pellets (e.g., Rohr, 1986; Collin *et al.*, 2011). Moreover, wood debris bearing identical anatomical features obtained from the coprolites indicate that termites from the Early

Cretaceous of the Huolinhe Basin had wood-feeding habits. A larger number of coprolites and clustering characters exhibited give an opportunity to indirectly understanding the evolution of the division of labor in termite sociality.

Geological setting

All fossil coprolites presented herein were collected from the Yilong open-cast coal mine ($N45^{\circ}32'49.1''$, $E119^{\circ}35'12.6''$) in Huolin Gol, eastern Inner Mongolia, northeastern China (Fig. 1). The Huolin Gol is located in the Huolinhe Basin, which is known as one of the important coal-bearing sedimentary basins formed during the Late Jurassic and Early Cretaceous (Li *et al.*, 1982; Deng, 1995). Within the basin the Huolinhe Formation (Fig. 1) is a sequence of terrestrial and fluvio-lacustrine-swamp deposits, up to 1700 m thick, which lies on the Late Jurassic–Early Cretaceous Xing'anling Volcanic Group (Li *et al.*, 1982; Deng, 1995). The Huolinhe Formation is further sub-divided into six members in ascending order based on the lithological characters: sandy conglomerate member, lower mudstone member, lower coal-bearing member, upper mudstone member, upper coal-bearing member, and top mudstone member (Fig. 1). Among these most of the high-quality coal strata and lignite seams occur in the lower coal-bearing member (Fig. 1; Deng, 1995).

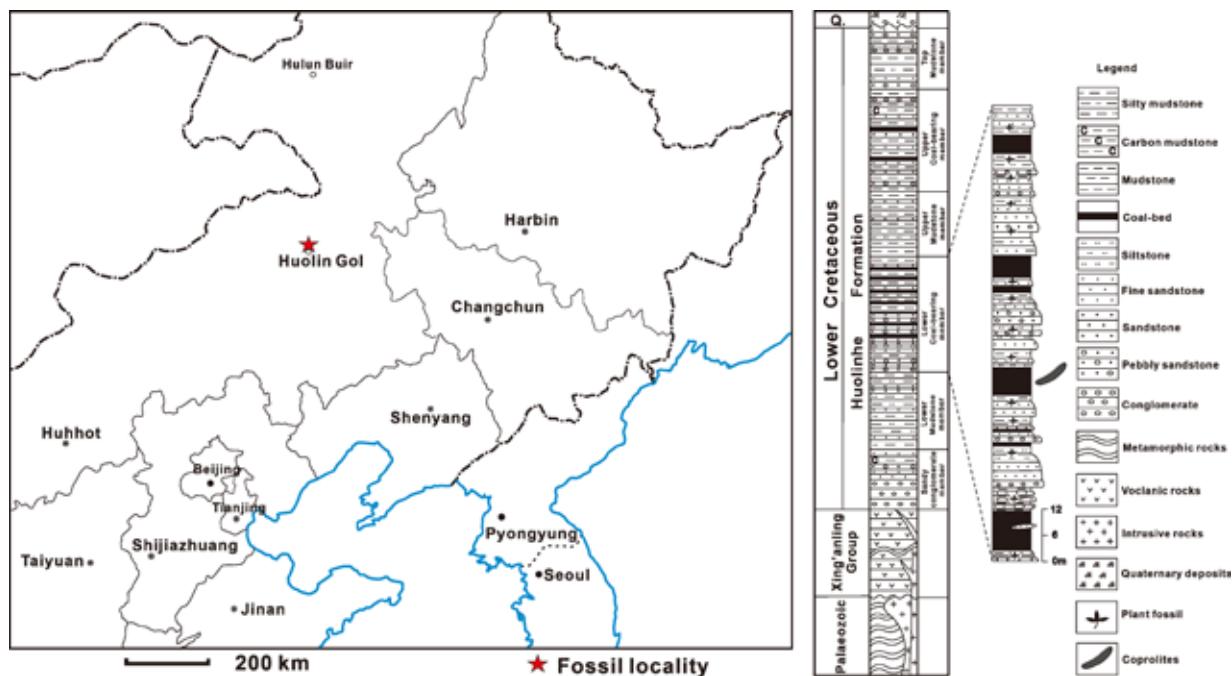


FIGURE 1. Locality map showing termite coprolites from the Yilong open-cast coal mine ($N45^{\circ}32'49.1''$, $E119^{\circ}35'12.6''$) in Huolin Gol, eastern Inner Mongolia, northeastern China (left) and the stratigraphic column of the Huolinhe Basin and the horizon of the lower coal-bearing member in the Lower Cretaceous Huolinhe Formation where the fossil were collected (right, revised from Deng, 1995).

All termite coprolites were selected from one block of unconsolidated lignite collected at the intermediate seam of the lower coal-bearing member in the Huolinhe Formation (Fig. 1), which yields abundant well-preserved compressed fossils, charcoal fossils and silicified plant fossils (e.g., Deng, 1995; Mei & Cui, 1994; Cui, 1995; Guo, 1995; Shi *et al.*, 2021b). A maximum age of the Huolinhe Formation is constrained to be 125.6 ± 1.0 Ma (late Barremian–early Aptian) age according to U-Pb geochronology analyses on the recently discovered volcanic ash layer in the lowest part of the “lower coal-bearing member” (Shi *et al.*, 2021a). Furthermore, a late Barremian–earliest Aptian for the maximum age of the Huolinhe Formation is also supported by palynological assemblages associated with the ash layer (Shi *et al.*, 2021a).

Material and methods

Lignite samples were disaggregated in soap and water, cleaned with dilute hydrochloric and hydrofluoric acids. Specimens were then thoroughly washed and soaked in distilled water for one week, with changes of water every half day. The samples were then dried in air. Fossil coprolites were selected under a stereomicroscope with tweezers. The selected intact coprolites and broken fossil that could show cross-sections were mounted on standard stubs with conductive tape, coated with gold, and then observed and photographed using a SU 3500 scanning electron microscope (SEM) operated at 5–12 kV and 80–90 Pa, with working distances ranged from 5 to 25 mm, at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). To observe the cross-sections of fossil coprolites under the light microscope, we embedded some coprolites with resin. Then they were cut along the transverse section and ground to 30 μm thickness for transmitted light microscopy.

Besides, in order to examine the internal contents of coprolites, some of them were physically broken into pieces and were then cleaned with dilute hydrochloric and hydrofluoric acids and followed by maceration in nitric acid. After that, several pieces of wood debris were selected with a dissecting needle from the broken fossil pellets under a stereomicroscope, followed by mounted on permanent slides and visualized with Light Microscope (LM) and SEM. Light micrographs of transverse thin sections and wood debris were examined and photographed with different inference contrast illuminations using an Olympus BX53 microscope equipped with an Olympus DP73 camera system. The coprolites and their SEM stubs,

thin sections as well as wood debris slices are all stored in the NIGPAS.

For assessing the grouping features of these selected fossil coprolites from the Lower Cretaceous of the Huolinhe Basin, we measured the lengths and diameters of 200 fossil coprolites, all data of which are shown in Table 1. Linear relationship analysis for fossil lengths and diameters was completed in MATLAB R2014b. Additionally, the measured data formed three clusters using a *k*-means clustering algorithm in MATLAB R2014b. *K*-means clustering uses *k* previously established data clusters, then assigned each object to a cluster with the closest mean, according to Euclidean distance. These reassignments are repeatedly made until every observation remains in the cluster to which it was assigned before being compared with all other cluster means.

Results

Morphology

All fossil coprolites studied here are preserved as carbonaceous fossil without special internal organic texture. To obtain the statistically significant morphological features and size range of coprolites, we generally examined more than 200 fossil coprolites selected from the lignite samples from the Lower Cretaceous Huolinhe Formation of the Huolinhe Basin in eastern Inner Mongolia, Northeast China.

Coprolites herein are not squashed in preservation, fully exhibiting morphology in 3D version (Figs 2, 3). These coprolites are oval, elongated oblong to hexagonally cylindrical in shape (Figs 2, 3). They usually display one characteristic pointed end, with the other end often blunt, sometimes with a shallow central dimple (Figs 2, 3). According to the biometrical data from the measurements, our collected coprolites vary in size (Table 1). Their range in length is from 0.67 mm to 3.21 mm, most of them however usually between 0.8 mm and 1.5 mm (Figs 2, 3; Table 1). The diameter of coprolites is 0.25 mm to 1.16 mm, however most often between 0.40 mm to 0.62 mm (Figs 2, 3; Table 1). The outer surface of the coprolites is rough to slightly smooth in general. Ridges along the longitudinal axis are often obvious on the outer surface, extending from the pointed end to the other blunt end (Figs 2, 3). Small wood or plant fragments with unexplained features were sometimes observed attached to the outer surface. The cross-section of the coprolites generally is hexagonal, sub-hexagonal or elliptical in outline, with slightly rounded edges (Fig. 4A, B). All cross-sections were provided without special biological features both under the LM and SEM.

TABLE 1. Length (L) and diameter (D) data of termite coprolites from the intermediate lignite seam of the “lower coal-bearing member” of the Lower Cretaceous Huolinhe Formation at the Huolinhe Basin, eastern Inner Mongolia, China.

| No. | L (μm) | D (μm) | No. | L (μm) | D (μm) | No. | L. (μm) | D. (μm) | No. | L. (μm) | D. (μm) |
|-----|--------|--------|-----|--------|--------|-----|---------|---------|-----|---------|---------|
| 001 | 1311 | 515 | 051 | 981 | 974 | 101 | 957 | 459 | 151 | 1562 | 470 |
| 002 | 1238 | 527 | 052 | 1106 | 551 | 102 | 1655 | 506 | 152 | 1146 | 427 |
| 003 | 1399 | 637 | 053 | 1146 | 579 | 103 | 1836 | 672 | 153 | 1016 | 520 |
| 004 | 1184 | 564 | 054 | 1156 | 475 | 104 | 1282 | 562 | 154 | 1744 | 662 |
| 005 | 1446 | 623 | 055 | 1105 | 399 | 105 | 1176 | 531 | 155 | 1224 | 522 |
| 006 | 1337 | 434 | 056 | 925 | 413 | 106 | 1306 | 472 | 156 | 1330 | 466 |
| 007 | 1059 | 513 | 057 | 1172 | 494 | 107 | 1434 | 473 | 157 | 1161 | 518 |
| 008 | 1221 | 551 | 058 | 909 | 306 | 108 | 1695 | 464 | 158 | 1361 | 544 |
| 009 | 1309 | 543 | 059 | 1068 | 525 | 109 | 1676 | 481 | 159 | 1098 | 377 |
| 010 | 1279 | 581 | 060 | 1025 | 615 | 110 | 1583 | 414 | 160 | 964 | 499 |
| 011 | 1928 | 1165 | 061 | 1048 | 252 | 111 | 1336 | 440 | 161 | 900 | 448 |
| 012 | 1607 | 735 | 062 | 1032 | 538 | 112 | 1310 | 505 | 162 | 709 | 387 |
| 013 | 1586 | 654 | 063 | 707 | 389 | 113 | 1515 | 485 | 163 | 847 | 415 |
| 014 | 1071 | 508 | 064 | 940 | 462 | 114 | 1383 | 418 | 164 | 892 | 537 |
| 015 | 1724 | 476 | 065 | 1020 | 393 | 115 | 1106 | 188 | 165 | 766 | 327 |
| 016 | 1223 | 450 | 066 | 1036 | 491 | 116 | 1095 | 479 | 166 | 755 | 383 |
| 017 | 2880 | 805 | 067 | 1054 | 478 | 117 | 1171 | 426 | 167 | 863 | 487 |
| 018 | 2856 | 818 | 068 | 1019 | 483 | 118 | 1199 | 444 | 168 | 701 | 387 |
| 019 | 1891 | 479 | 069 | 867 | 448 | 119 | 1328 | 445 | 169 | 726 | 323 |
| 020 | 2865 | 759 | 070 | 762 | 380 | 120 | 1283 | 608 | 170 | 1017 | 345 |
| 021 | 2993 | 788 | 071 | 1062 | 614 | 121 | 1361 | 546 | 171 | 918 | 352 |
| 022 | 1354 | 556 | 072 | 2341 | 671 | 122 | 1361 | 546 | 172 | 733 | 384 |
| 023 | 1816 | 592 | 073 | 2785 | 775 | 123 | 1158 | 605 | 173 | 978 | 492 |
| 024 | 1585 | 465 | 074 | 1493 | 680 | 124 | 1295 | 566 | 174 | 1135 | 555 |
| 025 | 3208 | 725 | 075 | 1764 | 457 | 125 | 1093 | 456 | 175 | 1046 | 481 |
| 026 | 1296 | 465 | 076 | 995 | 519 | 126 | 1091 | 580 | 176 | 1107 | 518 |
| 027 | 2866 | 781 | 077 | 1681 | 529 | 127 | 1109 | 590 | 177 | 870 | 403 |
| 028 | 2924 | 590 | 078 | 1682 | 435 | 128 | 1073 | 465 | 178 | 792 | 340 |
| 029 | 2716 | 701 | 079 | 1543 | 646 | 129 | 1126 | 528 | 179 | 1025 | 448 |
| 030 | 2729 | 662 | 080 | 2588 | 668 | 130 | 1429 | 416 | 180 | 772 | 501 |
| 031 | 1053 | 550 | 081 | 3068 | 695 | 131 | 1027 | 482 | 181 | 1753 | 1028 |
| 032 | 1215 | 885 | 082 | 2790 | 550 | 132 | 1400 | 512 | 182 | 970 | 561 |
| 033 | 1922 | 541 | 083 | 2762 | 738 | 133 | 1112 | 572 | 183 | 1152 | 561 |
| 034 | 2246 | 629 | 084 | 1262 | 439 | 134 | 1241 | 506 | 184 | 827 | 470 |
| 035 | 1687 | 582 | 085 | 2798 | 728 | 135 | 891 | 432 | 185 | 907 | 491 |
| 036 | 1962 | 512 | 086 | 1730 | 554 | 136 | 947 | 472 | 186 | 1033 | 474 |
| 037 | 1363 | 443 | 087 | 1551 | 475 | 137 | 1005 | 470 | 187 | 972 | 431 |
| 038 | 1782 | 500 | 088 | 1111 | 542 | 138 | 1252 | 552 | 188 | 1042 | 593 |
| 039 | 2200 | 576 | 089 | 2735 | 801 | 139 | 1109 | 568 | 189 | 884 | 466 |
| 040 | 2239 | 594 | 090 | 2629 | 638 | 140 | 1131 | 472 | 190 | 951 | 446 |
| 041 | 1580 | 552 | 091 | 1547 | 557 | 141 | 1294 | 507 | 191 | 1181 | 541 |
| 042 | 2008 | 572 | 092 | 1597 | 587 | 142 | 1034 | 521 | 192 | 2170 | 1018 |
| 043 | 1524 | 446 | 093 | 2276 | 690 | 143 | 1071 | 548 | 193 | 1447 | 513 |
| 044 | 1826 | 504 | 094 | 2602 | 653 | 144 | 1258 | 523 | 194 | 959 | 493 |
| 045 | 2114 | 550 | 095 | 1227 | 532 | 145 | 1296 | 465 | 195 | 1055 | 426 |
| 046 | 1345 | 461 | 096 | 1301 | 456 | 146 | 931 | 453 | 196 | 966 | 550 |
| 047 | 1998 | 544 | 097 | 672 | 421 | 147 | 1431 | 403 | 197 | 1421 | 517 |
| 048 | 2092 | 542 | 098 | 1041 | 480 | 148 | 1033 | 406 | 198 | 1123 | 500 |
| 049 | 1806 | 514 | 099 | 1029 | 543 | 149 | 977 | 587 | 199 | 1165 | 531 |
| 050 | 1168 | 632 | 100 | 1531 | 749 | 150 | 977 | 535 | 200 | 1338 | 464 |

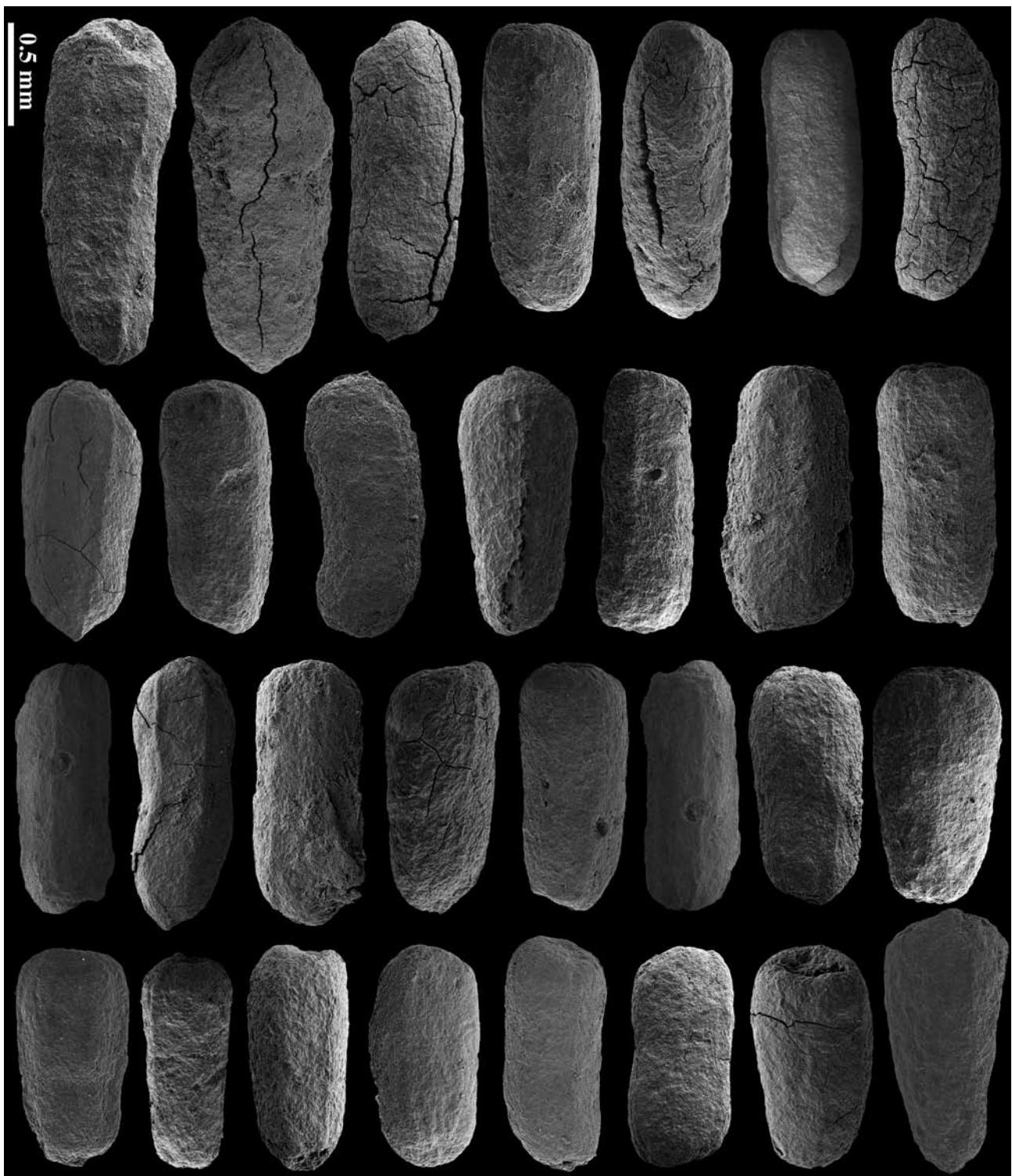


FIGURE 2. SEM images of small lignite termite coprolites from the Lower Cretaceous Huolinhe Formation showing their morphology.

Internal wood debris contained in coprolites

Through bulk maceration of physically broken coprolites, we obtained some identical wood debris from fossil coprolites (Fig. 5A–N). In general, most of the wood debris are radial sections, strip to amorphous, ranging from 100 µm to 500 µm in length and 10 µm to 100 µm in width, exhibiting several tracheid pits (Fig. 5B, C, D,

G, H, K, M), cross-fields (Fig. 5E, H, I), xylem rays (Fig. 5J), bundle of fibres (Fig. 5A), and fragmented secondary wood (Fig. 5L). In general, the tracheids are generally flattened, *ca.* 22–28 µm in diameter, bearing some uniseriate bordered pits which are circular to elliptical, *ca.* 15–20 µm in diameter, separated from each other (Fig. 5B, C, G). Walls between adjacent cells are clearly

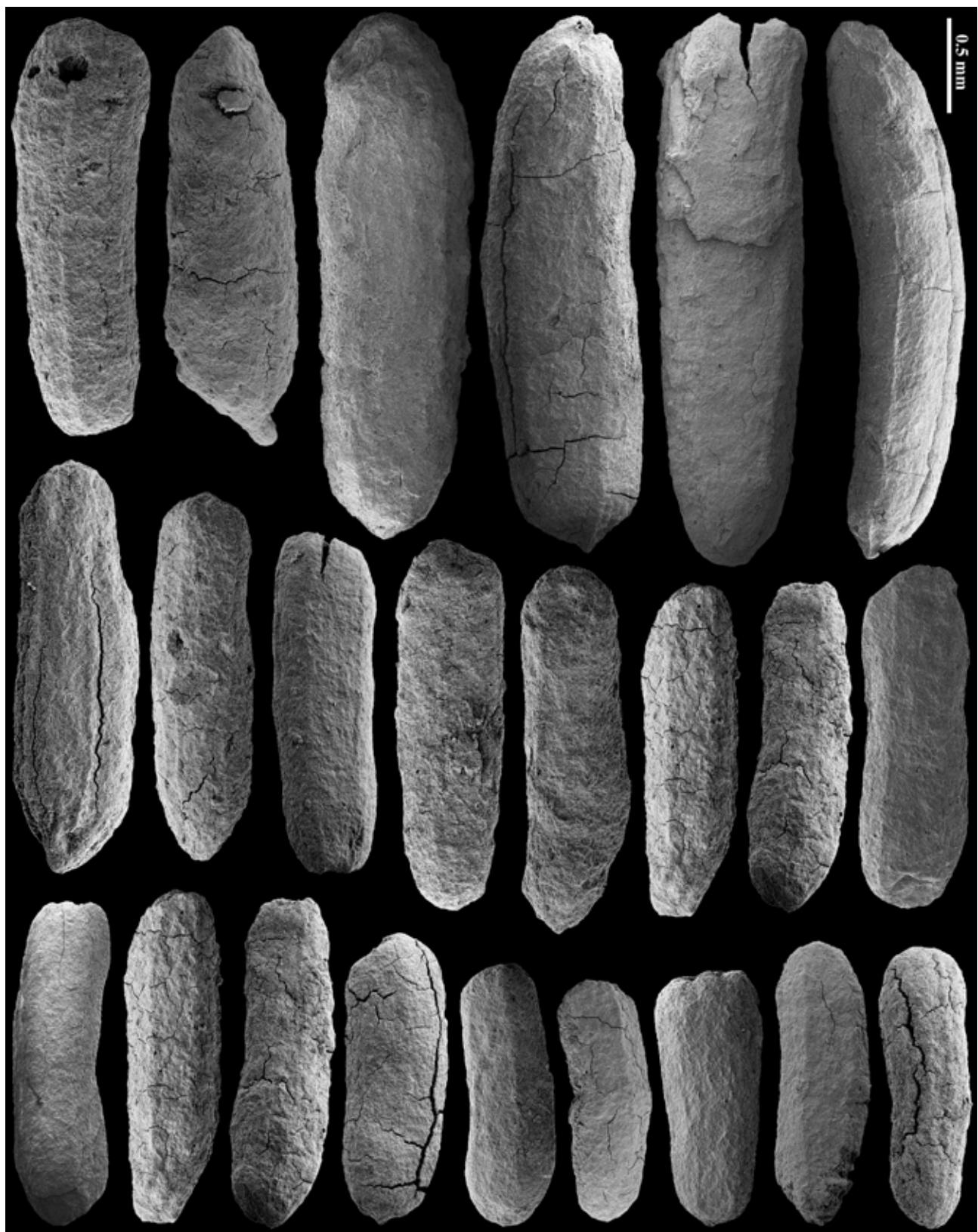


FIGURE 3. SEM images of moderate and large lignite termite coprolites from the Lower Cretaceous Huolinhe Formation showing their morphology.

homogenized and vary in width from 2 μm to 5 μm (Fig. 5J, K). Cross-fields are window-like, isodiametric, *ca.* 18–25 μm in length, and each bears one circular pit filling

almost the whole cross-field (Fig. 5E, H, I). Besides, a couple of uniserial xylem rays were also detected from the wood debris in SEM images (Fig. 5J, N).

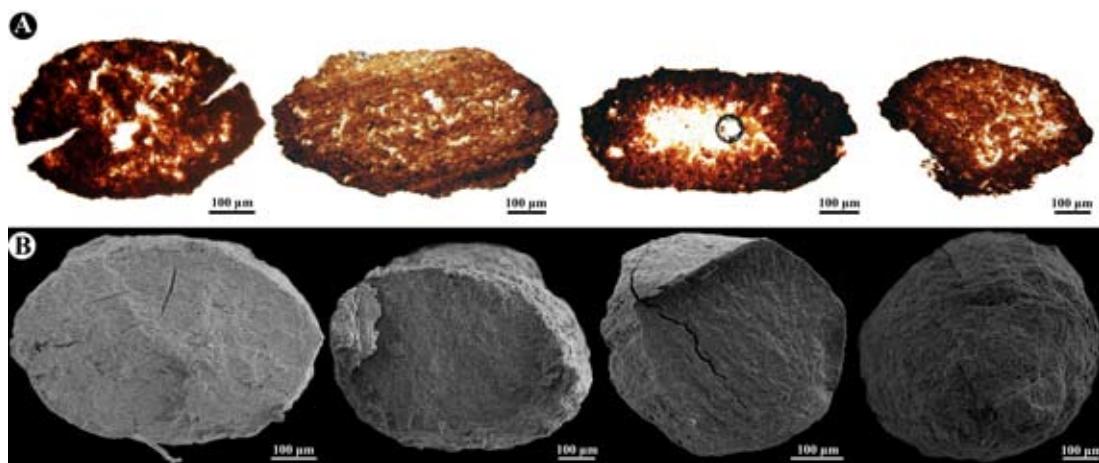


FIGURE 4. Light micrographs (A) and scanning electron micrographs (B) of transversal sections of termite coprolites showing hexagonal to rounded shape.

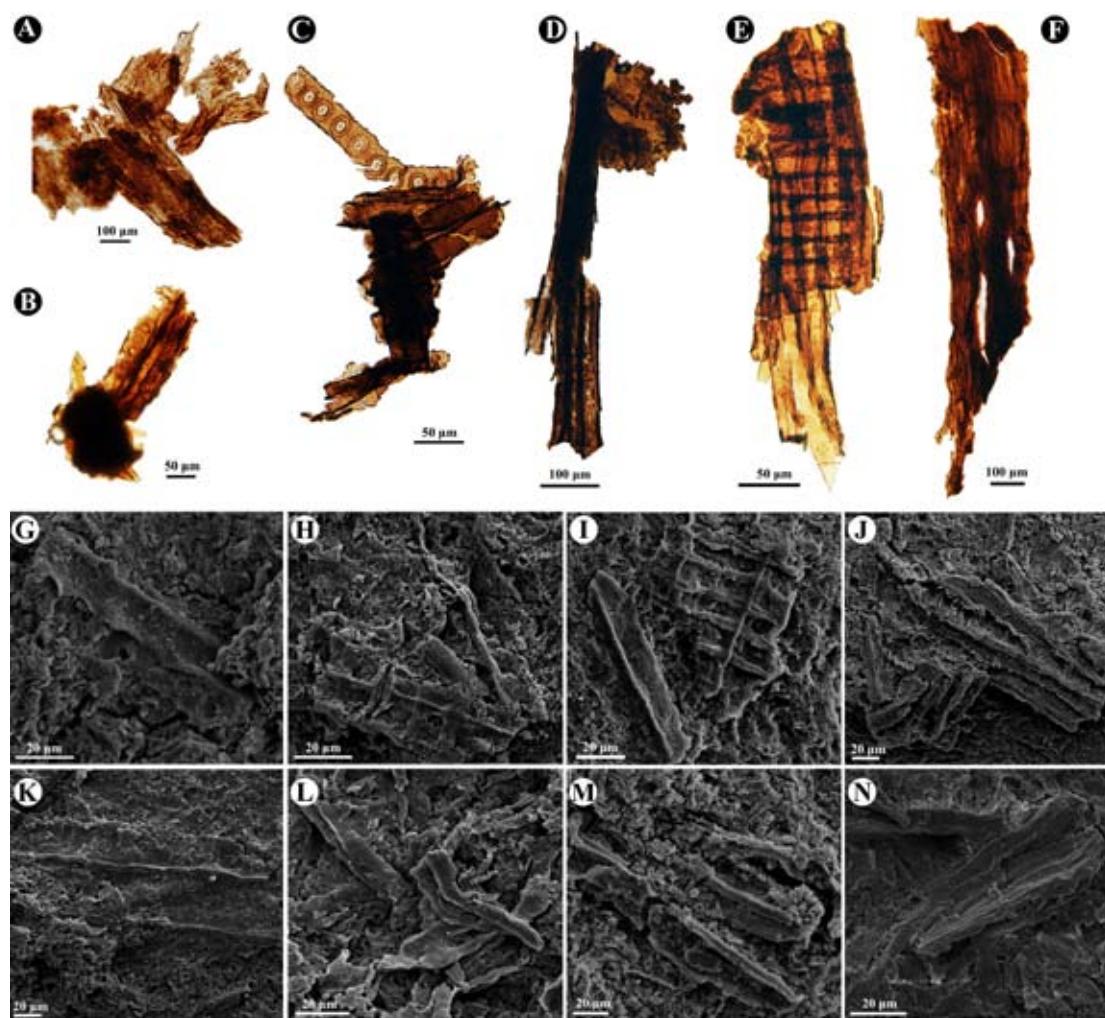


FIGURE 5. Light micrographs (A–F) and scanning electron micrographs (G–N) of wood debris macerated from the Lower Cretaceous Huolinhe Formation. **A**, Wood debris showing a bundle of fibres. **B**, Wood debris in radial section showing tracheid with separate uniseriate pits. **C**, Wood debris in radial section showing uniseriate tracheid pits. **D**, Wood debris in radial section showing tracheid. **E**, Wood-debris in radial section showing cross-field pits. **F**, Wood debris of radial section of structureless. **G**, Wood debris in radial section showing tracheid with uniserial tracheid bordered pits. **H–I**, Wood debris in radial section showing cross-field pits with homogenized cell walls. **J**, Wood debris in radial section showing uniseriate xylem rays. **K**, Wood debris in radial section showing tracheid with homogenized cell walls. **L**, Fragmented secondary wood. **M**, Wood debris of tracheid with homogenized cell walls. **N**, Wood debris in radial section showing uniseriate xylem rays.

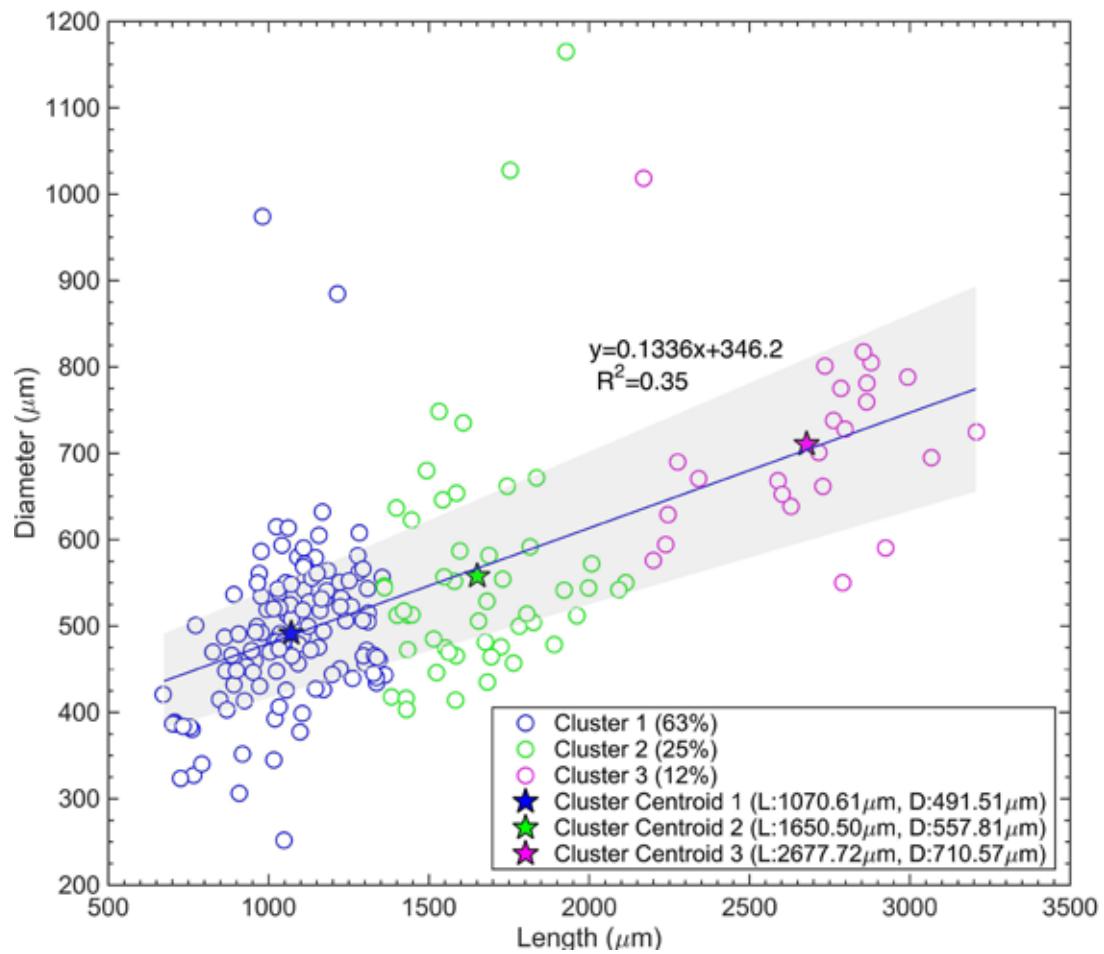


FIGURE 6. Scatter plots (N=200) and linear regression lines of the length and diameter of termite coprolites from the Lower Cretaceous Huolinhe Formation in eastern Inner Mongolia, China. The grey shading represents the 95% confidence interval of linear relationship. Note scatter plots depicting a *k*-means clustering analysis reveals three groups, indicated by circles of different colours; stars of different colour mean the clusters centroids which are the average length and diameter.

Linear regression and k-means cluster analysis based on length and diameter of coprolites

Our measurement data (Table 1) based on 200 fossil materials shows that these coprolites are mostly ranging from *ca.* 0.7 mm to 3.15 mm in length and *ca.* 0.31 to 0.81 mm in diameter, with a length/diameter ratio ranging from 1.0 to 5.9 (Fig. 6). According to the linear regression analysis of the length to diameter, we found that the coprolite length has a low positive relationship with diameter ($R^2=0.35$; Fig. 6).

The *k*-means algorithm is a clustering algorithm based on iterative solution. It uses distance as the index of similarity, meaning that the closer the two data points are, the greater the similarity. In this study, a *k*-means clustering analysis (Fig. 6) was performed on the dataset measured on coprolites collected from the Early Cretaceous of the Huolinhe Basin. With simultaneous measurements of length and diameter of coprolites, three clusters were categorised and interpreted (Fig. 6). In these clusters, cluster 1 accounted for 63% of the total fossil coprolites.

Coprolites in cluster 1 range from 0.67 mm to 1.35 mm in length, with an average length of *ca.* 1.07 mm, and they range from 0.25 mm to 0.65 mm in diameter, with an average diameter of *ca.* 0.49 mm (Fig. 6). Coprolites in cluster 2 accounted for 25% of the measurement data, which are 1.35 mm to 2.15 mm in length and 0.40 mm to 1.17 mm in diameter, with an average length of *ca.* 1.65 mm and an average diameter of *ca.* 0.56 mm (Fig. 6). Coprolites in cluster 3 are fewer, which accounted for 12% of the total coprolites data. Coprolites in cluster 3 are more elongated, generally longer and slightly thicker, ranging from 2.2 mm to 3.21 mm in length and 0.56 mm to 1.02 mm in diameter, with an average length of *ca.* 2.68 mm and an average diameter of *ca.* 0.71 mm (Fig. 6).

Discussion

Identification of coprolites

In general, coprolites studied here are no more than 3.15

mm in length and 0.81 mm in diameter, with numerous wood debris present in their internal contents, suggesting that they were produced by wood-feeding insects rather than other animals. Among modern insects, wood-feeding habits are most common in termites, beetles, and some cockroaches (Eaton & Hale, 1993). Larvae of many wood-boring beetle groups feed on wood, and they produce pellets that are much smaller than the Huolinhe Basin fossil pellets, besides they are generally ellipsoid or rounded in shape rather than hexagonal (Cichan & Taylor, 1982; Francis & Harland, 2006). The extant wood-eating cockroach *Cryptocercus* (Cryptocercidae) provides solid faecal pellets that look like cylindrical in shape and have six ridges running from one end to another, but they are usually larger, with length can up to *ca.* 4.5 mm (Sweetman, 1965; Rohr, 1986), which differs in the Huolinhe Basin coprolites in bearing a range of lengths no more than 3.15 mm (Figs 1, 6; Table 1). However, some modern cockroach species produce faecal pellets are variable in size, which makes it difficult to completely preclude the coprolites studied here from those of cockroach droppings only based on the slight difference in the lengths. Termites are a group of cellulose-feeding insects that produce droppings with varied appearance depending on the kind of species. However, they are generally small with oval to cylindrical shapes, possessing one rounded end and one pointed end, and six-sides running from one end to the other (Boucot, 1990; Genise, 1995; Collin *et al.*, 2011). Coprolites studied here closely resemble faecal pellets of modern termites in having the following combination of characters: (a) longitudinally striated and oval to cylindrical shaped; (b) one end pointed and the other blunt, sometimes with a shallow central dimple; (c) hexagonal, sub-hexagonal to elliptical in cross-section; (d) six longitudinal ridges present on outer surface; (e) lacking internal organic texture (e.g., Rohr, 1986; Boucot, 1990; Genise, 1995; Collin *et al.*, 2011).

Among modern termites, Kalotermitidae (e.g., *Kalotermes*) and Mastotermitidae (*Mastotermes*) produce faecal pellets that typically are longitudinally striated and hexagonal cylinders with one end blunt and the other more pointed; each side has a longitudinal groove, formed by three pairs of anal muscles (Collin *et al.*, 2011). Coprolites from the Lower Cretaceous of the Huolinhe Basin fit quite well with these morphological features. Besides, both of these two modern termite taxa provide solid pellets more susceptible to fossilization, whereas other termite families produce pasty to liquid faeces or pellets often losing their distinctive shape and forming amorphous clumps (Rohr, 1986; Collin *et al.*, 2011). Most similar to the coprolites studied here are the pellets of the modern taxa *Mastotermes darwiniensis* (Mastotermitidae) and *Kalotermes* spp. (Kalotermitidae), both of which exhibit an oblong, oval or cylindrical shape, a hexagonal cross-

section, and one blunt end and the other more pointed end (Colin *et al.*, 2011; Moreau *et al.*, 2019). Faecal pellets of modern *Kalotermes* spp. and *M. darwiniensis* were figured by Collin *et al.* (2011), in which they described pellets of modern *Kalotermes* spp. are 0.65 mm long and 0.3 mm wide, and modern *M. darwiniensis* are 1.0–1.2 mm long. It seems that both above-mentioned extant taxa of termites provide smaller pellets than the coprolites (0.67–3.21 mm long and 0.8–1.5 mm wide) from the Lower Cretaceous of the Huolinhe Basin. The sizes of the pellets of *M. darwiniensis* measured by Colin *et al.* (2011) are within the size range of the Huolinhe Basin coprolites. However, the size of extant termite faecal pellets look like they were counted by Colin *et al.* (2011) based only on a couple of samples, whereas the sizes of the coprolites studied here are measured from a series of datasets based on a larger number of pellets (over 200). Therefore, we suppose that coprolites from the Lower Cretaceous of the Huolinhe Basin are most comparable to those of *M. darwiniensis* among extant termites. It is interesting that *M. darwiniensis* is resolved as the most ‘inclusive’ living termite in the phylogenetic analyses based on both molecular and morphological data (e.g., Lo *et al.*, 2000; Terry & Whiting, 2005; Kjer *et al.*, 2006; Pellens *et al.*, 2007; Inward *et al.*, 2007; Wipfler *et al.*, 2019; Jouault *et al.*, 2021). However, these coprolites are preserved just as trace fossils, whole body fossils or fragments of termites have never been found in the Lower Cretaceous Huolinhe Formation in the eastern Inner Mongolia. Thus, it is not possible to ascribe these coprolites to any precise family of modern termites.

We cannot conclude if the differences observed in the lengths among the smaller (0.67–1.35 mm) coprolites cluster, the moderate (1.35–2.15 mm) and the larger clusters (2.20–3.21 mm) correspond to different species. However, all the coprolites analysed here were selected from a lignite sample collected from one block, while no similar fossil faecal pellets were found in other blocks from the same collection site. Therefore, it is suggested that all coprolites in this study most likely came from the same nest. Moreover, a large number of extant cumulative faecal pellets are generally found in the termite nests, often used as building materials (Stuart, 1969), indirectly supporting the hypothesis that the Huolinhe Basin coprolites are most probably from the same nest.

Termite coprolites have never been reported from any deposits of China, but worldwide they are rather common in the Cretaceous and Cenozoic fossil records including preserved in wood borings, lignified sediments, and amber (Colin *et al.*, 2011). However, most termite coprolites records are either simple reports lacking detailed features or those with poor preservation, which leads to a difficult comparison with the Early Cretaceous coprolites from the Huolinhe Basin, Northeast China.

Rogers (1938) first formally assigned some pellets in wood borings from the Pliocene of California to termites based on a characteristic hexagonal cross-section. Lance (1946) latter identified similar termite coprolites from the Pleistocene of California, and he further attributed to species of *Kalotermes* (Kalotermitidae). Afterwards well-preserved termite coprolites were sequentially recognised in wood borings from the Early Cretaceous of the UK, the Late Cretaceous of western USA, the Eocene–Oligocene of France, and early Miocene of New Zealand (Table 2; Rohr, 1986; Sutherland, 2003; Francis & Harland, 2006; Moreau *et al.*, 2019). All these above-mentioned termite coprolites are similar to those from the Huolinhe Basin in having hexagonal or sub-hexagonal cross-sections; besides, the range of their size is also within the one of the Inner Mongolia coprolites. Coprolites records of termites found in wood-boring from the Lower Cretaceous of Brazil (Berriasian) exhibit similar hexagonal cross-section with the coprolites studied here, but have a relatively smaller size (0.07–0.32 mm long and 0.16–0.23 mm wide) (Pires & Sommer, 2009). Rozefelds & De Baar (1991) identified some termite coprolites that they assigned to the Kalotermitidae from an Oligocene rainforest in

central Queensland, Australia; these Oligocene coprolites fit well with the larger ones from the Lower Cretaceous of the Huolinhe Basin, in oblong oval shape, hexagonal cross-section, as well as in the length and diameter (Table 2). However, the Queensland material is more uniform in size (2.0–2.6 mm long and 0.8–1.0 mm wide), while those of the Huolinhe Basin include a wider range of size (0.67–3.21 mm in length and 0.25–1.16 mm in diameter). Zhao *et al.* (2020a, b) mentioned coprolites preserved associated with several termite bodies in colonies from the mid-Cretaceous Burmese amber. The Burmese amber termite coprolites are different from those of the Huolinhe Basin in their irregular or rice-shapes with inconspicuous lateral ridges. Similar well-preserved coprolites from the mid-Cretaceous amber-bearing or lignified sediments of France were attributed to termites and recognized as *Microcarpolithes hexagonalis* (Colin *et al.*, 2011); they resemble the coprolites studied here in exhibiting ovoid or cylinder shapes and hexagonal cross-sections. However, the larger coprolites observed from the mid-Cretaceous of France are no more than 1.45 mm long, and most often between 0.50 mm and 0.75 mm, thus smaller than those from the Huolinhe Basin (Fig. 6; Table 2).

TABLE 2. Comparison of coprolites studied here to termite coprolites with detailed features reported from the Cretaceous and the Cenozoic.

| References | Age | Region | Preservation | Shape | Cross-section | Length (mm) | Diameter (mm) |
|------------------------------------|--------------------------------|-------------|--|------------------------|--------------------------|-------------|---------------|
| This study | late Barremian–earliest Aptian | China | lignite | ovoid, cylinder | hexagonal, sub-hexagonal | 0.67–3.21 | 0.25–1.16 |
| Pires & Sommer, 2009 | Berriasian | Brazil | wood borings | ? | hexagonal | 0.07–0.32 | 0.16–0.23 |
| Francis & Harland, 2006 | Barremian | UK | wood borings | ? | hexagonal | 0.4–0.6 | 0.4–0.5 |
| Colin <i>et al.</i> , 2011 | Late Albian to Cenomanian | France | lignitic clay, amber-bearing sediments | oblong? | hexagonal | 0.26–1.45 | 0.30–0.40 |
| Zhao <i>et al.</i> , 2020a, b | Cenomanian | Burmese | amber | irregular, rice-shaped | ? | 0.66–0.73 | 0.26–0.35 |
| Rohr, 1986; Grimaldi & Engel, 2005 | Upper Maastrichtian | USA | wood-borings | ? | Sub-hexagonal | 0.75 | 0.5 |
| Moreau <i>et al.</i> , 2019 | Eocene–Oligocene | France | wood-borings | oblong | hexagonal | 0.47–0.615 | 0.22–0.325 |
| Rozefelds & De Baar, 1991 | Oligocene | Australia | lignified silcrete blocks | oblong oval | hexagonal | 2.0–2.6 | 0.8–1.0 |
| Sutherland, 2003 | Early Miocene | New Zealand | wood-borings | ? | hexagonal | 1.0 | 0.5 |
| Roger, 1938 | Pliocene | USA | wood-borings | elongate | hexagonal | 0.7–0.9 | 0.3–0.5 |

Feeding habits of coprolites' producers

Most termites, especially the 'lower' termites, in nature feed solely on wood, which is primarily made up of cellulose (Cleveland, 1923). 'Lower' termites can consume and digest cellulose because they are equipped with special mouthparts for chewing wood as well as they have microorganisms such as bacteria and protozoans in their hind guts, which enable termites to break down cellulose into digestible substances (e.g., Bignell & Eggleton, 2000; Traniello & Leuthold, 2000). Such feeding habits make termites as ones of the Earth's most abundant and active decomposers of lignocellulosic plant materials in terrestrial ecosystems (Dangerfield *et al.*, 1998). According to their feeding habits, modern termites often are divided into three groups: dry-wood termites, damp-wood termites, and subterranean termites (Rohr, 1986). Subterranean termites live partly or entirely within the ground and produce liquid faeces. Dry-wood termites and damp-wood forms live inside wood, and both produce solid faecal pellets, which can more easily retain their shape and be fossilised (Rohr, 1986). The shape of the termite coprolites studied here were preserved as solid pellets and provided with detailed morphological features, suggesting their producers were wood-feeding habits. Moreover, the soil-feeding habit of higher termites did not appear until the Cenozoic (Engel, 2009; Buček *et al.*, 2019), the earlier termites from the Mesozoic were generally known as the lower ones and involved with wood-feeding. Therefore, the termites producing these coprolites from the Lower Cretaceous of the Huolinhe Basin were obviously feeding on wood, just like those modern 'lower' termites.

As termite diet consists of cellulose from wood, their faecal pellets are easily containing small undigested wood debris, some of which even keep certain original wood's microstructural features including tracheid pits and cross-field pits. Thus, an indirect insight into what termites from the Early Cretaceous of the Huolinhe Basin ate can be obtained by examining undigested wood debris contained in the coprolites. According to the presence of the tracheid with very flattened uniserial circular to elliptical bordered pits and homogenised cell walls, the window-like cross-fields occupied by circular pits, as well as uniseriate xylem rays and the bundle of fibres (Fig. 5A–N), these fossil debris contained in fossil coprolites from the Huolinhe Basin are most likely from coniferous wood. Thus, although wood-borings with termite traces have not been found from the Early Cretaceous of the Huolinhe Basin, we supposed the producers of these termites' coprolites mainly fed on wood of conifers and probably dwelled in coniferous wood. It is consistent with the fact that carbonised-wood fossils found from the Lower Cretaceous Huolinhe Formation are also mainly

conifers, including Podocarpaceae (*Podocarpoxylon* and *Phyllocladoxylon*), Pinaceae (*Prorocedroxylon* and *Cedroxylon*), Taxaceae (*Taxoxylon*), and *Xenoxylon* (Mei & Cui, 1994; Cui, 1995).

Social behavior of coprolites' producers

All extant termites are eusocial, with individuals having specialized tasks divided in reproduction, foraging, and commonly defence and brood care (Wilson & Hölldobler, 2005). According to the division of labor, termite caste differentiation can be further divided into two kinds: reproductive individuals and sterile individuals, the latter including workers and soldiers. Each caste in the termite's nest performs its own functions, which are interdependent. The soldiers defend the colony from attack, while worker termites are responsible for building nests, caring for the immatures or the queen, and searching out and collecting food for the termite colony (Wilson & Hölldobler, 2005). Therefore, the workers, soldiers and/or immatures in a eusocial colony are the key clues for tracing the social behaviours of the termites.

The morphological specializations of the different termite castes and eusocial aggregations from colonies in mid-Cretaceous have been reported from Burmese amber, suggesting that the termites possessed advanced eusociality as earlier as in the mid-Cretaceous (Engel *et al.*, 2016a, b; Zhao *et al.*, 2019, 2020a). However, the divergence time of termites was suggested as occurring in at least the earliest Lower Cretaceous based on both fossil records and molecular data (Bourguignon *et al.*, 2015; Engel *et al.*, 2016a, b; Evangelista *et al.*, 2019; Jouault *et al.*, 2021). According to the *k*-means cluster analysis for 200 termite coprolites studied here, three clusters of coprolites were identified based on their differences in lengths and diameters (Fig. 6). In a mature modern termite nest, workers make up the majority and the soldiers are minor in the colony, while the rest, excepting for a very small population of reproductive individuals, are larvae/immatures (Zhao *et al.*, 2020b). It is of interest that three clusters and their proportions obtained in clustering analysis correspond quite well with the population and compositing proportion in a modern termite nest. The coincident fact plus the assumption that coprolites were from the same nest together indicate the producers of the new coprolites were representing the different termite castes, perhaps separately representing workers, soldiers, and immatures. Therefore, although body fossils of termites are unknown, these coprolites and their clusters' feature would suggest that a division of the society into casts corresponding to different body sizes was already present in the corresponding termite species, supporting the hypothesis that eusociality among termites has evolved even by the Early Cretaceous (late Barremian to early Aptian).

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References

Bignell, D.E. (2019) Termite ecology in the first two decades of the 21st century: a review of reviews. *Insects*, 10, 1–10. <https://doi.org/10.3390/insects10030060>

Bignell, D.E. & Eggleton, P. (2000) *Termites in ecosystems*. In: Abe, T., Bignell, D.E. & Higashi, M. (Eds), *Termites: evolution, sociality, symbioses, ecology*. Kluwer Academic Publications, Dordrecht, pp. 363–387. https://doi.org/10.1007/978-94-017-3223-9_17

Boucot, A.J. (1990) *Evolutionary paleobiology of behavior and coevolution*. Elsevier, New York, 750 pp.

Bourguignon, T., Lo, N., Cameron, S.L., Šobotník, J., Hayashi, Y., Shigenobu, S., Watanabe, D., Roisin, Y., Miura, T. & Evans, T.A. (2015) The evolutionary history of termites as inferred from 66 mitochondrial genomes. *Molecular Biology and Evolution*, 32, 406–421. <https://doi.org/10.1093/molbev/msu308>

Buček, A., Šobotník, J., He, S., Shi, M., McMahon, D.P., Holmes, E.C., Roisin, Y., Lo, N. & Bourguignon, T. (2019) Evolution of termite symbiosis informed by transcriptome-based phylogenies. *Current Biology*, 29, 1–7. <https://doi.org/10.1016/j.cub.2019.08.076>

Cleveland, L.R. (1923) Correlation between the food and morphology of termites and the presence of intestinal protozoa. *American Journal of Hygiene*, 3, 444–461. <https://doi.org/10.1093/oxfordjournals.aje.a118946>

Colin, J.P., Néraudeau, D., Nel, A. & Perrichot, V. (2011) Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. *Revue de Micropaléontologie*, 54, 129–139. <https://doi.org/10.1016/j.revmic.2011.06.001>

Cui, J.Z. (1995) Studies on the fusinized-wood fossils of Podocarpaceae from Huolinhe Coalfield, Inner Mongolia, China. *Acta Botanica Sinica*, 37, 636–640. [In Chinese with English abstract]

Dangerfield, J.M., McCarthy, T.S. & Ellery, W.N. (1998) The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology*, 14, 507–520. <https://doi.org/10.1017/S0266467498000364>

Deng, S.H. (1995) *Early Cretaceous flora of Huolinhe Basin, Inner Mongolia, Northeast China*. Geological Publishing House, Beijing. pp. 1–115.

Eaton, R.A. & Hale, M.D.C. (1993) *Wood. Decay, pests and protection*. Chapman and Hall, London, 546 pp.

Eggleton, P. (2011) *An introduction to termites: biology, taxonomy and functional morphology*. In: Bignell, D.E., Roisin, Y., Lo, N. (Eds), *Biology of termites: A modern synthesis*. Springer, Netherlands, pp. 1–26. https://doi.org/10.1007/978-90-481-3977-4_1

Engel, M.S. & Delclòs, X. (2010) Primitive termites in Cretaceous amber from Spain and Canada (Isoptera). *Journal of the Kansas Entomological Society*, 83, 111–128. <https://doi.org/10.2317/JKES0908.06.1>

Engel, M.S., Grimaldi, D.A. & Krishna, K. (2007) Primitive termites from the Early Cretaceous of Asia (Isoptera). *Stuttgarter Beiträge zur Naturkunde Serie B*, 371, 1–32.

Engel, M.S., Grimaldi, D.A. & Krishna, K. (2009) Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *American Museum Novitates*, 3650, 1–27. <https://doi.org/10.1206/651.1>

Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.P. & Perrichot, V. (2011) New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. *Palaeodiversity*, 4, 39–49. <http://hdl.handle.net/1808/13199>

Engel, M.S., Barden, P., Riccio, M.L. & Grimaldi, D.A. (2016a) Morphologically specialized termite castes and advanced sociality in the early cretaceous. *Current Biology*, 26, 522–530. <https://doi.org/10.1016/j.cub.2015.12.061>

Engel, M.S., Barden, P.M. & Grimaldi, D.A. (2016b) A replacement name for the cretaceous termite genus *Gigantotermes* (Isoptera). *Novitates Paleoentomologicae*, 14, 1–2. <https://doi.org/10.17161/np.v0i14.5694>

Evangelista, D.A., Wipfler, B., Béthoux, O., Donath, A., Fujita, M., Kohli, M.K., Legendre, F., Liu S.L., Machida, R., Misof, B., Peters, R.S., Podsiadlowski, L., Rust, J., Schuette, K., Tollenaar, W., Ware, J.L., Wappler, T., Zhou, X., Meusemann, K. & Simon, S. (2019) An integrative phylogenomic approach illuminates the evolutionary history of cockroaches and termites (Blattodea). *Proceedings of the Royal Society B*, 286, 20182076. <https://doi.org/10.1098/rspb.2018.2076>

Francis, J.E. & Harland, B.M. (2006) Termite borings in Early Cretaceous fossil wood, Isle of Wight, UK. *Cretaceous Research*, 27, 773–777. <https://doi.org/10.1016/j.cretres.2006.02.001>

Genise, J.F. (1995) Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. *Ichnos*, 3, 287–299.
<https://doi.org/10.1080/10420949509386399>

Grimaldi, D.A., Engel, M.S. & Krishna, K. (2008) The species of Isoptera (Insecta) from the Early Cretaceous Crato Formation: A Revision. *American Museum Novitates*, 3626, 1–30.

Guo, C.J. (1995) Sporopollen from the lower part of the Huolinhe Formation, Huolinhe Basin, Inner Mongolia and its significance. *Petroleum Exploration and Development*, 22, 37–44. [In Chinese with English abstract]

Inward, D.J., Vogler, A.P. & Eggleton, P. (2007) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters*, 3, 331–335.
<https://doi.org/10.1098/rsbl.2007.0102>

Jarzembowski, E.A. (1981) An early Cretaceous termite from southern England (Isoptera Hodotermitidae). *Systematic Entomology*, 6, 91–96.
<https://doi.org/10.1111/j.1365-3113.1981.tb00018.x>

Jouault, C., Legendre, F., Grandcolas, P. & Nel, A. (2021) Revising dating estimates and the antiquity of eusociality in termites using the fossilized birth-death process. *Systematic Entomology*, 46, 592–610.
<https://doi.org/10.1111/syen.12477>

Kjer, K.M., Carle, F.L., Litman, J. & Ware, J. (2006) A molecular phylogeny of Hexapoda. *Arthropod Systematics Phylogeny*, 64, 35–44.

Klass, K.D. & Meier, R. (2006) A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. *Entomologische Abhandlungen*, 63 (12), 3–50.

Klass, K.D., Nalepa, C. & Lo, N. (2008) Wood-feeding cockroaches as models for termite evolution (Insecta: Dictyoptera): *Cryptocercus* vs. *Parasphaeria boleiriana*. *Molecular Phylogenetics and Evolution*, 46, 809–817.
<https://doi.org/10.1016/j.ympev.2007.11.028>

Korb, J. (2010) *The ecology of social evolution in termites, ecology of social evolution*. Springer Verlag, Berlin Heidelberg, pp. 151–174.
https://doi.org/10.1007/978-3-540-75957-7_7

Korb, J. & Thorne, B. (2017) Society in termites. In: Rubenstein, D.R. & Abbot, P. (Eds), *Comparative social evolution*. Cambridge University Press, New York, pp. 124–153.
<https://doi.org/10.1017/9781107338319.006>

Lacasa-Ruiz, A. & Martínez-Delclòs, X. (1986) *Maiatermes. Nuevo género fósil de insecto isóptero (Hodotermitidae) de las calizas Nocomienses del Montsec (Provincia de Lérida, España)*. Institut d'Estudis Ilerdencs, Lleida. 65 pp.

Lance, J.F. (1946) Fossil arthropods of California. 9. Evidence of termites in the Pleistocene asphalt of Carpinteria, California. *Southern California Academy of Sciences Bulletin*, 45, 21–27.

Li, S.T., Huang, J.F., Yang, S.G., Zhang, X.M., Cheng, S.T., Zhao, G.R., Li, D.N., Li, G.L. & Ding, J.L. (1982) Depositional and structural history of the Late Mesozoic Huolinhe Basin and its characteristics of coal accumulation. *Acta Geologica Sinica*, 3, 244–254. [In Chinese with English abstract]

Lo, N., Tokuda, G., Watanabe, H., Rose, H., Slaytor, M., Maekawa, K., Bandi, C. & Noda, H. (2000) Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Current Biology*, 10, 801–804.
[https://doi.org/10.1016/S0960-9822\(00\)00561-3](https://doi.org/10.1016/S0960-9822(00)00561-3)

Maksoud, S., Azar, D., Granier, B. & Gèze, R. (2017) New data on the age of the Lower Cretaceous amber outcrops of Lebanon. *Palaeoworld*, 26, 331–338.
<https://doi.org/10.1016/j.palwor.2016.03.003>

Mei, M.T. & Cui, J.Z. (1994) Analysis of coal-forming plants from underlying coal-bearing member, Huolinhe Formation, Huolinhe Coal Field, Inner Mongolia. *Coal Geology of China*, 6, 19–21. [In Chinese]

Moreau, J.D., Trincal, V., Nel, A., Simon-Coinçon, R., Sallé, V., Couls, M.L., Néraudeau, D. & Fernandez, V. (2019) Hidden termite coprolites revealed by synchrotron microtomography inside Eocene–Oligocene filled wood-borings from the Malzieu Basin, Lozère, southern France. *Lethaia*, 53, 106–117.
<https://doi.org/10.1111/let.12344>

Pellens, R., D'Haese, C.A., Belle's, X., Piulachs, M.D., Legendre, F., Wheeler, W.C. & Grandcolas, P. (2007) The evolutionary transition from subsocial to eusocial behaviour in Dictyoptera: phylogenetic evidence for modification of the “shift-independent-care” hypothesis with a new subsocial cockroach. *Molecular Phylogenetics and Evolution*, 43, 616–626.
<https://doi.org/10.1016/j.ympev.2006.12.017>

Pires, E.F. & Sommer, M.G. (2009) Plant-arthropod interaction in the Early Cretaceous (Berriasian) of the Araripe Basin, Brazil. *Journal of South American Earth Sciences*, 27, 50–59.
<https://doi.org/10.1016/j.jsames.2008.09.004>

Ren, D., Lu, L.W., Guo, Z.G. & Ji, S.A. (1995) *Fauna and stratigraphy of Jurassic-Cretaceous in Beijing and the adjacent areas*. Geological Publishing House, Beijing, 222 pp. [In Chinese with English summary]

Rogers, A.F. (1938) Fossil termite pellets in opalized wood from Santa Maria, California. *American Journal of Sciences*, 86, 389–392.
<https://doi.org/10.2475/ajs.s5-36.215.389>

Rohr, D.M., Boucot, A.J., Miller, J. & Abbott, M. (1986) Oldest termite nest from the Upper Cretaceous of West Texas. *Geology*, 14, 87–88.
[https://doi.org/10.1130/0091-7613\(1986\)14<87:OTNFTU>2.0.CO;2](https://doi.org/10.1130/0091-7613(1986)14<87:OTNFTU>2.0.CO;2)

Rozefelds, A.C. & De Baar, M. (1991) Silicified Kalotermitidae (Isoptera) frass in conifer wood from a mid-Tertiary rainforest in central Queensland, Australia. *Lethaia*, 24, 439–442.
<https://doi.org/10.1111/j.1502-3931.1991.tb01498.x>

Shi, G.L., Li, J.G., Tan, T., Dong, C., Li, Q.L., Wu, Q., Zhang, B.L., Yin, S.X., Herrera, F., Herendeen, P.S. & Crane, P.R. (2021a) Age of the Houlihan Formation in the Huolinhe Basin, eastern Inner Mongolia, China: Evidence from U-Pb zircon dating

and palynological assemblages. *Journal of Stratigraphy*, 45 (1), 69–81.

Shi, G.L., Herrera, F., Herendeen, P.S., Elizabeth, G.C. & Crane, P.R. (2021b) Mesozoic cupules and the origin of the angiosperm second integument. *Nature*, 594, 223–226. <https://doi.org/10.1038/s41586-021-03598-w>

Stuart, A.M. (1969) *Social behavior and communication*. In: Krishna, K. & Weesner, T.M. (Eds), *Biology of termites*. Academic Press, New York and London, pp. 193–232. <https://doi.org/10.1016/B978-0-12-395529-6.50011-8>

Sutherland, J.I. (2003) Miocene petrified wood and associated borings and termite faecal pellets from Ukatere Peninsula, Kaipara Harbour, North Auckland, New Zealand. *Journal of the Royal Society of New Zealand*, 33, 395–414. <https://doi.org/10.1080/03014223.2003.9517736>

Sweetman, H.L. (1965) *Recognition of structural pests and their damage*. Dubuque, Iowa, W.C. Brown, 371 pp.

Terry, M.D. & Whiting, M.F. (2005) Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics*, 21, 240–257. <https://doi.org/10.1111/j.1096-0031.2005.00062.x>

Thorne, B.L., Grimaldi, D.A. & Krishna, K. (2000) *Early fossil history of termites*. In: Abe, T., Bignell, D.E. & Higashi, M. (Eds), *Termites: evolution, sociality, symbioses, ecology*. Dordrecht, Kluwer Academic Publishers, pp. 77–93. https://doi.org/10.1007/978-94-017-3223-9_4

Traniello, J.F.A. & Leuthold, R.H. (2000) *Behavior and ecology of foraging in termites*. In: Abe, T., Bignell, D.E. & Higashi, M. (Eds), *Termites: evolution, sociality, symbioses, ecology*. Kluwer, Dordrecht, pp. 141–168. https://doi.org/10.1007/978-94-017-3223-9_7

Vršanský, P. & Aristov, D. (2014) Termites (Isoptera) from the Jurassic/Cretaceous boundary: Evidence for the longevity of their earliest genera. *European Journal of Entomology*, 111, 137–141. <https://doi.org/10.14411/eje.2014.014>

Wipfler, B., Letsch, H., Frandsen, P.B., Kapli, P., Mayer, C., Bartel, D., Buckley, T.R., Donath, A., Edgerly-Rooks, J., Fujita, M., Liu, S.L., Machida, R., Mashimo, Y., Misof, B., Niehuis, O., Peters, R., Petersen, M., Podsiadlowski, L., Schütte, K., Shimizu, S., Uchifune, T., Wilbrandt, J., Yan, E., Zhou, X. & Simon, S. (2019) Evolutionary history of Polyneoptera and its implications for our understanding of early winged insects. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 3024–3029. <https://doi.org/10.1073/pnas.1817794116>

Wilson, E.O. & Hölldobler, B. (2005) Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 13367–13371. <https://doi.org/10.1073/pnas.0505858102>

Zhao, Z.P., Eggleton, P., Yin, X.C., Gao, T.P., Shih, C.K. & Ren, D. (2019) The oldest known mastotermitids (Blattodea: Termitidae) and phylogeny of basal termites. *Systematic Entomology*, 44, 612–623. <https://doi.org/10.1111/syen.12344>

Zhao, Z.P., Yin, X.C., Shih, C.K., Gao, T.P. & Ren, D. (2020a) Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. *National Science Review*, 7, 381–390. <https://doi.org/10.1093/nsr/nwz141>

Zhao, Z.P., Shih, C.K., Gao, T.P. & Ren, D. (2020b) Termite communities and their early evolution and ecology trapped in Cretaceous amber. *Cretaceous Research*, 117, 104612. <https://doi.org/10.1016/j.cretres.2020.104612>