







## 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 closet 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 (Jarzembowski, 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

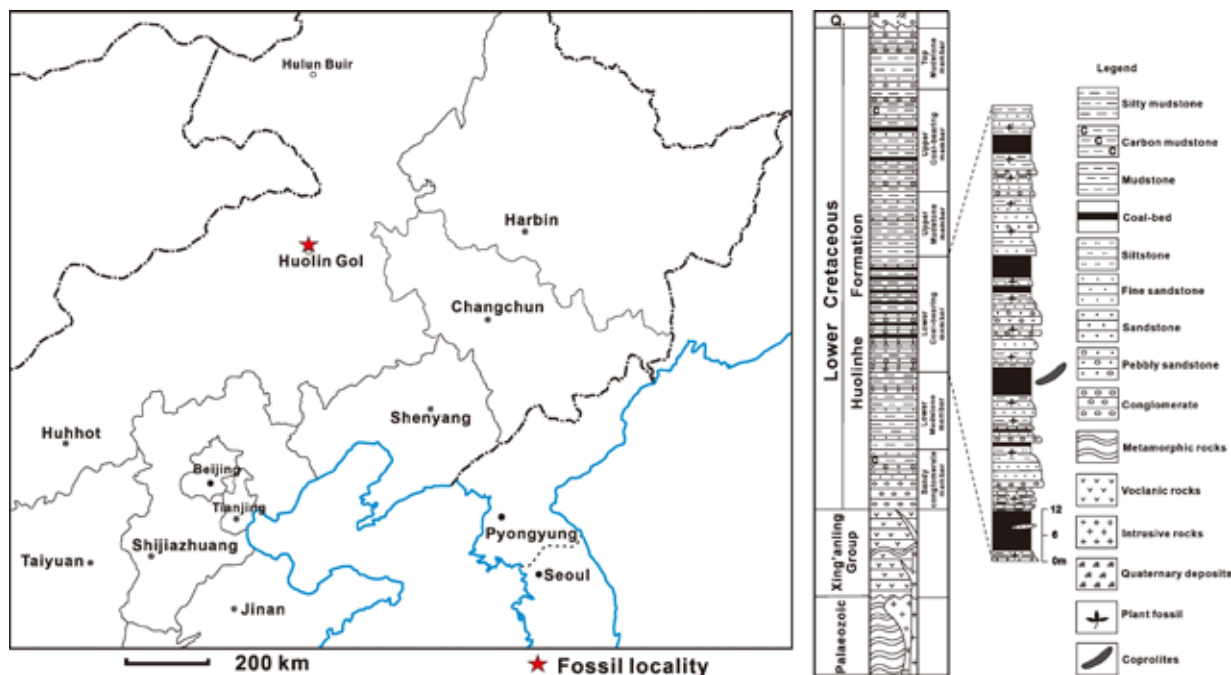
the Lebanese amber termites represent ones of the oldest termites so far known. Besides, termite coprolites in a wood-boring reported from the Berriasian of Brazil (Pires & Sommer, 2009) could represent the earliest termites in the trace fossil record. Numerous ‘basal’ termites reported by recent fossil 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°32′49.1″, E119°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°32′49.1″, E119°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  $125.6 \pm 1.0$  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  $\mu$ m 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

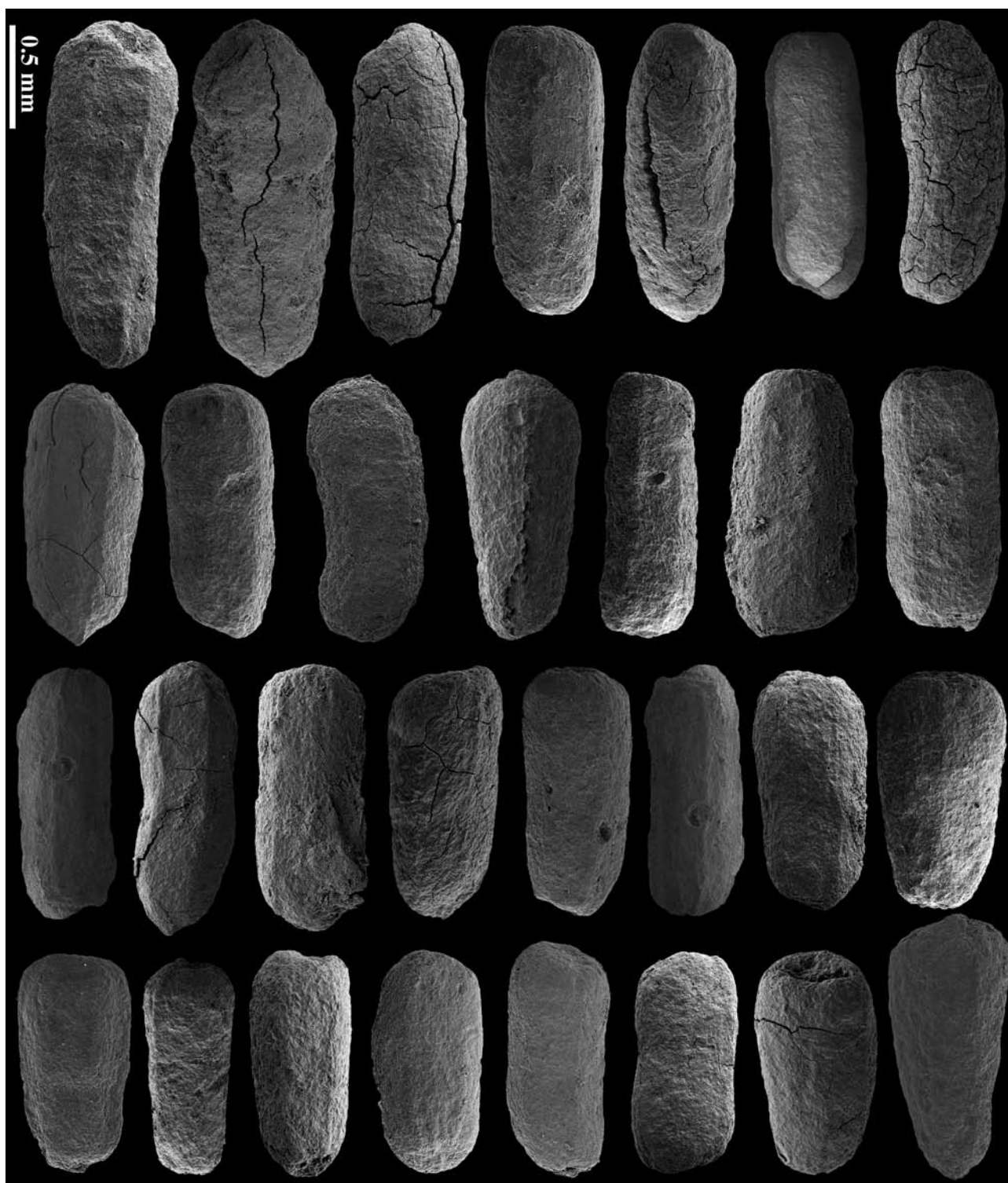
### Morphology

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

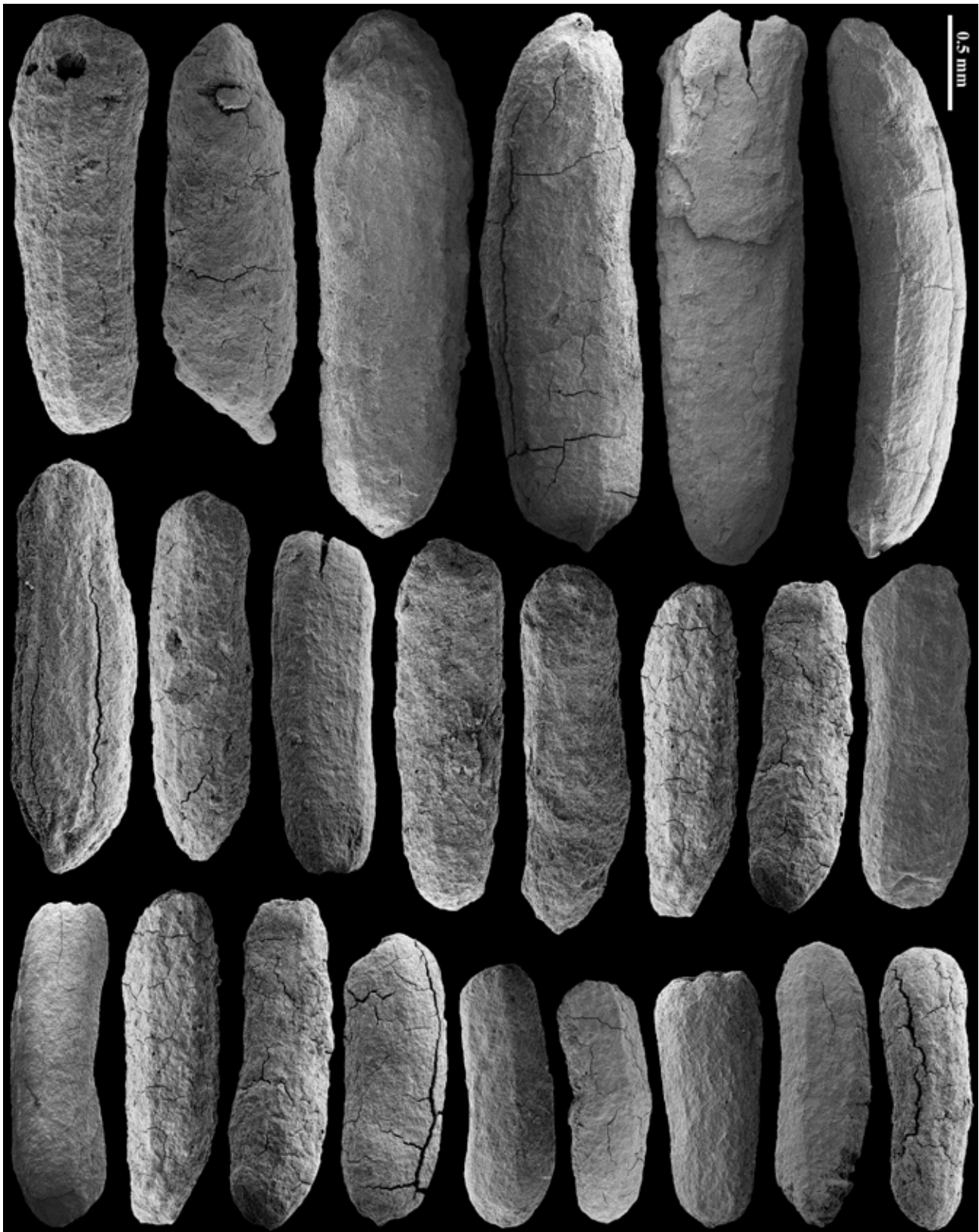


**FIGURE 2.** SEM images of small lignite termite coprolites from the Lower Cretaceous Huolinhe Formation showing their morphology.

#### *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  $\mu\text{m}$  to 500  $\mu\text{m}$  in length and 10  $\mu\text{m}$  to 100  $\mu\text{m}$  in width, exhibiting several tracheid pits (Fig. 5B, C, D,

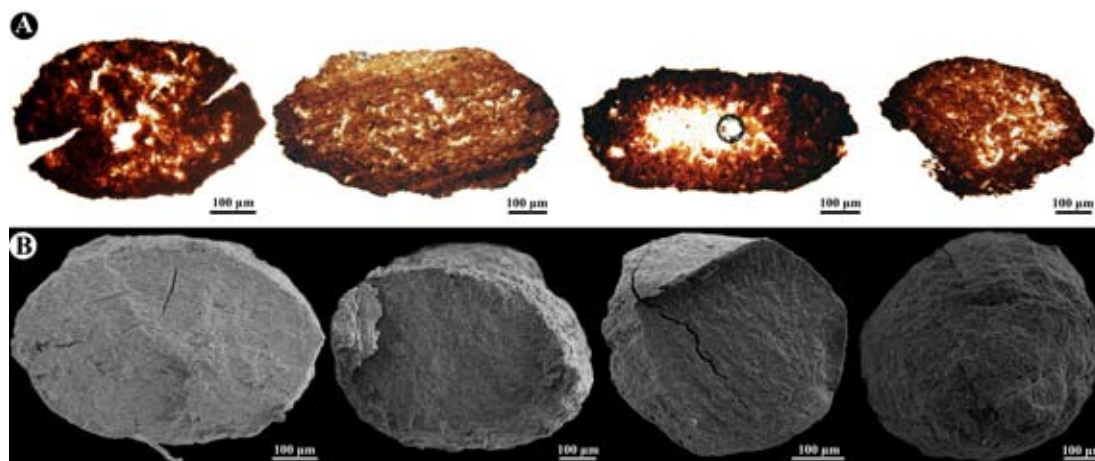
G, H, K, M), cross-fields (Fig. 5E, H, I), xylem rays (Fig. 5J), bundle of fibres (Fig. 5A), and fragmented secondary wood (Fig. 5L). In general, the tracheids are generally flattened, *ca.* 22–28  $\mu\text{m}$  in diameter, bearing some uniseriate bordered pits which are circular to elliptical, *ca.*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



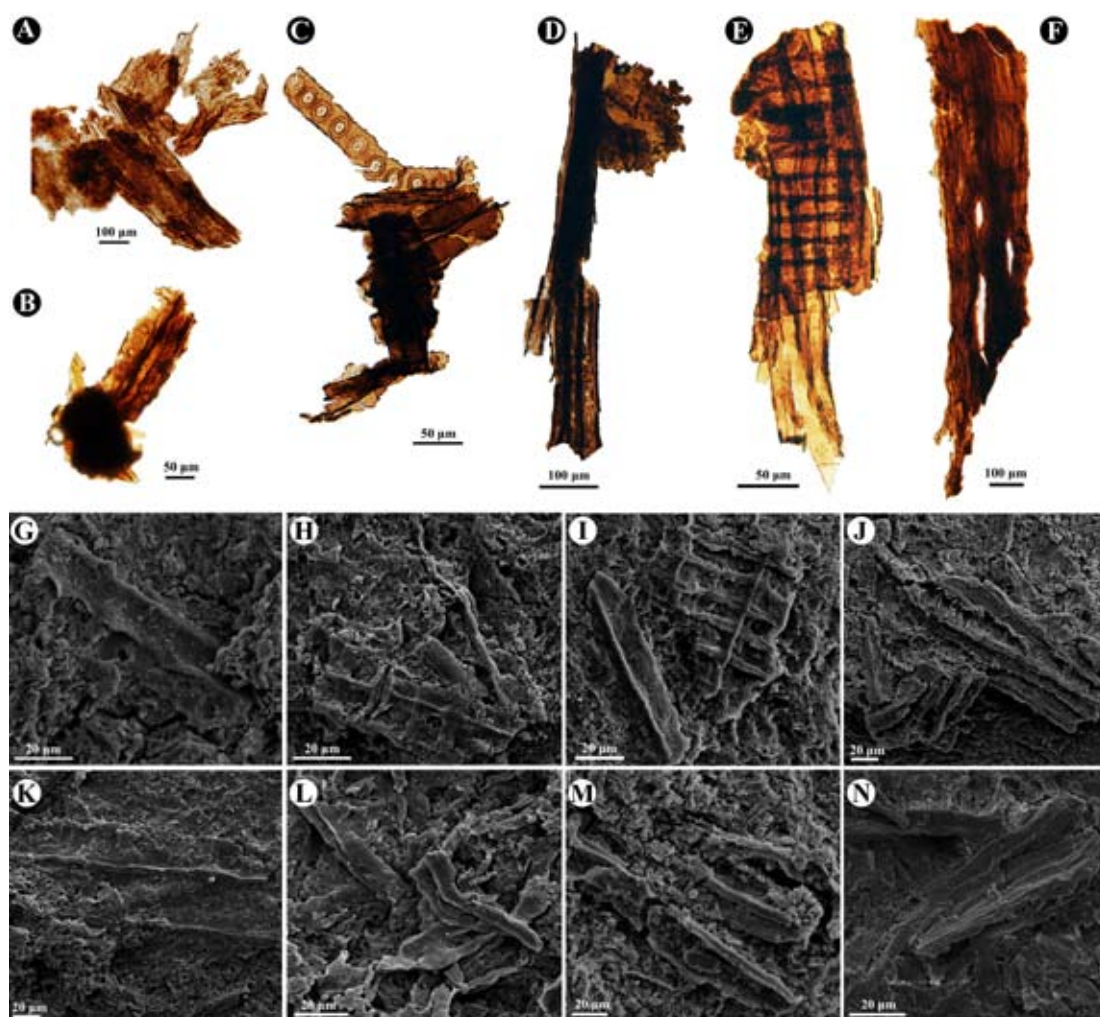
**FIGURE 3.** SEM images of moderate and large lignite termite coprolites from the Lower Cretaceous Huolinhe Formation showing their morphology.

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

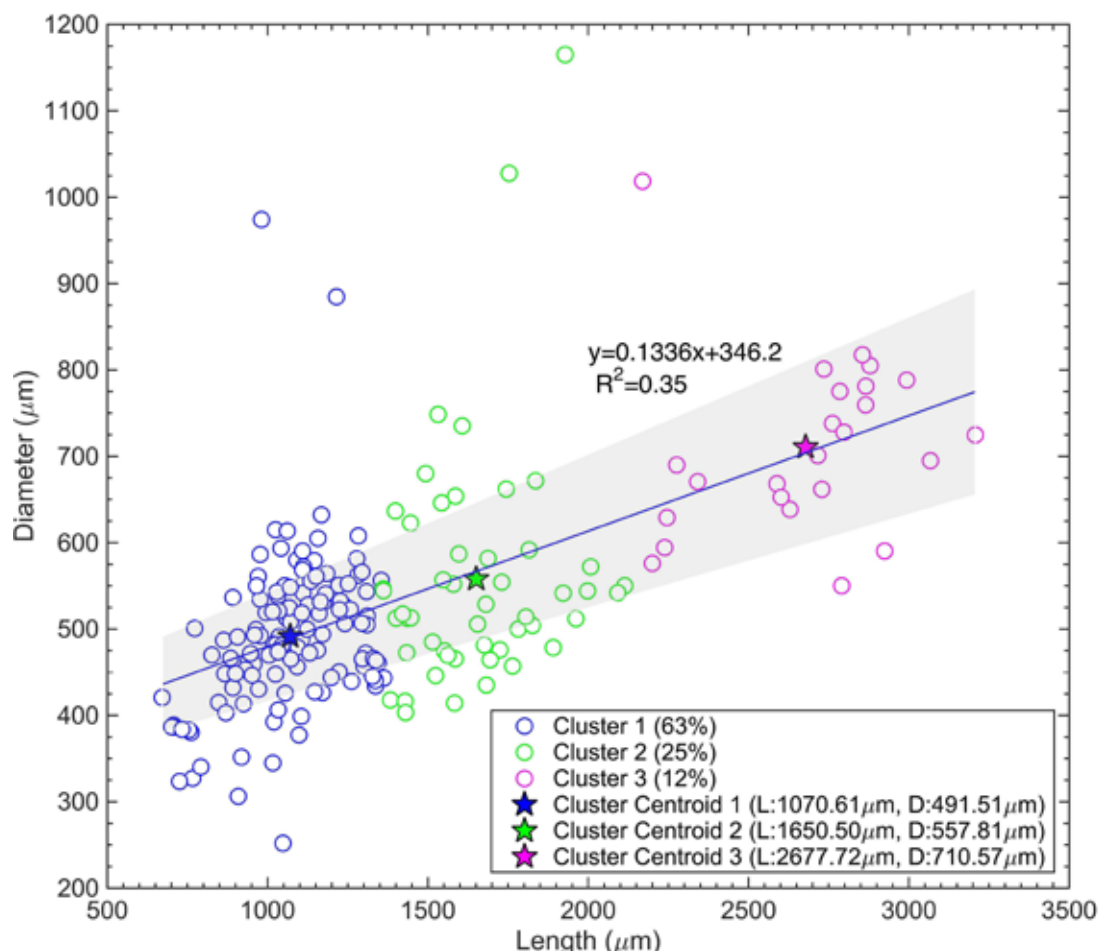
almost the whole cross-field (Fig. 5E, H, I). Besides, a couple of uniseriate xylem rays were also detected from the wood debris in SEM images (Fig. 5J, N).



**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 lignite coprolites collected 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 uniseriate 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.*, *Kaloterмес*) and Mastotermitidae (*Mastoterмес*) 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 *Mastoterмес darwiniensis* (Mastotermitidae) and *Kaloterмес* 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 (Collin *et al.*, 2011; Moreau *et al.*, 2019). Faecal pellets of modern *Kaloterмес* spp. and *M. darwiniensis* were figured by Collin *et al.* (2011), in which they described pellets of modern *Kaloterмес* 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 Collin *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 Collin *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 (Collin *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 *Kaloterme*s (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 being 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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