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# Cretohisteridae, a new beetle family from the Early Cretaceous of China, and its implications for the early evolution of the basal group of Histeroidea (Coleoptera)

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**Abstract.** A new beetle family Cretohisteridae **fam.n.** is described from the Lower Cretaceous Yixian Formation (~125 Ma) at Huangbanjigou of Beipiao City, Liaoning Province, Northeastern China based on a well preserved fossil beetle, *Cretohister sinensis* gen., **sp.n.** This discovery has established the oldest fossil record for the superfamily Histeroidea, backdating the minimum age of the group by 25 Ma from the earliest Cenomanian (~99 Ma) to the Barremian of the Cretaceous Period. Based on cladistic analyses of a comprehensive morphological dataset, Cretohisteridae is unambiguously recovered as the sister group of Histeridae, exhibiting several character states that bridge the span between Sphaeritidae, Synteliidae and Histeridae. The discovery of the new fossil family sheds new light on the early evolution and diversity of the Histeroidea in the Early Cretaceous, and provides new clues to solving the long-ambiguous phylogenetic relationships among the modern families of Histeroidea.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:C3F85BBB-D60E-44BC-87C8-B6D54374EE00>.

## Introduction

The beetle superfamily Histeroidea, with three closely related families Histeridae, Sphaeritidae and Synteliidae, forms a well-defined group within polyphagan beetles (Beutel, 2016). These families have been separately classified in the past, but since the landmark study of Sharp & Muir (1912) of the male genitalia in Coleoptera, these taxa, and then-separately treated Niponiidae, were recognized as ‘so closely related by the aedeagus, that they might form one family.’ Subsequently, Reichardt (1941) and Crowson (1955, 1981) considered these ‘four families’ to be closely related to Staphylinoidea and Hydrophiloidea

within the suborder Polyphaga. Lawrence & Newton (1982) expanded the concept of Hydrophiloidea and subsumed Histeroidea within this superfamily, largely based on larval characters shared by Histeridae and Hydrophilidae, as pointed out by Böving & Craighead (1931). Since then, Histeroidea and Hydrophiloidea have been treated as sister clades, closely related to Scarabaeoidea or to Staphylinoidea, but following comprehensive study of Hansen (1997) they are regarded as separate superfamilies (Crowson, 1974; Ôhara, 1994; Caterino & Vogler, 2002; Bocak *et al.*, 2014; McKenna *et al.*, 2015; Beutel, 2016).

Histeroidea comprises the hyperdiverse and globally widespread family Histeridae (11 subfamilies, at least 3900 species; Mazur, 2011), and the monogeneric and mostly Holarctic families Sphaeritidae (seven species) and Synteliidae (nine species) (Löbl, 1996; Löbl & Háva, 2002; Zhou & Yu, 2003; Gusakov, 2004, 2017; Newton, 2016). However, the phylogenetic relationships between histeroid

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families are not well established and are still controversial. Morphology-based phylogenetic research (Hansen, 1997; Ślipiński & Mazur, 1999; Caterino & Vogler, 2002) recovered a basal Sphaeritidae, with Synteliidae more closely related to Histeridae, sharing a distinctly geniculate antenna, much longer antennal scape, pedicel at least as long as antennomere 3, shorter legs with strong teeth on tibiae, and the loss of a frontoclypeal suture. This relationship is not supported by molecular studies (Caterino *et al.*, 2005; Bocak *et al.*, 2014; McKenna *et al.*, 2015) recovering Sphaeritidae as more closely related to Histeridae. The unique relationships of ((Sphaeritidae + Synteliidae) + Histeridae) + some Hydrophilidae + remaining Hydrophilidae were found in a general beetle phylogeny by Lawrence *et al.* (2011).

The fossil record of Histeroidea is sparse, and so far three Burmese amber (~99 Ma) inclusions of Histeridae constitute the oldest records of the superfamily (Poinar & Brown, 2009; Caterino *et al.*, 2015; Caterino & Maddison, 2018). Several fossil Histeridae, classified in Trypanaeinae, Saprininae and Histerinae, have been reported from various younger deposits (see Caterino *et al.*, 2015), but only *Trypanaeus hispaniolus* Chazimanolis *et al.* (2006) from Dominican amber has been adequately described. No fossil taxa of Sphaeritidae or Synteliidae have been reported so far.

Studies of the fossil record are significant for providing estimates of palaeodiversity, contributing valuable information about the time of origin and extinction of lineages, and in tracing beetle evolution. Here, we present results of our research on an exquisitely preserved fossil beetle from the Lower Cretaceous (c. 125 Ma) Yixian beds in Northern China. Our discovery represents the earliest known definitive member of Histeroidea. To evaluate its systematic placement within the superfamily, we performed phylogenetic analyses of morphological characters under the maximum parsimony criterion with outgroup taxa including Agyrtidae and three families of Hydrophiloidea. The new family, Cretohisteridae, is proposed, and it is classified as a sister group to Histeridae. This significant discovery provides some credibility to the claims that modern families of Histeroidea existed well before the Early Cretaceous, and dating the origin of superfamily back to the late Triassic (Toussaint *et al.*, 2017).

## Material and methods

### Material, drawing and photography

This study is based on a single specimen (with part and counterpart) collected from the Jianshangou Bed of the Yixian Formation at Huangbanjigou, Beipiao, Liaoning, northeastern China. This stratum represents the famous Jehol Biota known for its feathered dinosaurs, angiosperms and numerous other exceptionally preserved fossils (Barrett, 2000; Pan *et al.*, 2013). The 225- to 4000-m-thick Yixian Formation, varying in thickness and lithology in different areas, is mainly composed of tuff, andesite, basalt, mudstone, tuffaceous shale, sandstone, conglomerate and siltstone. Organisms that lived

in the Early Cretaceous volcanic-influenced environments were buried in lacustrine and rarely fluvial sediments, where many turned into exceptionally preserved fossils. Its geological age has been indicated as the Early Cretaceous, some 125 Ma (Swisher III *et al.*, 1999), and it is now considered to be one of the most important Mesozoic insect Lagerstätten (Zhou, 2014).

The type specimen was examined dry and under alcohol using a Leica M205C dissecting microscope. It was photographed using the Visionary Digital BK Lab Plus system (Austin, Texas) (<http://www.duninc.com/bk-plus-lab-system.html>) and Micropublisher5 digital camera (Canada) mounted on a Leica compound microscope. The source images were aligned and stacked in HELICON FOCUS (Ukraine) and manipulated in Adobe PHOTOSHOP CC 2015 to obtain fully sharpened and balanced images. The interpretive line drawings were executed with Wacom Intuo Draw tablet (PM ctl-680) using COREL DRAW X7.

The morphological terminology follows Ôhara (1994), Ślipiński & Mazur (1999), Caterino & Vogler (2002) and Caterino & Tishechkin (2015). The measurements were taken as follows: body length from apex of mandible to posterior margin of abdomen; body width as maximum width of body; head length (HL) from apex of clypeus to posterior margin of head; head width (HW) as maximum width of head across the eyes; antenna length from first to last antennomere; pronotum length (PL) as maximum length of pronotum; pronotum width (PW) as the maximum width of pronotum; elytral length (EL) from anterior margin to apex; elytral width (EW) as maximum width of elytra.

### Taxon sampling, characters and phylogenetic analysis

We selected four outgroups – *Necrophilus* (Agyrtidae, Staphylinidae), *Helophorus* (Helophoridae), *Spercheus* (Spercheidae), *Hydrochus* (Hydrochidae) – and 14 ingroups, including two species of *Sphaerites* (Sphaeritidae), one *Syntelia* (Synteliidae) species and 11 species of Histeridae, representing all subfamilies (Table 1). The fossil taxon was included as one of the ingroups.

In all, 66 external characters were scored from adult beetles covering all important characters used in previous phylogenies of Histeroidea and Hydrophiloidea (Tables 2, 3; Fig. 5), in particular in Hansen (1997), Ślipiński & Mazur (1999), Caterino & Vogler (2002), Fikáček *et al.* (2012) and Lawrence *et al.* (2011).

The morphological matrix was analysed using TNT v.1.1 (Goloboff *et al.*, 2008) under the implicit enumeration algorithm, with all characters unweighted and unordered. All characters were treated as nonadditive and were optimized on cladograms using unambiguous optimization in WINCLADA (Nixon, 2002). Gaps were treated as missing characters. The character states were mapped on the tree in Winclada under unambiguous optimisation. The Bremer support (Table 4) was calculated in TNT, from 4697 suboptimal trees that were up to five steps longer than the shortest tree. Five thousand bootstrap (BS) replicates were run in PAUP\* (Swofford, 2002; v 4.0a.159).

**Table 1.** Taxa sampled for this study.

	Superfamily/family/subfamily	Species		
Outgroups	Staphylinoidea	Agyrtidae	<i>Necrophilus subterraneus</i> (Dahl)	
	Hydrophiloidea	Spercheidae	<i>Spercheus emarginatus</i> (Schaller)	
		Hydrochidae	<i>Hydrochus elongates</i> (Schaller)	
		Helophoridae	<i>Helophorus brevipalpis</i> Bedel	
Ingroups	Histeroidea	†Cretohisteridae fam.nov.	† <i>Cretohister sinensis</i> <b>sp.n.</b>	
		Sphaeritidae	<i>Sphaerites glabratus</i> (Fabricius)	
		Sphaeritidae	<i>Sphaerites politus</i> Mannerheim	
		Synteliidae	<i>Syntelia histeroides</i> Lewis	
		Histeroidea: Histeridae	Abraeinae	<i>Abraeus</i> sp.
			Chlamydopsinae	<i>Chlamydopsis</i> sp.
			Dendrophilinae	<i>Dendrophilus pygmaeus</i> (Linnaeus)
			Haeteriinae	<i>Satrapes sartorii</i> (Redtenbacher)
			Histerinae	<i>Pelorusus</i> sp.
			Niponiinae	<i>Niponius</i> sp.
			Onthophilinae	<i>Onthophilus striatus</i> (Forster)
			Saprininae	<i>Philothis arabicus</i> Mazur
			Tribalinae	<i>Epierus</i> sp.
			Trypanaeinae	<i>Trypaneus ensifer</i> Marseul
		Trypeticinae	<i>Pygocoelis africanus</i> (Lewis)	

**Table 2.** List of characters used for the analysis of the phylogenetic position of fossil family Cretohisteridae **fam.n.**

1.	Frontoclypeal suture: (0) grooved; (1) visible but not grooved [Fig. 5 (A1, A3)]; (2) not distinct (Fig. 5 (A2)).
2.	Clypeus shape: (0) transverse [Fig. 5 (A3)]; (1) square, extended forwards [Fig. 5 (A1)].
3.	Head: (0) not constricted behind eyes [Fig. 5 (A2)]; (1) abruptly constricted immediately behind eyes; (2) with constricted neck well behind eyes.
4.	Supraorbital stria: (0) absent [Fig. 5 (A3)]; (1) present, entire [Fig. 5 (A2)]; (2) present, not entire.
5.	Gular sutures: (0) broadly separated; (1) fused together; (2) narrowly separated.
6.	Subentum: (0) anterior margin not dentate; (1) anterior margin dentate.
7.	Anterior margin of mentum (position): (0) between anterior margin of eye and the middle of eye; (1) more backwards, behind the middle of eye; (2) more forwards, before the anterior margin of eye.
8.	Right mandible on inner side: (0) with two teeth [Fig. 5 (B2)]; (1) with one tooth [Fig. 5 (B1)]; (2) without tooth; (3) with three to four teeth.
9.	Stipes of maxilla: (0) elongate, at least as long as combined length of basal three palpomeres; (1) normal, no longer than combined length of two basal palpomeres.
10.	Shape of terminal maxillary palpomere (4th): (0) subconical; (1) cylindrical.
11.	Maxillary palpomere 4: (0) at least as large as 3; (1) markedly smaller than 3.
12.	Antenna: (0) 11-segmented; (1) 10-segmented; (2) less than 10-segmented.
13.	Antenna: (0) not geniculate; (1) geniculate.
14.	Scape: (0) gradually expanded apically; (1) strongly expanded apically; (2) super-expanded apically, triangular-shaped.
15.	Scape length: (0) at least as long as or much longer than three terminal antennomeres combined; (1) much shorter than terminal three terminal antennomeres combined.
16.	Antennal pedicel: (0) conical, narrower distally than basally; (1) bulbous; (2) club-like, narrower basally than distally.
17.	Pedicel length comparing to scape length: (0) shorter than scape; (1) less than half of scape length; (2) slightly longer than scape.
18.	Antennomere 3: (0) distinctly longer than 2; (1) shorter than 2; (2) as long as 2.
19.	Antenna: (0) without cupuliform segments [Figure S3 (from Niponiinae to Abraeinae)]; (1) with cupuliform segment proceeding three segmented club [Figure S3 (from Hydrophiloidea to Trypanaeinae)].
20.	Antennae: (0) filiform, or with gradually developed club of about five segments; (1) with club of three densely pubescent segments; (2) with three apical loose antennomeres.
21.	Annuli of antennal club: (0) distinct, straight [Figure S3 (Sphaeritidae, Synteliidae)]; (1) outwardly arcuate [Figure S3 (Niponiinae)]; (2) inwardly arcuate [Figure S3 (Dendrophilinae)]; (3) obsolete, club entirely pubescent [Figure S3 (Abraeinae)]; (4) obsolete, club sclerotized on bases of upper and lower surfaces [Figure S3 (Trypanaeinae)]; (5) obsolete, club sclerotized otherwise.
22.	Antennal groove: (0) present between eye and gular suture; (1) absent.
23.	Antennal groove: (0) paired at each side of prosternal process [Fig. 5 (C3)]; (1) with paired of cavities on anterior angle of pronotum (prosternal alae) [Fig. 5 (C2)]; (2) absent [Fig. 5 (C1)].
24.	Posterior margin of pronotum: (0) arcuate; (1) bisinuate, medially projected backwards.
25.	Connection between base of prothorax and rest of thorax: (0) not co-adaptive with each other; (1) tightly co-adaptive with each other.

**Table 2.** Continued.

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26.	Posterolateral pits on pronotum: (0) absent; (1) present.
27.	Lateral margin of pronotum: (0) smooth; (1) slightly to moderately crenulate; (2) strongly and sharply denticulate.
28.	Protibia: (0) narrow, with small spines on external margin; (1) distinctly expanded, with dentate or arcuate external margin.
29.	Procoxal cavity: (0) externally open [Fig. 5 (C1–3)]; (1) externally closed.
30.	Procoxal cavities: (0) open internally [Fig. 5 (C1–3)]; (1) closed internally.
31.	Prosternal intercoxal process: (0) not widened behind procoxae [Fig. 5 (C1)]; (1) distinctly widened behind procoxae [Fig. 5 (C2, 3)].
32.	Prosternum length: (0) at least about one-third of pronotum length [Fig. 5 (C1)]; (1) less than one-third of pronotum length [Fig. 5 (C2, 3)].
33.	Prosternal lobe: (0) large projecting, defined by more or less distinct transverse line [Fig. 5 (C2)]; (1) missing [Fig. 5 (C1)].
34.	Prosternal keel: (0) missing [Fig. 5 (C1)]; (1) present, excavate laterally for reception of the protibial spur; (2) present, without lateral excavation [Fig. 5 (C2, 3)].
35.	Separation of procoxae: (0) broad, about procoxal diameter [Fig. 5 (C3)]; (1) narrow, much less than procoxal diameter [Fig. 5 (C1, 2)].
36.	Protrochantin: (0) visible externally (Fig. 5 (C1)); (1) hidden [Fig. 5 (C2, 3)].
37.	Procoxae: (0) not projecting; (1) projecting.
38.	Mesocoxa: (0) globular or slightly elongate; (1) transverse, at least one-third wider than long.
39.	Mesoscutellum: (0) finger-shaped; (1) small; (2) large, tongue-shaped.
40.	Elytra: (0) smooth, without any grooves or carinae [Figure S2 (A)]; (1) either with grooves or carinae or densely punctate [Figure S2 (C2, 3)].
41.	Elytra: (0) not truncate posteriorly, completely concealing abdomen or leaving extreme apex visible; (1) truncate posteriorly, completely exposing at least one abdominal tergite.
42.	Hind leg: (0) projecting beyond abdominal sides [Figure S2 (B)]; (1) not projecting beyond abdominal sides [Figure S2 (F)].
43.	Mesocoxal cavity: (0) externally open; (1) externally closed.
44.	Transverse ridge on mesoventrite: (0) absent; (1) present.
45.	Meso- and metatarsomere 1: (0) long, at least as long as tarsomere 2; (1) short, much shorter than tarsomere 2.
46.	Mesocoxal cavities: (0) separated by at least of mesocoxal width; (1) separated by much less than mesocoxal width.
47.	Meso and metaventrite: (0) fused [Fig. 5 (D2, 3)]; (1) not fused [Fig. 5 (D1)].
48.	Mesotarsi length: (0) quite elongate [Fig. 5 (G1)], as long as mesotibiae; (1) quite compact [Fig. 5 (G2, 4)], distinctly shorter than mesotibiae.
49.	Mesotibiae: (0) strongly dentate externally [Fig. 5 (G4)]; (1) with regular small spines [Fig. 5 (G1)].
50.	Mesotrochantin: (0) distinctly exposed externally; (1) concealed, invisible.
51.	Meso- and metatibiae: (0) not grooved for reception of tarsi [Fig. 5 (G1, 2, 4)]; (1) grooved for reception of tarsi [Fig. 5 (G3)].
52.	Distance between metacoxae: (0) more than 1.5× width of coxa; (1) 1.0–1.5× width of metacoxa; (2) < 1× metacoxa width.
53.	Meso-metaventral junction: (0) arcuate backwards [Fig. 5 (D1)]; (1) straight [Fig. 5 (D2, 3)].
54.	Metaventrite: (0) with paired postcoxal lines; (1) without postcoxal lines.
55.	Metakatepisternal suture: (0) present [Fig. 5 (D1)]; (1) absent [Fig. 5 (D2, 3)].
56.	Metendosternite stalk: (0) long, over half the length of metaventrite; (1) medium length, between one-third and half length of metaventrite; (2) very short, distinctly less than one-third length of metaventrite.
57.	Metepimeron: (0) not fused to metanepisternum [Fig. 5 (D3)]; (1) fused to metanepisternum [Fig. 5 (D2)].
58.	Metacoxae: (0) subcircular or subtriangular [Fig. 5 (D2, 3)]; (1) transverse [Fig. 5 (D1)].
59.	Anterior-median margin of abdominal tergite IV: (0) distinctly projecting forwards [Fig. 5 (E3)]; (1) gradually projecting forwards [Fig. 5 (E2)]; (2) arcuate [Fig. 5 (E1)].
60.	Abdominal tergite: (0) tergite VII and/or VIII (and sometimes the following) well sclerotized; (1) IV, and the following abdominal terga well sclerotized; (2) III (sometimes also II), and the following abdominal terga well sclerotized.
61.	Median groove in abdominal tergite IV: (0) absent [Fig. 5 (E1)]; (1) present [Fig. 5 (E2, 3)].
62.	Abdominal terga-sternal membrane: (0) long on segments 1–6 (–7); (1) long on segments 1–3 (and partly 4), very short on following segments.
63.	Abdominal ventrite 1: (0) as long as or slightly longer than ventrite 2; (1) 1.5× longer of ventrite 2.
64.	Abdominal segment 8: (0) exposed at least dorsally (when elytra opened); (1) completely invaginated within segment 7 [Fig. 5 (F2)].
65.	Propygidium: (0) with spiracle; (1) without spiracle.
66.	Median process on ventrite 1: (0) subtruncate [Fig. 5 (F2)]; (1) sharply projecting [Fig. 5 (F1)]; (2) arcuate.

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## Results

### *Phylogenetic assessment of Lower Cretaceous histeroid family*

The implicit enumeration search in TNT returned a single maximum parsimony tree (MP), 143 steps long, with a consistency index (CI) of 0.62 and a retention index (RI) of 0.80 (Fig. 1; Figure S1). The phylogeny recovers the new fossil taxon as an intermediate clade between Synteliidae and Histeridae, and additionally supports the following relationships:

1 Histeroidea, including the new fossil taxon, forms a distinct clade [98% bootstrap support (BS)], separated from a monophyletic Hydrophiloidea (98% BS). The clade is based on six unambiguous synapomorphies: (13,1) antennae geniculate; (14,1) antennal scape strongly expanded apically; (41,1) elytra truncate posteriorly, completely exposing at least one abdominal tergite; (60, 2) abdominal tergites 3 posterad well sclerotized; (63,1) abdominal ventrite 1 about 1.5× the length of ventrite 2; and (64,1) abdominal segment 8 completely invaginated within 7.

**Table 3.** Morphological dataset used for the analysis of the phylogenetic position of fossil family Cretohisteridae **fam.n.**

Characters	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3					
Characters	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9			
<i>Necrophilus subterraneus</i> Agyrtidae	1	0	0	0	0	0	2	2	1	1	0	0	0	0	1	1	1	2	0	0	–	1	2	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	1	1		
<i>Helophorus brevipalpis</i> Helophoridae	0	0	1	0	2	0	2	1	1	1	0	2	0	0	1	0	0	2	1	2	–	1	2	1	1	1	2	0	0	1	0	1	1	0	1	0	1	0	0	0	1	
<i>Spercheus emarginatus</i> Spercheidae	1	0	1	0	0	0	0	1	1	1	0	2	0	0	1	1	0	1	2	–	1	2	0	1	1	2	0	0	1	0	1	1	0	1	0	0	0	1	0	0	1	
<i>Hydrochus elongates</i> Hydrochidae	0	1	1	0	2	0	2	1	1	1	0	2	0	0	1	0	1	0	1	2	–	1	2	1	1	1	0	0	1	1	1	0	1	1	0	1	1	0	0	1		
<i>Sphaerites glabratus</i> Sphaeritidae	1	1	0	0	0	0	2	0	0	1	0	0	1	1	1	1	0	1	1	0	–	1	2	1	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	2		
<i>Sphaerites politus</i> Sphaeritidae	1	1	0	0	0	0	2	0	0	1	0	0	1	1	1	1	0	1	1	0	–	1	2	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	2			
<i>Cretohister sinensis</i> Cretohisteridae	1	1	0	0	?	0	2	0	?	1	0	0	1	1	0	2	2	1	0	1	0	–	1	2	1	0	0	0	0	?	?	?	?	?	0	1	?	0	0	?		
<i>Syntelia histeroides</i> Synteliidae	2	–	0	0	2	0	2	3	0	1	0	0	1	1	0	1	1	1	1	0	0	–	2	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0		
<i>Trypaneus ensifer</i> Trypanaeinae	2	–	0	0	1	0	2	0	1	0	0	0	1	1	0	1	1	1	1	4	–	1	2	0	1	0	0	1	0	0	0	1	1	2	1	1	0	0	1			
<i>Pelorusus</i> sp. Histerininae	1	0	0	1	0	0	1	1	1	0	0	1	1	0	1	1	0	1	0	1	0	–	1	0	1	0	0	1	0	0	1	0	0	1	0	0	2	1	1	0	0	1
<i>Philothis arabicus</i> Sapriniinae	2	–	0	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	0	1	3	–	1	0	0	1	0	0	1	0	0	1	0	0	2	1	1	0	0	1		
<i>Epierus</i> sp. Tribalinae	1	0	0	0	1	0	0	2	1	1	0	0	1	1	0	2	1	1	0	1	0	–	1	1	0	1	0	0	1	0	0	1	0	0	2	1	1	0	0	1		
<i>Dendrophilus pygmaeus</i> Dendrophilinae	2	–	0	1	2	0	1	1	1	1	0	0	1	1	0	1	1	1	0	1	2	–	1	0	0	1	0	0	1	0	0	1	0	0	1	1	1	0	0	1		
<i>Abraeus</i> sp. Abraeinae	2	–	0	2	1	0	0	1	1	1	0	0	1	1	0	1	1	0	0	1	3	–	1	0	0	1	0	0	1	0	0	1	0	0	2	0	1	0	0	1		
<i>Satrapes sartorii</i> Haeteriinae	2	–	0	0	1	0	1	2	1	1	0	0	1	2	0	1	1	1	0	1	5	–	1	1	0	0	1	0	0	1	0	0	2	1	1	0	0	1	0	1		
<i>Niponius</i> sp. Niponiinae	2	–	0	0	1	1	2	0	1	1	0	0	1	1	0	1	1	0	1	1	0	–	2	0	1	0	0	1	0	0	1	0	1	0	1	2	1	1	0	0	1	
<i>Pygocoelis africanus</i> Trypeticinae	1	0	0	0	1	0	2	2	1	0	0	0	1	1	0	1	1	0	1	4	–	1	0	0	1	0	0	1	0	0	1	0	2	1	1	0	0	1	0	1		
<i>Chlamydopsis</i> sp. Chlamydopsinae	2	–	0	0	1	0	0	1	1	0	1	0	1	2	0	1	1	1	0	1	3	–	1	1	0	1	0	0	1	0	0	0	0	2	1	1	0	0	1			
<i>Onthophilus striatus</i> Onthophilinae	2	–	0	1	1	0	2	1	1	1	0	0	1	1	0	1	1	1	0	1	0	–	1	0	1	0	0	1	0	0	1	0	0	2	0	1	0	0	1			

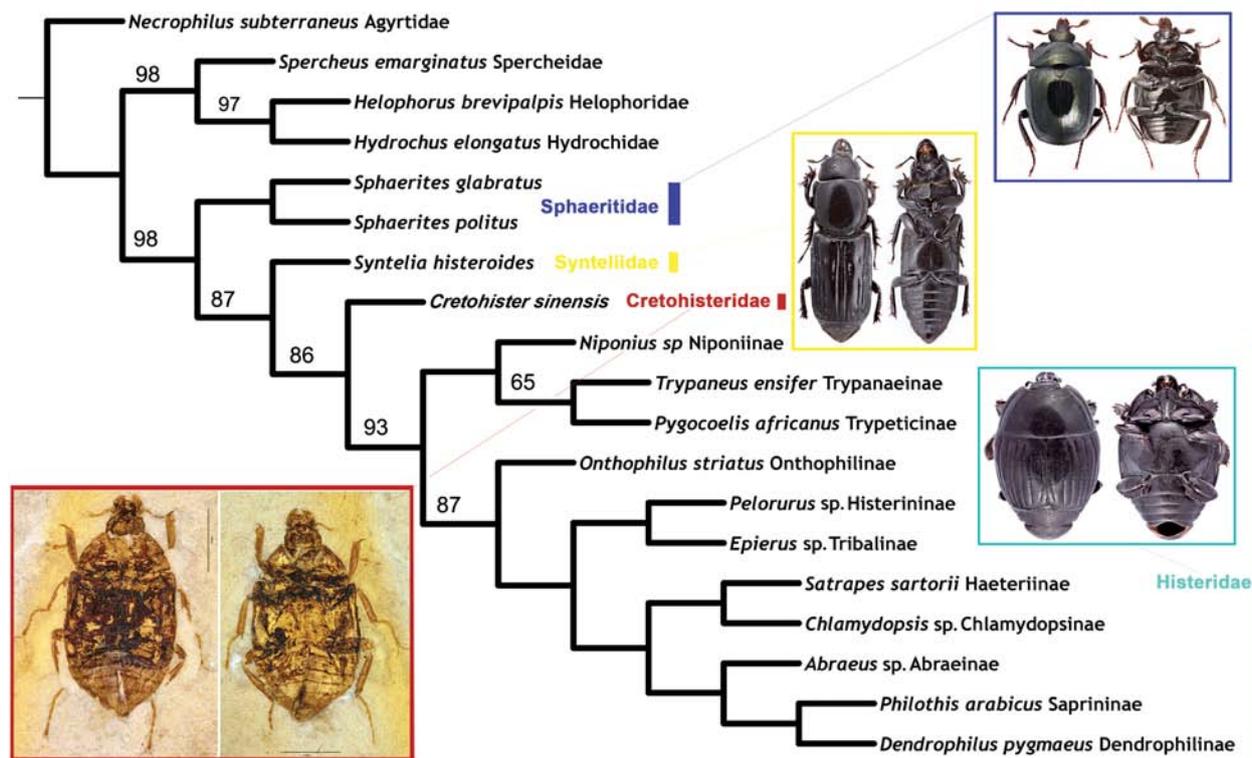
  

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<i>Necrophilus subterraneus</i> Agyrtidae	0	0	0	0	0	0	1	1	0	1	0	0	2	0	1	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Helophorus brevipalpis</i> Helophoridae	0	0	0	0	0	1	1	1	1	0	1	0	0	2	0	1	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Spercheus emarginatus</i> Spercheidae	0	0	0	0	0	0	1	1	0	1	0	0	2	0	1	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Hydrochus elongates</i> Hydrochidae	0	0	0	1	0	0	1	1	0	1	0	0	2	0	1	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Sphaerites glabratus</i> Sphaeritidae	0	1	0	0	0	0	1	1	0	1	0	0	2	0	1	0	0	0	1	2	2	0	0	0	1	1	0	0	1	1	0	1	0	1	0	1	0	1	0	1	
<i>Sphaerites politus</i> Sphaeritidae	0	1	0	0	0	0	1	1	0	1	0	0	2	0	1	0	0	0	1	2	2	0	0	1	2	0	0	1	1	0	1	0	1	0	1	0	1	0	1		
<i>Cretohister sinensis</i> Cretohisteridae	0	1	0	0	0	0	0	0	0	1	?	0	0	1	0	1	1	?	0	2	1	?	0	0	0	1	?	0	0	1	?	2									
<i>Syntelia histeroides</i> Synteliidae	1	1	0	0	0	0	1	0	0	0	0	0	2	0	1	1	0	0	1	2	0	0	1	2	0	0	1	1	1	1	0	1	1	0	1	1	0	1	1		
<i>Trypaneus ensifer</i> Trypanaeinae	0	1	1	0	0	0	0	0	0	0	0	1	0	2	1	0	1	2	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2		
<i>Pelorusus</i> sp. Histerininae	1	1	1	0	0	0	0	0	1	0	1	0	1	1	0	1	2	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0		
<i>Philothis arabicus</i> Sapriniinae	1	1	1	0	0	0	0	0	1	0	1	0	1	1	0	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0		
<i>Epierus</i> sp. Tribalinae	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	1	2	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0		
<i>Dendrophilus pygmaeus</i> Dendrophilinae	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	2	0	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0		
<i>Abraeus</i> sp. Abraeinae	0	1	1	0	0	0	0	0	1	1	1	0	0	1	0	1	2	1	0	1	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0		
<i>Satrapes sartorii</i> Haeteriinae	1	1	1	0	0	0	0	0	1	1	1	0	1	0	1	0	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0		
<i>Niponius</i> sp. Niponiinae	0	1	1	0	0	0	0	0	0	0	1	0	2	1	0	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2			
<i>Pygocoelis africanus</i> Trypeticinae	0	1	1	0	0	0	0	0	0	0	1	0	2	1	0	1	2	1	0	1	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2			
<i>Chlamydopsis</i> sp. Chlamydopsinae	1	1	1	0	0	0	0	0	1	1	1	1	0	1	0	1	2	0	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2			
<i>Onthophilus striatus</i> Onthophilinae	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	1	2	0	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2			

**Table 4.** Bremer support value of main clades.

Main clade	Bremer support
Hydrophiliodea: Spercheidae + Hydrochidae + Helophoridae	5
Histeroidea: Sphaeritidae + Cretohisteridae + Synteliidae + Histeridae	5
Hydrophiliodea + Histeroidea	5
Cretohisteridae + Histeridae	5
Cretohisteridae + Synteliidae+Histeridae	4

2 Sphaeritidae with two unique apomorphies: (39,2) large, tongue-shaped scutellum and (55,0) metakatepisternal suture present, forms the most basal clade (96% BS) in Histeroidea, and is the sister clade of (Synteliidae [Cretohisteridae+Histeridae]) (87% BS). The latter is supported by four unique synapomorphies: (15,0) antennal scape at least as long as three terminal antennomeres combined; (18,1) antennomere 3 shorter than 2; (32,0) prosternum length at least one-third of pronotum length; and (47,0) meso- and metaventrites fused. Other characters that map to this branch include (31, 1) prosternal intercoxal process distinctly widened behind procoxae; (36,1) protochantin hidden, though these could not be observed in *Cretohister*.



**Fig. 1.** The most parsimonious tree obtained from implicit enumeration method in TNT. Numbers above branches denote significant bootstrap values. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

- 3 Synteliidae exhibits three unique apomorphies: (8,3) right mandible on inner side with 3–4 teeth; (29,1) procoxal cavities closed externally; and (39,0) mesoscutellum finger-shaped.
- 4 Cretohisteridae as a new family is supported by one unambiguous autapomorphy: (17,2) pedicel slightly longer than scape (Fig. 3C). Other characters supporting this branch include: (16,2) antennal pedicel club-like, narrower basally than distally (Fig. 3C); (24,1) posterior margin of pronotum bisinuate (Fig. 3D); (52,0) hind coxae separated by 1.0–1.5× metacoxa width (Fig. 3E); and (63,0) abdominal ventrite 1 as long or slightly longer than ventrite 2 (Fig. 2B, D).
- 5 The clade of Cretohisteridae + Histeridae (86% BS) is supported by five unambiguous synapomorphies: (46,0) mesocoxal cavities separated by at least mesocoxal width; (53,1) meso and metaventral junction straight; (54,0) metaventricle with postcoxal lines; (58,0) metacoxae subcircular or subtriangular; and (60,1) abdominal tergites 4 posterad well sclerotized.
- 6 Histeridae is a strongly supported, monophyletic group (93% BS), supported here by three unambiguous synapomorphies: (34,2) prosternal keel present, but without lateral excavation with exception in Dendrophilinae; (42,1) hind leg not projecting beyond abdominal sides; and (62,1) abdominal tergal-sternal membrane long on segments 1–3 (and partly 4), very short on following segments. Relationships within

Histeridae are beyond the scope of this analysis and are not addressed further.

#### Systematic palaeontology

Superfamily Histeroidea Gyllenhal, 1808

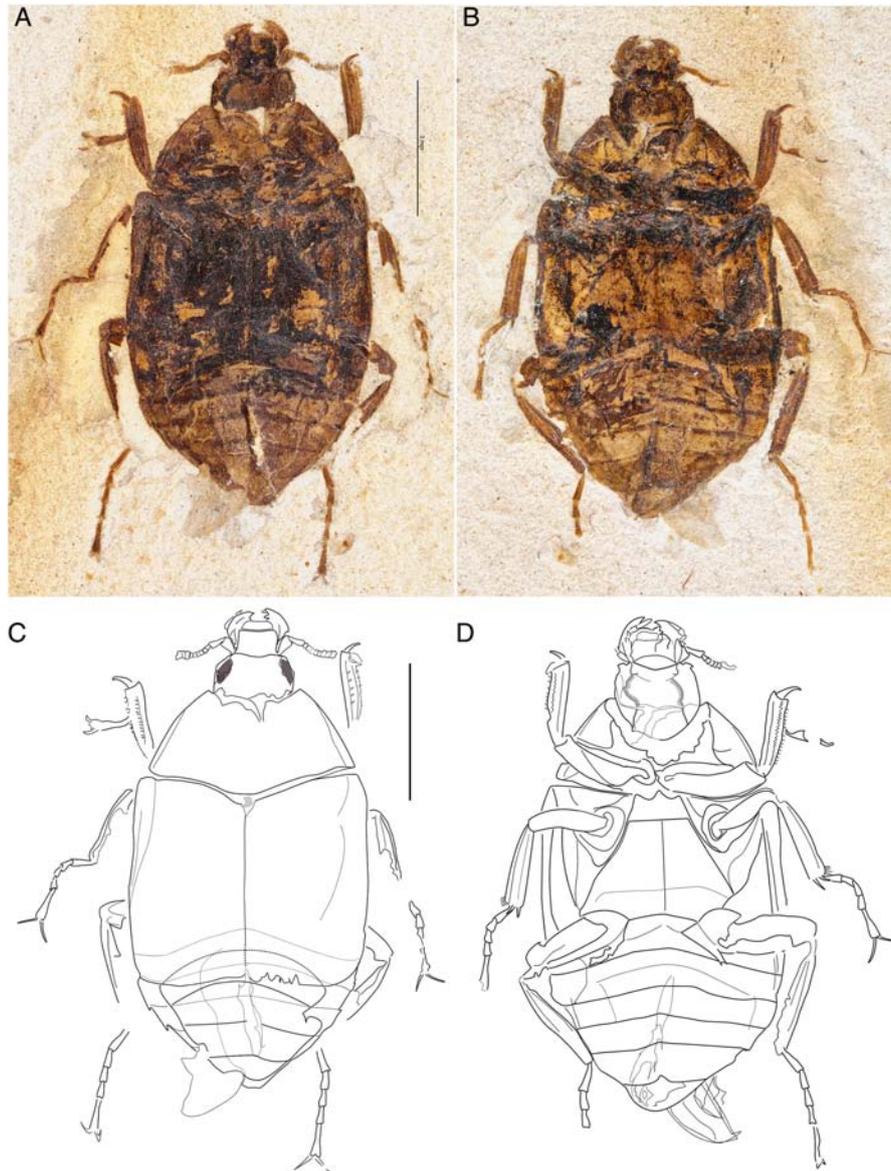
#### † Cretohisteridae fam.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:0F319412-70BE-468E-BFCD-77DC53EA40E2>

*Type genus.* † *Cretohister* **gen.n.**

**Diagnosis.** Cretohisteridae can be diagnosed as belonging to Histeroidea by combination of the following characters: geniculate antennal scape, compact three-segmented antennal club (Fig. 3C); truncate mesoventral process (Fig. 3E); truncate elytra (Fig. 2A, C); and abdominal segment VIII completely invaginated within VII.

This family can be easily distinguished from all known members of Histeridae, Sphaeritidae and Synteliidae by the following combination of characters. Head prognathous, not constricted behind eyes, with large, square clypeus and free labrum (Fig. 3A); antenna geniculate with scape short, cup-like; pedicel as long as scape; antennal club small, compact three-segmented



**Fig. 2.** Photographs and schematic drawings of holotype (NIGP166874a, b) of †*Cretohister sinensis* sp.n. of Cretohisteridae fam.n.: dorsal habitus (A, C) and ventral habitus (B, D). Scale bar, 3 mm. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

(Fig. 3C). Elytra nearly smooth, without grooves, striae or carinae, exposing 2 or 3 abdominal tergites (Fig. 2A, C). Prosternum short, with blunt triangular hypomeron laterally (Fig. 4A), procoxae not separated (Fig. 3E). Mesoventrite with paired coxal rests anteriorly (Fig. 3E); mesocoxae small, and broadly separated (Fig. 3E). Metaventrte with complete postcoxal lines (Fig. 2B, D), distinct middle discrimen extending the full length of the metaventrte, truncate metaventral process (Fig. 3E). Metacoxae transversely oval (Fig. 4C), moderately broadly separated. Propygidium without spiracle. Legs long (Figs 1A, B, 4D); tibiae with external margins not dentate but bearing two rows of small spines, meso-tarsomeres and meso-claws extraordinarily large (Figs 1A, B, 4D).

† *Cretohister* gen.n.

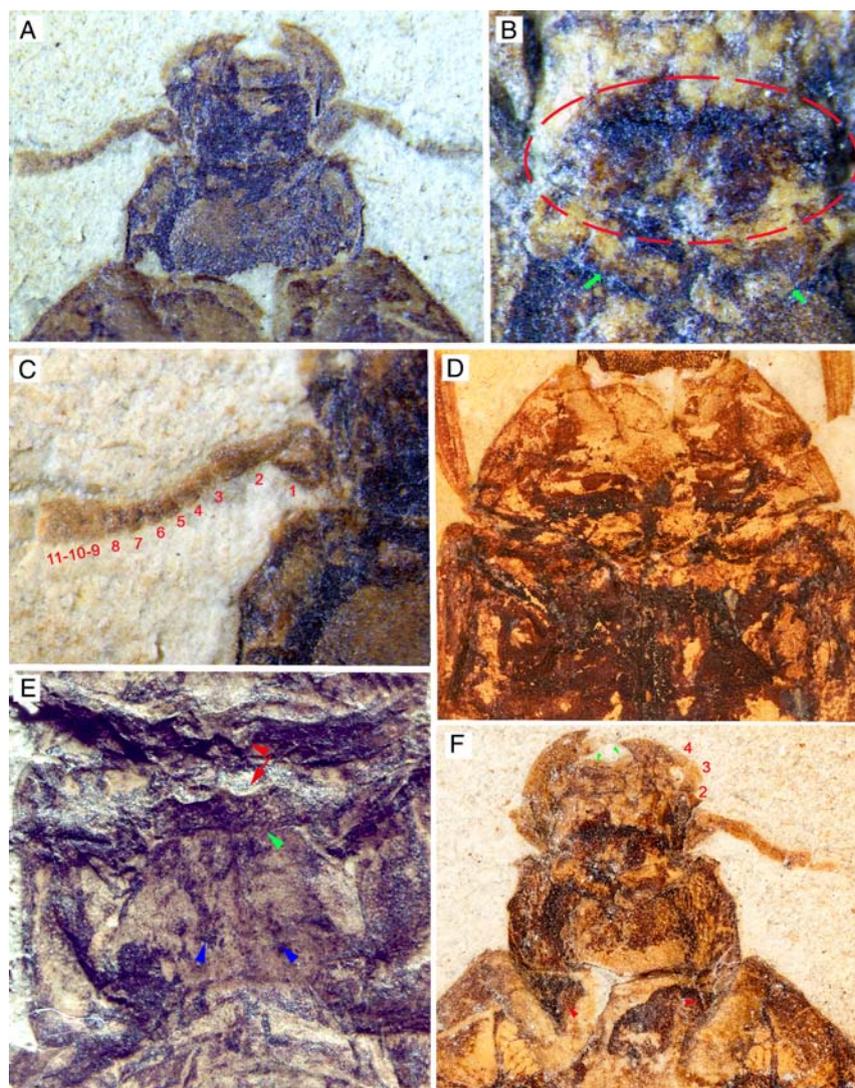
<http://zoobank.org/urn:lsid:zoobank.org:act:DC11290C-8439-46FB-ABC6-F368637C74F1>

*Type species.* † *Cretohister sinensis* sp.n.

*Diagnosis.* As for the family above.

† *Cretohister sinensis* sp.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:74E8D15F-0E66-4227-AAD9-B86A599EEC80>



**Fig. 3.** †*Cretohister sinensis* sp.n.: (A) head (NIGP166874a); (B) mentum (within red dotted line) and basal line of submentum (green arrow) (NIGP166874b); (C) antenna (NIGP166874a); (D) pronotum, (NIGP166874a); (E) meso- and metaventrite (NIGP166874b) (red arrows, procoxa and procoxal rest on mesoventrite; green arrow, boundary line between meso- and metaventrite; blue arrows, anterior margin of stalk); (F) head (NIGP166874b, maxillary palpomeres 2–4; green arrows, brushy galea; red arrows, gular sutures). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

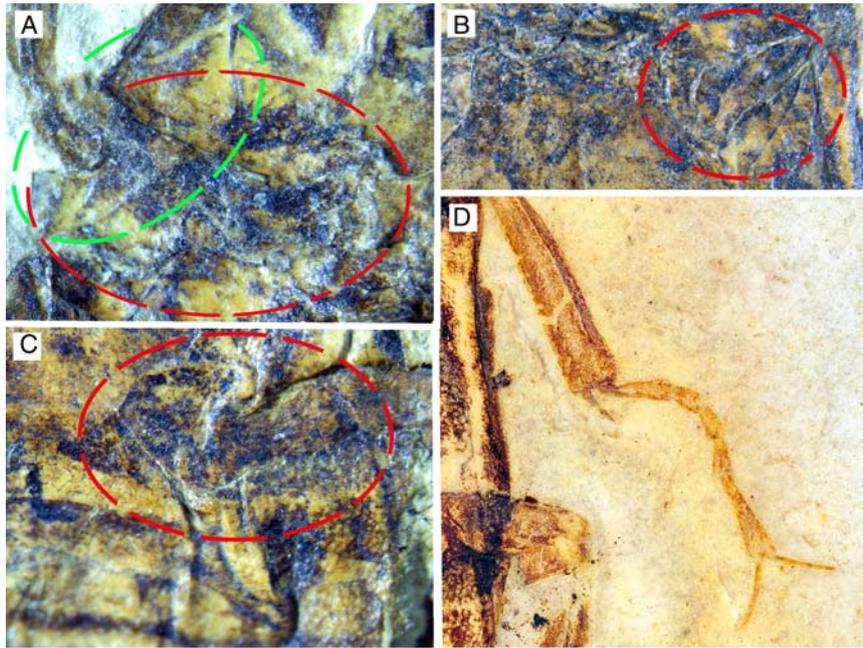
**Material.** Holotype, NIGP166874. The fossil beetle is very well preserved and nearly complete. Dorsal counterpart (NIGP166874a) and ventral counterpart (NIGP166874b) preserve most of details, except for a part between head and prosternum – the prosternal process appears partly crushed – and distortions on the ventral part of abdominal segments in dorsal part (a). The type specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu Province, China.

**Occurrence.** Lower Cretaceous Yixian Formation (Barremian, *c.* 125 Ma); Huangbanjigou, Beipiao, Liaoning, northeastern China.

#### Description

Body large, 10.3 mm long, maximum width across elytra 4.6 mm. Surfaces deeply and densely punctate on postgenae, metanepisternum and lateral sides of abdomen and especially on complete sternite VII (Figs 1A, B, 3F).

Head prognathous, with distinctly transverse vertex (HL = 1.3 mm; HW = 0.8 mm), not constricted behind eyes. Eyes oval and not projecting, 0.6 mm long, nearly occupying half of head length (Fig. 3A). Labrum large and distinctly transverse, length 0.3× width (Fig. 3A). Clypeus square-shaped (Fig. 3A), length 0.45× width, two times longer than labrum; separated from frons by distinct frontoclypeal suture (slightly



**Fig. 4.** †*Cretohister sinensis* sp.n.: (A) base of front leg (within red dotted line) and prothoracic hypomeron (within green dotted line) (NIGP166874b); (B) mesocoxa (within red dotted line) (NIGP166874b); (C) metacoxa (within red dotted line), (NIGP166874b); (D) mid-leg (NIGP166874a). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

emarginate medially). Mandibles asymmetrically dentate, with at least two teeth on right incisor edge (left side not visible). Maxilla partially preserved, ultimate palpomere cylindrical, and longer than penultimate, with a long brushy galea between mandibles (Fig. 3F). Antenna 11-segmented and geniculate (Fig. 3C), *c.* 1.4 mm long; scape slightly elongate, 0.4 mm long, subpyramidal, slightly longer than pedicel; pedicel elongate, length approximately equal to combined antennomeres 3–6; antennal club three-segmented, compact and small, *c.* 0.3 mm long. Mentum obscure, apparently oval (Fig. 3B), separated from gula by thin medially emarginate suture. Anterior margin of submentum situated before anterior margin of eye (Fig. 3B). Gular plate very broad, probably artificially depressed at anterior two-thirds (Fig. 3F).

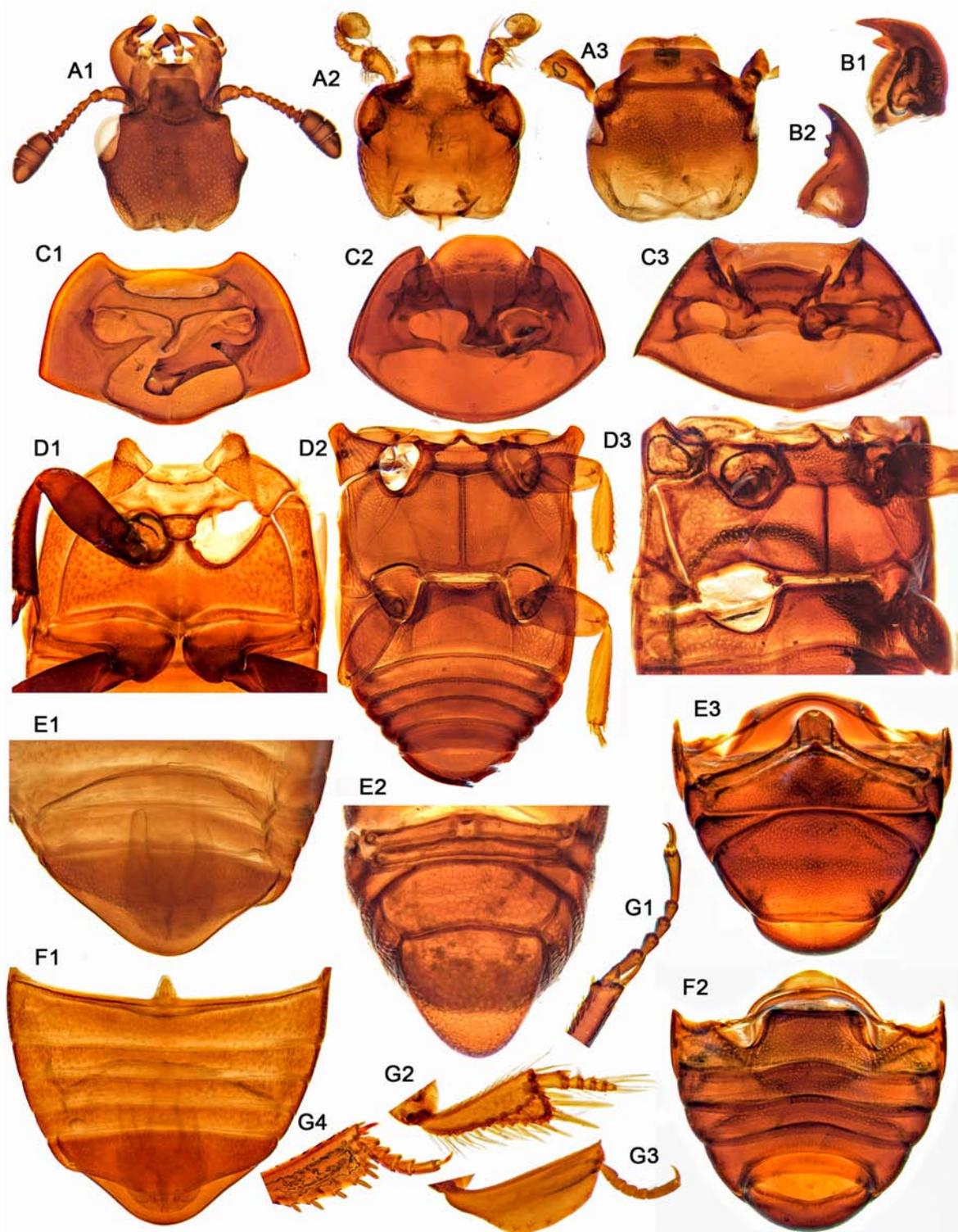
Prothorax transverse (PL = 2.3 mm, PW = 4.4 mm), nearly trapezoidal, widest at base and distinctly narrowing anteriorly (Fig. 3D). Base of prothorax not tightly co-adapted with rest of thorax. Posterior margin sinuate medially, projecting posteriorly. Anterior angle distinct but not projecting; lateral pronotal margin with sub-lateral carina extending from apical to posterior angles. Hypomeron blunt, triangular (Fig. 4A). Prosternum damaged anteriorly, but apparently short and without median lobe or keel (Fig. 3E). Procoxae apparently narrowly separated, subcontiguous (Fig. 3E); prosternal process damaged. Procoxal cavity transverse, externally open; protrochantin not clearly visible; notosternal sutures complete, sinuate.

Pterothorax (Figs. 2A–D, 3E, 4B, C). Scutellum indistinct. Elytra (EL = 5.2 mm, EW = 4.6 mm) rectangular, 2× longer than pronotum length, with well-developed humeral angles, exposing three tergites, but right elytron partly damaged apically

(Fig. 2C). Hindwing well-developed, partly visible and extending beyond apex of abdomen (Fig. 2A, C). Elytral disc appears to be smooth without puncture rows, grooves or carinae; epipleuron wide and probably complete (Fig. 2A, C). Mesoventrite transverse, at least as wide as mesocoxal diameter; anteriorly with paired coxal rests (Fig. 3E). Mesocoxae small (Fig. 4B); mesocoxal cavities triangular, externally open. Metaventrite with postcoxal lines, truncate metaventral process and distinct discri-men. Metendosternite visible through sternum, with stalk about one-third length of metaventrite (Fig. 3E). Metanepisternum broader than elytral epipleuron. Metacoxae transversely oval (Fig. 4C), separated by weakly arcuate intercoxal process, which is broader than metacoxa.

Legs (Fig. 2C, E, 4D). Protibia with single large spur apically (length *c.* 0.5 mm) and with two rows of spines on the outer and median surface (Fig. 2C, D). Mesotibia with two subequal apical spurs (Fig. 4D). Both mid- and hind tibiae with two rows of spines and grooves on each surface. Mid- and hind legs quite long (> 7 mm). Metafemur with inner apical tooth; tarsal formula 5-5-5; tarsi (especially in mid- and hind legs) with long claws (*c.* 0.14 mm); terminal tarsomere as long as preceding two combined; basal tarsomere longer than tarsomere 2.

Abdomen (Fig. 2A–D). Distinctly narrowing apically with five ventrites of subequal length. Dorsal side somewhat unclear and appears to contain three exposed tergites but the first exposed tergite was probably artificially extended during fossilization. Abdominal tergite IV arcuate anteriorly, terga IV–VII well sclerotized. Propygidium without apparent spiracle. Abdominal tergo-sternal membrane long on segments 1–6 (–7). Abdominal segment VIII completely invaginated within



**Fig. 5.** Some characters used in phylogenetic analyses. (i) *Sphaerites glabratus* (Fabricius): A1, head; C1, prosternum; D1, meso- and metaventrite; E1, tergites IV–VII; F1, ventrites; G1, mid-leg; (ii) *Pelorurus* sp. (Histerinae): B1, mandibles; D3, meso- and metaventrite; E3, tergites IV–VII; F2, ventrites; G4, mid-leg; (iii) *Philothis arabicus* Mazur (Saprininae): A2, head; E2, tergites IV–VII; G2, mid-leg; (iv) *Epiurus* sp. (Tribalinae): A3, head; C2, prosternum; D2, meso- and metaventrite; (v) *Abraeus* sp. (Abraeinae): C3, prosternum; *Dendrophilus pygmaeus* (Linnaeus) (Dendrophilinae): G3, mid-leg; (vi) *Niponius* sp. (Niponiinae): B2, mandibles. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

**Table 5.** Published phylogenetic studies related to Histeroidea.

Systematic relationships	Morphological dataset				Mixture	Molecular dataset		
	Larva	Larva + adult	Adult	Adult + Fossil	Adult + 18S	18S	Eight nuclear genes	18S + 28S
Sphaeritidae+ (Synteliidae + Histeridae)	B		A–C	H	D			
Synteliidae+ (Sphaeritidae + Histeridae)						D	F	G
Histeridae+ (Sphaeritidae+Synteliidae)		E						
(Synteliidae+ ((Hydrophilidae + (Sphaeritidae deep positioned inside Histeridae)))	H based on E							

A, Hansen (1997); B, Caterino & Vogler (2002); C, Ślipiński & Mazur (1999); D, Caterino *et al.* (2005) (using two subfamilies of Histeridae); E, Lawrence *et al.* (2011); F, McKenna *et al.* (2015) (using three subfamilies of Histeridae); G, Bocak *et al.* (2014) (using 68 unplaced species); H, by our research.

segment VII; specimen may be a female, with one apparent coxite exposed beneath open pygidium.

## Discussion

Phylogenetic analyses based on adult, larval or combined morphological and molecular data have consistently supported the monophyly of Histeroidea, and the monophyly of the largest family Histeridae within this superfamily (Newton, 2016). However, there remain disagreements between the published phylogenies in whether Sphaeritidae, Synteliidae or Histeridae is the sister taxon to the other two families (Table 5; Ōhara, 1994; Hansen, 1997; Beutel, 1999; Ślipiński & Mazur, 1999; Caterino & Vogler, 2002; Caterino *et al.*, 2005; Hunt *et al.*, 2007; Lawrence *et al.*, 2011; Bocak *et al.*, 2014; McKenna *et al.*, 2015; Kovarik & Caterino, 2016).

The Lower Cretaceous *Cretohister* exhibits a somewhat transitional morphology among Histeroid families. Our phylogenetic results support the hypothesis that Sphaeritidae is the sister of the remaining Histeroidea, with Synteliidae the sister group of the new family plus Histeridae. Based on the character distributions on the cladogram we may hypothesize that, over time: (i) the body of Histeroidea evolved from rather loosely articulated (Sphaeritidae, Synteliidae, *Cretohister*) to very compact and co-adapted without free space between prothorax and elytra in Histeridae – this may have been facilitated by the broadening of the ventrites such that the meso- and metacoxal bases are well separated, as seen in *Cretohister* and all Histeridae; (ii) the well-developed frontoclypeal suture found in Hydrophiloidea, *Sphaerites*, and *Cretohister* disappeared in parallel in Synteliidae and Histeridae (the apparent epistomal suture in some histerid groups is probably not homologous with frontoclypeal suture); (iii) antennal organization and form changed from a nongeniculate base, bearing rather a distinctly divided club in Hydrophiloidea and Sphaeritidae, to the derived geniculate form in the Histeroidea, with antennomere 3 becoming shorter than pedicel and the antennal club progressively more compact; (iv)

the gular sutures broadly separated in the plesiomorphic Sphaeritidae and *Cretohister*, got much narrower in Synteliidae and became fused together within Histeridae.

*Cretohister* and Histeridae share a remarkable number of characters of the venter, while remaining superficially quite different. The broadly separated meso- and metacoxae, with broad, flat ventrites, is unmistakably histerid-like. However, apparently substantial differences in the prosternum preclude assignment of *Cretohister* to Histeridae. These characters are unfortunately difficult to interpret in the fossil. We suspect some level of damage to have obscured portions of the prosternum. Yet it is difficult to imagine that any kind of prominent prosternal keel would have been completely removed. So we consider its absence to be a reliable hypothesis. If this is accurate we might further hypothesize that the reposed position of the head was hypognathous, much as in *Sphaerites*, rather than prognathous, as preserved in the fossil. The abdomen also seems to differ significantly from that of Histeridae. The segments are rather loosely articulated, and do not appear to be at all telescoping, as are the ventrites in Histeridae and Synteliidae. In this and some other respects, the hypothesis that *Cretohister* is sister to Histeridae necessitates reinterpretation of several formerly presumed synapomorphies of Synteliidae and Histeridae.

Unfortunately, the habits of extant basal Histeroidea remain somewhat unclear. Adults of *Sphaerites glabratus* are usually associated with decaying matter and are known to be attracted to sap flows on stumps, and have been observed to feed on the sap and mate there (Nikitsky, 1976; Newton, 2016). However, the feeding of *Sphaerites* adults on sap, as opposed to the predatory behaviour of all Histeroidea larvae and adults of Synteliidae and most Histeridae, requires further confirmation (Newton, 2016). Basal habits within Histeridae are still unclear, as both basal relationships and feeding preferences of some putatively basal forms are unknown. Poinar & Brown (2009) suggested semi-aquatic habits for the Cretaceous *Pantostictus burmanicus*, one of the earliest true Histeridae, but this was based on interpretation of a single minor character (ventral tarsal setae). The comparably old *Cretonthophilus tuberculatus*

(Caterino *et al.*, 2015) and *Amplectister tenax* (Caterino & Maddison, 2018), all from ~99 Ma Burmese amber, exhibit very different morphologies, and the latter seem to indicate that inquilinism arose very early in Histerid evolution. It is becoming further apparent that none of these represents the family's earliest evolution, and further new fossil taxa awaiting description (Zhou *et al.*, unpublished data) show that Histeridae was very diverse and that most of the subfamilies were already established at the Middle Cretaceous.

Ongoing fossil discoveries will facilitate a complete reassessment of basal Histerid relationships. Although relationships between major clades recovered in our phylogenetic analyses are in part similar to those in Ślipiński & Mazur (1999) and Caterino & Vogler (2002), this weak agreement is still based on rather fragmentary analyses of extant diversity. Morphological convergences in cylindrical bark beetle predators (Niponiinae, Trypanaeninae, and Trypeticinae, all with superficial similarities to *Syntelia*) have probably misled previous analyses (Caterino & Vogler, 2002). Other early branching lineages of Histeridae include the poorly defined Onthophilinae, with some saprophagous taxa, Dendrophilini (presumably predators), Anapleini (habits unknown) and some Abraeinae (varied habits) (Kovarík & Caterino, 2016). Adequate samples of these remain to be included in larger analyses. Integration of newly discovered fossil taxa and more complete sampling of extant taxa will provide great new insights into the early branching patterns and ecomorphological evolution of this interesting group.

## Conclusions

The discovery of a new family of Histeroidea from the Lower Cretaceous Yixian Formation, with a combination of many plesiomorphic and derived morphological characters, provides an interesting picture of palaeodiversity of the early Histeroidea, and supports the basal position of Sphaeritidae in this superfamily. This finding, together with Jurassic fossils attributable to the sister group Hydrophiloidea (Ponomarenko, 1977; Prokin *et al.*, 2010; Fikáček *et al.*, 2012; Fikáček *et al.*, 2014) and already diverse fossils of Histeridae in Burmese amber, provides support for the Late Triassic age of origin for Histeroidea as advocated by Toussaint *et al.* (2017).

## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12300

**Figure S1.** The most parsimonious tree with significant bootstrap values and character states mapped using unambiguous optimization in WINCLADA.

**Figure S2.** Habitus of recent Histeroidea. (1) *Sphaerites glabratus* (Fabricius), dorsal view (A) and ventral view (B); (2) *Syntelia histeroides* Lewis, dorsal view (C) and ventral

view (D); *Hister nomas* Erichson, dorsal view (E) and ventral view (F).

**Figure S3.** The main types of antennal club in Hydrophiloidea and Histeroidea.

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