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# Early origin of parental care in Mesozoic carrion beetles

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The reconstruction and timing of the early stages of social evolution, such as parental care, in the fossil record is a challenge, as these behaviors often do not leave concrete traces. One of the intensely investigated examples of modern parental care are the modern burying beetles (Silphidae: *Nicrophorus*), a lineage that includes notable endangered species. Here we report diverse transitional silphids from the Mesozoic of China and Myanmar that provide insights into the origins of parental care. Jurassic silphids from Daohugou, sharing many defining characters of Nicrophorinae, primitively lack stridulatory files significant for parental care communications; although morphologically similar, Early Cretaceous nicrophorines from the Jehol biota possess such files, indicating that a system of parental care had evolved by this early date. More importantly, burying beetles of the genus *Nicrophorus* have their earliest first record in mid-Cretaceous Burmese amber, and document early evolution of elaborate biparental care and defense of small vertebrate carcasses for their larvae. Parental care in the Early Cretaceous may have originated from competition between silphids and their predators. The rise of the Cretaceous Nicrophorinae implies a biology similar to modern counterparts that typically feed on carcasses of small birds and mammals.

sociobiology | paleoethology | paleoecology

Understanding the early evolution of many complex or ephemeral behaviors is severely hampered by the frequent lack of fossilized traces. Among these behaviors, parental care represents a significant behavioral adaptation in life history traits and, as one of the core levels of arthropod sociality, has a wealth of sociobiological and behavioral ecological theory behind it (1). Parental care has evolved independently numerous times among animals, including various lineages of insects (1, 2), for which one of the notable examples is the famous burying beetle, otherwise so critical to forensic entomology. With fewer than 200 extant species, the family Silphidae are among the largest and most conspicuous of the staphylinoid Coleoptera (3) and comprise two well-defined subfamilies: the Silphinae and the Nicrophorinae, with the latter characterized by the presence of an epistomal sulcus and paired stridulatory files and the former by the absence of such features. Silphid parental care has been intensively studied (4, 5), with several attempts to explain its origin and subsequent evolution (6, 7). Fossil evidence that elucidates the origin and evolutionary history of this phenomenon is, not surprisingly, lacking, although modern-looking silphids have been discovered in the Tertiary (8–10). Recent discoveries in the Middle Jurassic and Early Cretaceous of northeastern China together provide a unique suite of evidence for the timing of origin of parental care in these beetles, and suggest an ancient and long history to this behavioral adaptation among silphids. Furthermore, evidence from olfactory structures preserved in minute detail on the antennae of these fossils reveals them to have already adapted to feeding on carrion, perhaps being important recyclers of small-bodied vertebrates during the Age of Dinosaurs.

The material studied herein includes 44 well-preserved specimens belonging to three distinct groups. The first group, characterized by the absence of abdominal stridulatory files, comprises 37 specimens from the Middle Jurassic Daohugou beds (~165 Mya) at Daohugou, Ningcheng County, Inner Mongolia of China. The second group, with distinct abdominal stridulatory files as in crown-group nicrophorine silphids, includes five specimens from the Lower Cretaceous Yixian Formation (~125 Mya) at Huangbanjigou, Beipiao City, Liaoning Province and Liutiaogou, Ningcheng County, Inner Mongolia. The third group, with lamellate apical antennomeres, comprises six individuals preserved in two mid-Cretaceous ambers (~99 Mya) from northern Myanmar.

## Results

All Jurassic and Cretaceous beetles are unambiguously referred to Silphidae, as evidenced by their general habitus, clubbed antennae, large mesoscutellum, truncate elytra, and well-separated mesocoxae (3, 11). The diverse transitional silphids extend the earliest records of the family by about 130 million y, the next oldest record being a compression fossil from the Late Eocene (~35 Mya) of Florissant, Colorado (9). With a body length ranging from 6.5 to 13.5 mm, these Mesozoic beetles are smaller than extant silphids (usually 12–20 mm long). The beetles are obviously suggestive of modern Nicrophorinae, the subfamily including the burying beetles, which locate and bury vertebrate carrion and use it to feed and care for their brood, sometimes with both mother and father contributing to the parental investment (3). The beetles share with Nicrophorinae the presence of a straight epistomal sulcus, relatively short elytra (Figs. 1*A*, *D*, and *E*, and 2*A–C*), and body shape (Figs. 1*A–E* and 2*A–C* and Figs. S1–S3). The

## Significance

We report on the unique discovery of Jurassic and Cretaceous carrion beetles (Silphidae) from China and Myanmar, early relatives of one of the most protected of beetle species in North America, and which clearly preserve evidence indicative of complex parental care. This finding represents the earliest evidence of parental care, a behavioral repertoire that is the first step in the development of truly social behavior and one that is intensely studied by ecologists, ethologists, and evolutionary biologists alike. Our fossils clearly span the origins of parent-offspring communication and allow us to provide a robust estimate of the time of origin for this complex behavior.

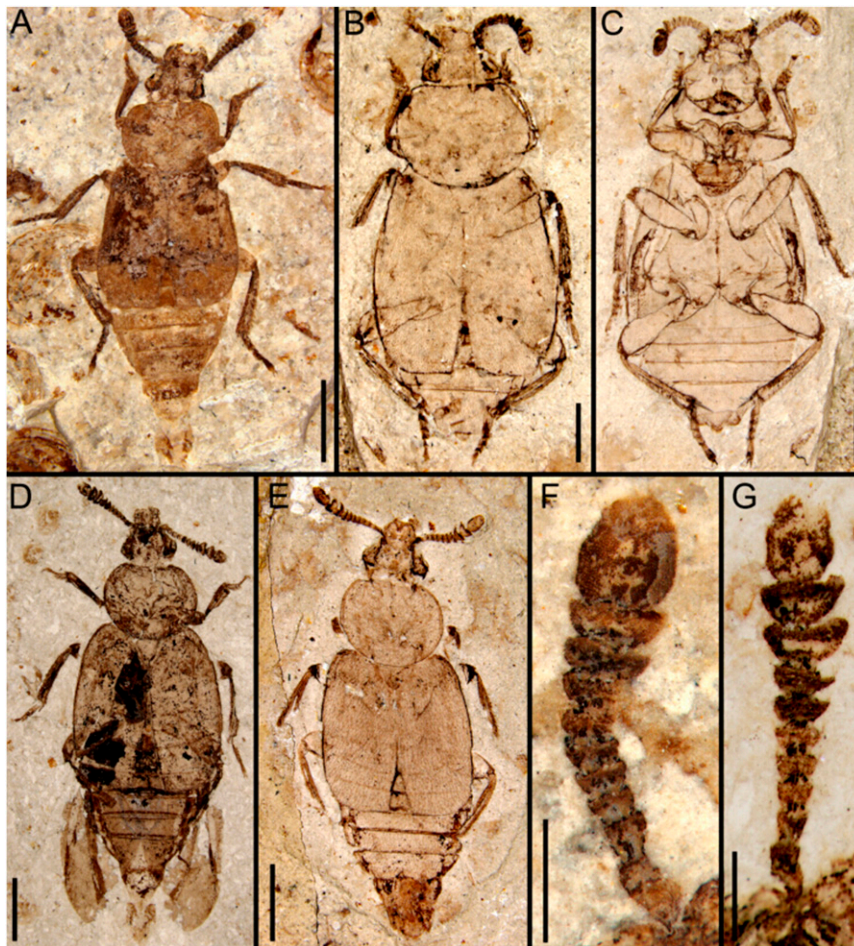
Author contributions: D.-Y.H. designed research; C.-Y.C. and D.-Y.H. performed research; M.K.T., A.F.N., B.W., and X.-D.W. contributed new reagents/analytic tools; C.-Y.C., M.K.T., M.S.E., A.F.N., J.O.-B., and D.-Y.H. analyzed data; and C.-Y.C., M.S.E., and D.-Y.H. wrote the paper.

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**Fig. 1.** Silphids from the Middle Jurassic of Daohugou. (A) 156144a, general habitus. (B) 156145a, part. (C) 156145b, counterpart. (D) 156146a, part. (E) 156147a, part. (F) Enlargement of A, left antenna. (G) Enlargement of D, left antenna. (Scale bars: 2 mm in A–E; 500  $\mu$ m in F and G.)

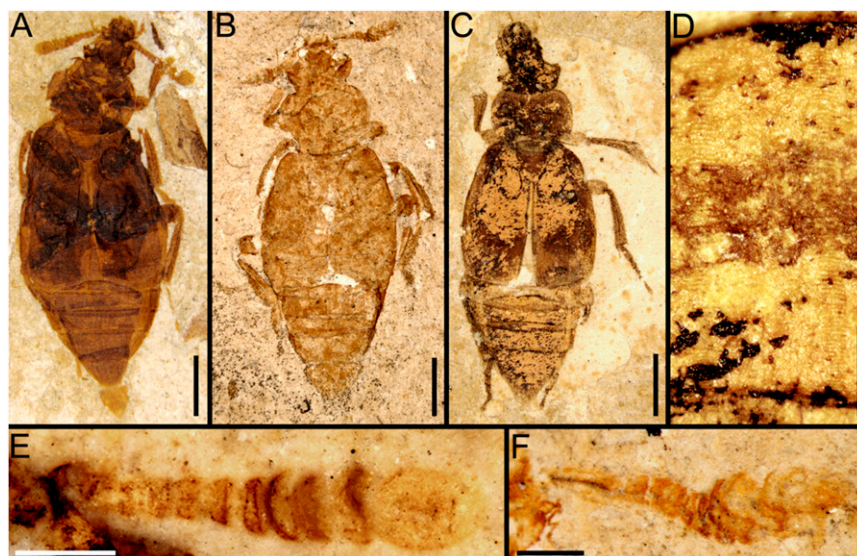
Mesozoic silphids display three distinct types of antennae: one is gradually widened from the base to the distal antennomere, resembling that of some extant silphines (Figs. 1F and 2E); the second is characterized by the apical three antennomeres being moderately to abruptly clubbed, but not lamellate (Figs. 1G and 2F), a feature suggestive of the modern nicrophorine genus *Ptomascopus*; and the third is characterized by a strongly clubbed antenna with lamellate apical antennomeres 8–10 (Fig. 3C) as those of the burying beetles *Nicrophorus* (Fig. 3D) (3). Given the similar morphological characters between the Mesozoic and Recent silphids, the former probably had the same feeding habits as modern ones. In most insects the principal olfactory receptors are located on the antennae, with auxiliary ones on the palpi (12, 13). Two types of sensory organs (or sensilla) are recognizable on the antennal club of the Jurassic silphids (Fig. 4C and Fig. S4 D, G, J, and K), perfectly corresponding to those in extant nicrophorine beetles (14), namely sensilla coelosphaerica (Fig. 4 D and E and Fig. S4 E, H, L, and M) and sensilla basiconica (Fig. S4 F and I). The former type is large, round, pit-like, and located on one side of the apical antennomere along its axis; the latter is smaller, hair-like, and distributed on the other side. The identical olfactory structures indicate that silphids in the Jurassic were already adapted to detecting sulfur-containing volatile organic compounds over long ranges, just as in extant nicrophorines and most silphines (15). Mesozoic silphids thus may have been significant scavengers and important to the breakdown and recycling of carcasses in such ancient ecosystems.

Notably, all Cretaceous silphids studied possess a pair of stridulatory files on abdominal tergite (Figs. 2D and 4B, and Fig. S5 D and E) and Y-shaped gular sutures (Fig. S3 K and L) like those found in Nicrophorinae (Fig. 4A and Fig. S5 A–C), so they are firmly placed in Nicrophorinae. The Cretaceous Nicrophorinae from China with the second type of antennae can be placed in more primitive *Ptomascopus*, whereas those from Myanmar with the third type are attributed to *Nicrophorus*. It is probable that the mid-Cretaceous and Recent *Nicrophorus* were derived from among the Early Cretaceous silphids. Together, the Jurassic and Cretaceous taxa form a grade leading to crown-group Nicrophorinae and spanning the origin of stridulatory structures used in parent–offspring communication (Fig. S6).

## Discussion

Evidence of parental care in the fossil record is exceptionally limited, reported mainly in dinosaurs (16–21), ostracod crustaceans (22), and rarely in insects (23). Despite extensive research on the ecology, physiology, and behavior of modern burying beetles, the origin of parental care within Nicrophorinae and broadly across all beetles remains elusive. Burying beetles exploit small vertebrate carcasses (usually rodents or birds) and bury them in soil as a source of nutrition for their larvae (3). The parents care for and feed the young as they grow, a condition necessary for sociality and more famously known in taxa such as bees, ants, and termites (24). The closely allied *Ptomascopus* is known to possess a simpler, possibly primitive, parental care in

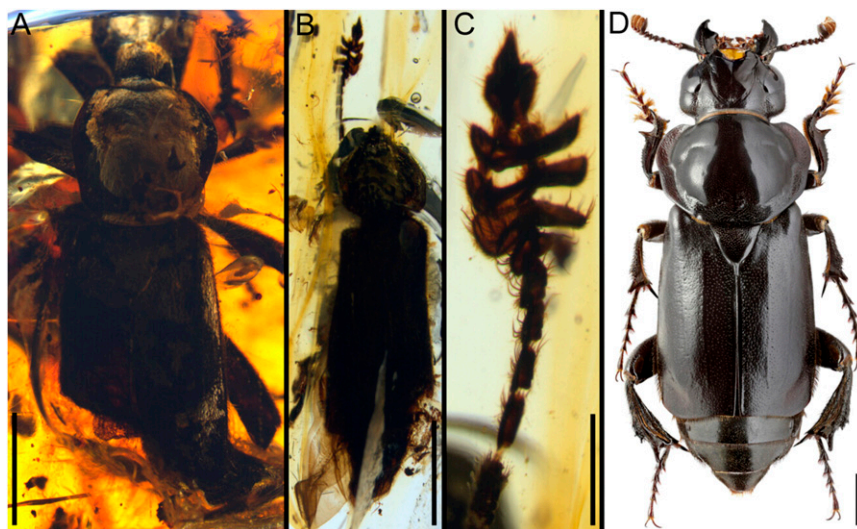




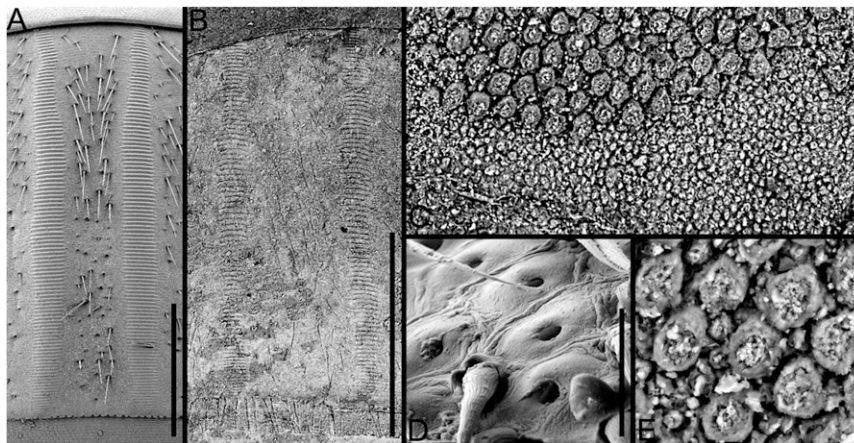
**Fig. 2.** Nicrophorine silphids from the Early Cretaceous of northeastern China. (A) 156150a, from Huangbanjigou, general habitus. (B) 156151 from Huangbanjigou. (C) 156152a from Liutiaogou. (D) Enlargement of abdominal tergite V of C, showing paired stridulatory files. (E) Enlargement of A, left antenna, mirror-imaged. (F) Enlargement of B, right antenna. (Scale bars: 2 mm in A–C; 200  $\mu$ m in D; 500  $\mu$ m in E and F.)

which adults guard small carcasses and their young against competition from both flies and predators, but without burying the carcasses (7). Parental care in Silphidae is confined to the subfamily Nicrophorinae and absent in Silphinae, although the latter are also carrion-feeding as larvae and adults. The innovation of stridulatory files in Nicrophorinae for parent–offspring communication and defense (25) seems to be critically linked to the origin of parental care, as inhibition of stridulation affects reproduction drastically in extant *Nicrophorus* males and affects brood care and survival of offspring in females (26). Our discovery of exquisitely preserved Mesozoic silphids sheds new light on the origin and early evolution of parental care. Although Jurassic silphids resemble *Ptomascopus*, stridulatory files are clearly absent in all individuals, suggesting that these scavengers did not care for their young, as in modern Silphinae. However, the Early Cretaceous nicrophorines having stridulatory files, including *Ptomascopus*

species, likely shared a similar behavior and biology, possessing a simple form of parental care whereby adults guarded small carcasses, alerting their brood to the presence of predators and defending them as necessary. More significantly, true burying beetles, *Nicrophorus*, with characteristic body shape and antennae, originated in the mid-Cretaceous, suggesting that they likely provided elaborate biparental care to their offspring, including exploiting small vertebrate carcasses (early birds or mammals) and burying them in soil as a source of nutrition for their larvae. This finding demonstrates that such significant adaptations, behavioral and morphological, associated with considerable parental investment, were already well established in the Cretaceous. Although parental care is widespread across the hyperdiverse Coleoptera and has evolved independently multiple times, this is the earliest documentation of such behavioral adaptations within the clade.



**Fig. 3.** Mid-Cretaceous and Recent burying beetles *Nicrophorus*. (A) 156194, dorsal view. (B) 156195, dorsal view. (C) Enlargement of B, left antenna. (D) *Nicrophorus satanas* Reitter, dorsal view. (Scale bars: 500  $\mu$ m in C; 2 mm A, B, and D.)



**Fig. 4.** Scanning electron micrographs of stridulatory files and antenna. (A) Detail of stridulatory files of *Nicrophorus orbicollis* Say, 1825. (B) Stridulatory files of Cretaceous silphid, 156152a (compare with Fig. 2D). (C) Enlargement of apical antennomere of 156148b, showing sensilla coelosphaerica and sensilla basiconica. (D) Enlargement of antennomere of modern *Nicrophorus orbicollis* Say, showing the pit-like sensilla coelosphaerica. (E) Enlargement of antenna of 156148b, showing detail of sensilla coelosphaerica. (Scale bars: 500  $\mu$ m in A and B; 50  $\mu$ m in C; 10  $\mu$ m in D; 20  $\mu$ m in E.)

Competition for resources and predation have been hypothesized as ecological factors important to the evolution of parental care (27, 28). Modern microphorines encounter intense biotic stress from two sources: competition with blow flies (Diptera: Calliphoridae) for food, and threat of predation, potentially by some derived staphylinine rove beetles (Coleoptera: Staphylinidae) (7, 29). Similar competitive pressures may have triggered the origin of parental care among ancient carrion beetles. Calliphorids and other schizophoran flies are unknown before the Tertiary, and even molecular estimates consider their radiation to have occurred around the K/T boundary (~65 Mya) (30, 31). Calliphorids were certainly not competitors for vertebrate carcasses during the Mesozoic, and although we cannot exclude the possibility of other extinct lineages serving such an ecological role, such evidence is presently not forthcoming. As for potential predators of silphids, these seem to be in abundance. The related rove beetles (Staphylinidae) have a relatively long evolutionary history extending into the early Jurassic (32). Jurassic staphylinids are well known and diverse, comprising several basal lineages (32, 33). Many of these taxa, with inconspicuous mandibles, were possibly mycophagous or saprophagous, like their modern counterparts. However, there was an apparent radiation of the derived subfamily Staphylininae during the Early Cretaceous (34). Interestingly, a diversity of staphylinines has been recovered from the Yixian Formation and many of them are characterized by very prominent, sharp mandibles (Fig. S6 B and C) and large bodies (Fig. S6 A and D–G), as in predaceous groups today. Potential predators of extant microphorine larvae include staphylinine genera such as the Staphylinina *Creophilus*, *Ontholestes*, and *Platydracus* (29); several of the Cretaceous rove beetles (Fig. S7) might have shared this life history, although the known Cretaceous taxa are not closely related to the often carrion-attracted Staphylinina (34). It is possible that the rise of predaceous Staphylininae influenced evolution of coeval silphids, perhaps being critical to the origin of parental investments in stem-group Microphorinae. Alternatively, or in addition, some early mammals or birds in the Early Cretaceous might have been predators influencing the evolution of silphid biology (see SI Text, *Paleodiversity of Contemporaneous Feathered or Haired Vertebrates*).

With the origin of crown Mammalia in the Late Triassic (35), early silphids might have already derived from their staphyliniform ancestors at that time. Mid-Jurassic silphids likely fed on carcasses of small mammals and perhaps even feathered dinosaurs, whereas Cretaceous species likely sought, as in modern microphorines (3), small mammals (Fig. S8) or birds. The Daohugou biota and adjacent localities have yielded feathered dinosaurs (36, 37) and some terrestrial mammals, including small-sized eutherians and allotherians (35, 38, 39), but no birds. In contrast, the younger Jehol biota preserves evidence of significant radiations for both early birds and mammals, with at least 39 avian and 15 mammalian species reported (40), and with taxa ranging in body size from dozens of grams to several kilograms (40, 41). In addition, bird feathers are well known from Burmese amber (42). Regardless, the Mesozoic diversity highlights an ancient time of origin for parental investment among carrion beetles, and emphasizes the complex interplay between locating a suitable and specialized food source (carrion) and defending against predation for the evolutionary development of extended parent-offspring interactions and communication (stridulation). It is fascinating that much paleoethology and paleoecology are embodied in the relatively minute remains of otherwise great recyclers during the mid-Mesozoic forests of China, and suggests a familiar ecological role and suite of influences in a foreign ecosystem.

## Methods

The material studied here is housed at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. The fossils were prepared using a sharp knife. Photographs were taken using a Zeiss Discovery V20 microscope system, with specimens moistened with 70% (vol/vol) alcohol (Figs. S1 E and I–M, S2 A–D, I, L, and M, and S3 K and L) or dry (remaining figures). Photomicrographs of stridulatory files on abdominal tergite V (Fig. 4 A and B and Fig. S5 B–F) and antennal sensilla (Fig. 4 C and D and Fig. S4) were taken with a LEO1530VP field-emission scanning electron microscope.

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# Supporting Information

Cai et al. 10.1073/pnas.1412280111

## SI Text

**Description of Mesozoic Silphidae and Remarks.** *Silphidae from the Middle Jurassic Daohugou biota.* With a body length ranging from 6.5 to 13.5 mm, these beetles (Figs. S1 and S2) are smaller than Recent silphids (length 7–45 mm, usually 12–20 mm). The general habitus is obviously suggestive of the extant subfamily Nicrophorinae. The robust body (Fig. S1 A–C and Fig. S2 A–K), including the head, bears fine and dense pubescence, whereas the prominent mandible is sharp and lacks preapical teeth. The antennae are of two distinct types: one type is gradually widened from the base to the distal antennomere, resembling that of some extant silphines (Fig. S1 L and M); the other is characterized by the apical three antennomeres being more abruptly clubbed (Fig. S2 L and M), a feature greatly resembling modern Nicrophorinae, especially the relatively primitive genus *Ptomascopus*. The second antennomere is distinct, slightly shorter than the third, not highly reduced as in modern Nicrophorinae (Figs. S1 L and M, and S2 L and M). At least the apical four antennomeres are asymmetrical and the antennal insertions are exposed (Figs. S1 L and M, and S2 L and M). The epistomal sulcus is present and straight (Fig. S1C), as found in modern Nicrophorinae, and the elytra are short and truncate, usually with four abdominal segments exposed (Fig. S2 G, J, and K). It is noteworthy that these superficially nicrophorine-like beetles retain several peculiar characters that differ from those of Nicrophorinae. The beetles bear narrowly separated gular sutures (Fig. S1D) that diverge anteriorly and posteriorly (in contrast to posteriorly fused and Y-shaped in Nicrophorinae), narrowly separated mesocoxae (Fig. S2 B, C, F, and I), a medially carinate sternite III (Fig. S1G) and tergite V lacking stridulatory files.

**Silphidae from the Early Cretaceous Jehol biota.** These beetles (Fig. S3), 12.5–14.0 mm long, are superficially similar to those from the Middle Jurassic Daohugou biota, including their general habitus, body size, and antennal morphology. Like the Jurassic silphids, the Cretaceous ones have two antennal types: one is gradually dilated apically, almost the same as one of the Jurassic types (Fig. S3 H and I); the other is characterized by an elongate scape and four evidently dilated apical antennomeres (Fig. S3J). The beetles also share a straight epistomal sulcus (Fig. S3 C and K), truncate elytra (Fig. S3 A–G), and a carinate sternite III (as in Fig. S2 A, D, and F). Unlike the Jurassic silphids, they possess Y-shaped, posteriorly fused gular sutures (Fig. S3 K and L), moderately separated mesocoxae (Fig. S3 A, D, and F) and, more significantly, abdominal tergite V with paired stridulatory files (Fig. S5 D–F).

**Remarks.** The Jurassic silphids distinctly combine features of the two subfamilies, as presently defined. These beetles share with Silphinae their antennal morphology (pedicel well-developed, rather than retracted into apex of scape) and absence of paired stridulatory files, both interpreted as primitive conditions, and with Nicrophorinae the presence of a straight epistomal sulcus, short elytra, and overall body shape. The Cretaceous forms appear nearly identical to those of the Jurassic, sharing body shape, antennal morphology, and truncate elytra, but differ most profoundly in the presence of paired stridulatory files and posteriorly fused gular sutures. Thus, the Cretaceous silphids can be assigned to the modern subfamily Nicrophorinae, closely resembling the modern genus *Ptomascopus*. Compared with the extant burying beetles, *Nicrophorus*, the Cretaceous taxa exhibit a simpler antennal morphology. *Nicrophorus* typically has a strongly clubbed antenna with lamellate antennomeres 8–10, but the Cretaceous taxa bear more silphine-like antennae, with apical antennomeres dilated but not lamellate.

**Fossil Record of Social or Subsocial Insects.** The origin and early evolution of insect societies is a fascinating and challenging issue in fossil insect studies. The evolution of eusociality occurred multiple times in different orders of insects, including termites (Blattodea: Termitidae), ambrosia beetles (Coleoptera: Scolytidae), gall-dwelling aphids (Hemiptera), Australian gall-dwelling thrips (Thysanoptera), and many Hymenoptera (i.e., bees, wasps, and ants) (1). It has been suggested that eusociality first evolved in the common ancestor of all termites in the Early Cretaceous and in the ancestor of all ants in the mid-Cretaceous, perhaps 115–120 Mya, and there is no fossil evidence that social insects existed before then. **Termites.** The oldest definitive termite, *Baissatermes lapideus* Engel, Grimaldi, and Krishna, 2007, is known from a single alate compression fossil from the Zaza Formation of Baissa, Russian Transbaikalia (2). The exact age of the Zaza Formation is disputed, usually estimated as Early Cretaceous (Neocomian–Aptian), but most paleoentomologists date it as Valanginian–Hauterivian (3). It is the earliest fossil termite known to date and the oldest known example of a social organism. In addition, termite borings are known from the Cretaceous and Tertiary, which also reflects their early history. The earliest termite workings, attributed to Kalotermitidae, are from the Late Cretaceous Javelina Formation of western Texas, United States (4), and represent the oldest social insect nest. (5) **Bees.** The oldest fossil bee, *Cretotrigona prisca* Engel, 2000, is from the Late Cretaceous (approximately 65 Mya) amber of New Jersey. *C. prisca* is a social bee, attesting to the antiquity of sociality in the corbiculate apines. Eusocial corbiculate bees evolved in the Late Cretaceous, and they appear to have reached their peak in their distribution and diversity in the Eocene (5).

**Ants.** The earliest known ant, *Gerontotormica cretacea* Nel, 2004, is based on a putative worker specimen from the Uppermost Albian amber of France (6). Another slightly younger definitive ant is known from the earliest Cenomanian Burmese amber (5). Origin of the ants was thus no later than latest Early Cretaceous and during the rise of angiosperms, but ants did not radiate extensively until the Tertiary. In addition, the worker-like structure of some sphecomyrmine ants from the Cretaceous indicates that the most primitive known ants were social (7).

**Wasps.** Vespids from the Mesozoic are rare and belong to the solitary or subsocial subfamilies; nevertheless, a polistine nest has been found from the Late Cretaceous of Utah (8–9), indicating that social forms were already present at that time. Thus, eusociality also seems to be ancient in vespids, and probably evolved in these wasps around the time it did in ants.

To date, no definitive ambrosia beetles are known from the Mesozoic, despite the fact that a number of ambrosia beetles are known from Early Miocene Dominican amber (10), Eocene Baltic amber (11), Late Eocene Rovno amber of Ukraine (12), and Late Eocene Florissant beds, Colorado, United States (13). The earliest fossil thrips, *Pernothrips longipennis* Martynov, 1935, can be traced back to the Permian (14). Even though true thrips became much more abundant by the Early Cretaceous, only one example indicating subsociality (food-provisioning for larvae) has been reported from the Early Cretaceous amber of Spain (15). Similarly, the oldest aphid, *Vosegus triassicus* Szweo and Nel, 2011, has been described recently from the Anisian (early Middle Triassic) of Vosges, northeastern France (16), but there is no fossil evidence suggesting that social aphids originated during the Mesozoic.

**Paleodiversity of Contemporaneous Feathered or Haired Vertebrates.** Because the extant *Nicrophorus* (burying beetles) and the more basal group *Ptomascopus* usually exploit small vertebrate carcasses

(rodents or birds) as a food source for their larvae, the contemporaneous feathered or haired vertebrates from the same stratum were probably the source of nutrition for the larvae of early silphids. In particular, the Middle Jurassic Daohugou biota and adjacent localities have yielded four feathered dinosaurs, such as *Anchiornis huxleyi* Xu et al., 2009 from the Middle Jurassic Tiaojishan Formation of Liaoning province (17); *Epidipteryx hui* Zhang et al., 2008 from Daohugou (18); *Pedopenna daohugouensis* Xu and Zhang, 2005 from Daohugou (19); and *Xiaotingia zhengi* Xu et al., 2011 from the Tiaojishan Formation at Linglongta, Jianchang, Liaoning province (20). Specifically, with a body length about 11.6-cm long, the smallest feathered dinosaur of them, *Xiaotingia zhengi*, is small-sized and about the weight of a domestic chick (20). In addition, four small-sized mammals are known from Daohugou and an adjacent locality, including *Castorocauda lutrasimilis* Ji et al., 2006 (body length: ~20 cm without tail) (21), *Pseudotribos robustus* Luo et al., 2007 (body length: ~8 cm without tail) (22), and *Volaticotherium antiquus* Meng et al., 2006 (body length: 12–14 cm) from Daohugou (23); additionally is *Juramaia sinensis* Luo et al., 2011 (body mass: about 15 g) from the Middle Jurassic at Tiaojishan Formation at Daxigou, Jianchang County of Liaoning province, China (24).

More discoveries have been made from the Early Cretaceous Yixian Formation and contemporaneous localities. At least 11 feathered dinosaurs are reported from Yixian Formation and contemporaneous localities, including *Beipiaosaurus inexpectus* Xu et al., 1999 (25); *Caudipteryx zoui* Ji et al., 1998 (26); *Dilong paradoxus* Xu et al., 2004 (27); *Jinfengopteryx elegans* Ji et al., 2005 (Qiaotou member of the Huajiyang Formation of Hebei Province) (28); *Protarchaeopteryx robusta* Ji and Ji, 1997 (29); *Similicaudipteryx yixianensis* He et al., 2008 (30); *Sinocalliopteryx gigas* Ji et al., 2007 (31); *Mei long* Xu and Norell, 2004 (32); *Sinornithosaurus millenii* Xu et al., 1999 (33); *Sinosauropteryx prima* Ji and Ji, 1996 (34); and *Yixianosaurus longimanus* Xu and Wang, 2003 (35). With body length more than 50 cm, all of these Cretaceous feathered dinosaurs had relatively large body sizes.

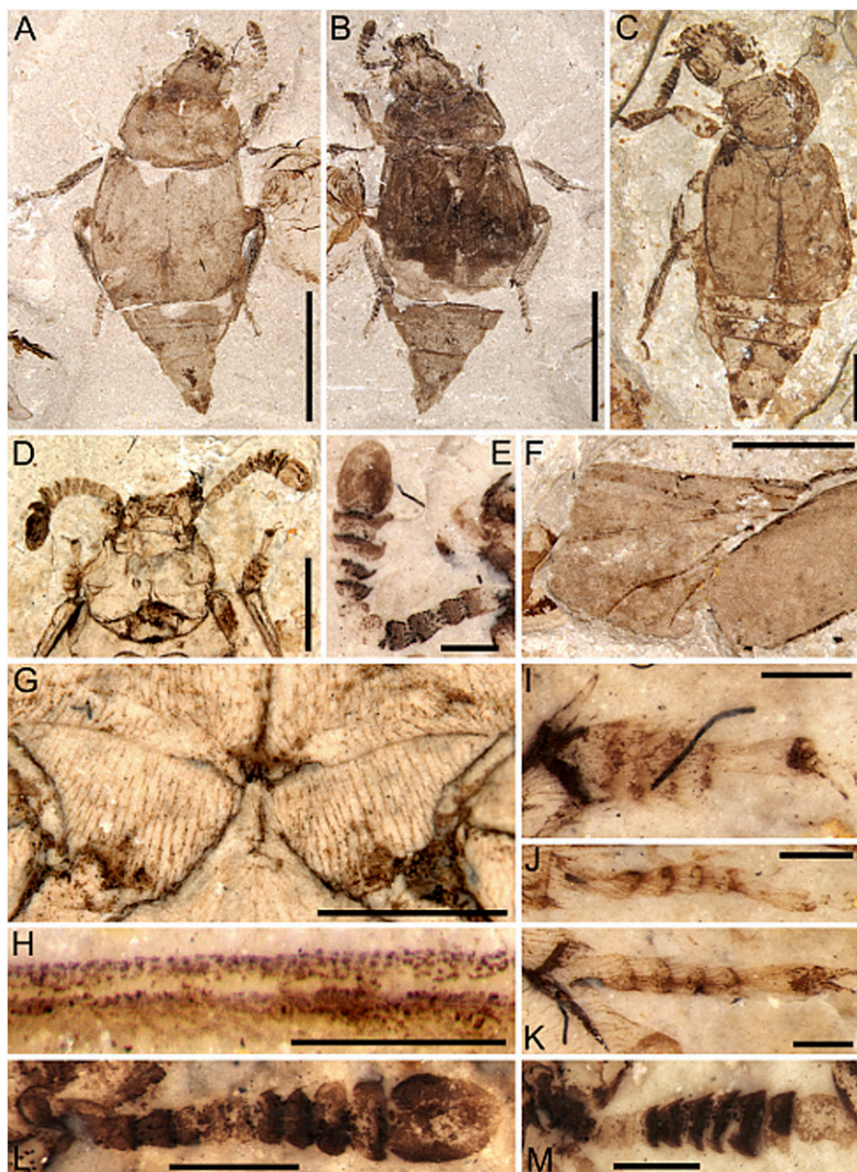
With at least eight mammal species discovered from the Yixian Formation to present, the early mammals have received extensive attention. Excavations in the Yixian Formation led to the discovery of two large mammals, *Repenomamus robustus* Li et al., 2000 (approximately 4–6 kg) (36) and *Repenomamus giganticus* Hu et al., 2005 (approximately 12–14 kg) (37), the largest mammals known to date from the Cretaceous. In particular, the discovery of a small dinosaur preserved in the stomach area of *R. robustus* provided the first direct evidence that mammals preyed on dinosaurs (37). The other mammals from the formation, *Akidolestes cifellii* Li and Luo, 2006 (38); *Eomaia scansoria* Ji et al., 2002 (39); *Sinobaatar linguanensis* Hu and Wang, 2002 (40); *Sinodelphys szalayi* Luo et al., 2003 (41); *Jeholodens jenkinsi* Ji et al., 1999 (42); and *Zhangheotherium quinquecuspidens* Hu et al., 1997 (43) are all small, with body length less than 15 cm. Interestingly, the little primitive mammal *J. jenkinsi* has a very small body size (body length approximately 5 cm, excluding the long tail) and its tooth structure suggest that it was an insectivore.

Even though no definitive birds have been discovered in the Middle Jurassic Daohugou, the birds from the younger Early Cretaceous Yixian Formation (and contemporaneous areas) are diverse. So far, at least eight primitive birds have been reported from the Yixian Formation: *Archaeorhynchus spathula* Zhou and Zhang, 2006 (44); *Changchengornis hengdaoziensis* Ji et al., 1999 (45); *Confuciusornis sanctus* Hou et al., 1995 (46); *Hongshanornis longicresta* Zhou and Zhang, 2005 (47); *Liaoxiornis delicatus* Hou and Chen, 1999 (48); *Longirostravis hani* Hou et al., 2004 (49); *Jeholornis prima* Zhou and Zhang, 2002 (50); and *Shenqiornis mengi* Wang et al., 2010 (Qiaotou member of the Huajiyang Formation, correlating with the Yixian Formation) (51). Among these, *C. sanctus*, with long wing and tail feathers, was about the size of a modern crow, with a wingspan of up to 0.7 m and a weight of up to 0.5 kg. In contrast, at only about 8-cm long, the sparrow-sized *L. delicatus* is the smallest bird known from the Mesozoic deposit (48).

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**Fig. S1.** Silphids from the Middle Jurassic of Daohugou, Ningcheng County, Inner Mongolia of China, characterized by antennae gradually widened from the base to the distal antennomere. (A) General habitus, mainly showing dorsal structures, 156148a. (B) 156148b, with a few ventral structures shown. (C) 157736, mainly showing dorsal structures. (D) Detail of 156145b, showing gradually widened antennae, narrowly separated gular sutures, and setose five-segmented protarsi. (E) Enlargement of B, showing gradually widened antenna and normal antennomere 2. (F) Hind wing and partial pubescent elytron, 156149. (G) Detail of 156145b, showing contiguous metacoxae and a small median carina on abdominal sternite III. (H) Intersegmental membrane between abdominal sternites VI and VII, showing brick-wall pattern. (I) Detail of 156145b, showing robust spur, five-segmented protarsus, and pretarsal claws. (J) Detail of 156145b, showing truncate apex of tibia and five-segmented mesotarsus. (K) Detail of 156145b, showing long spur, truncate apex of tibia, five-segmented metatarsus, and claws. (L) Detail of 156144, showing right antenna. (M) Detail of 157736, showing left antenna. (Scale bars: 5 mm in A and B; 2 mm in C, D, and F; 1 mm in G; 500  $\mu$ m in E, H–M.)



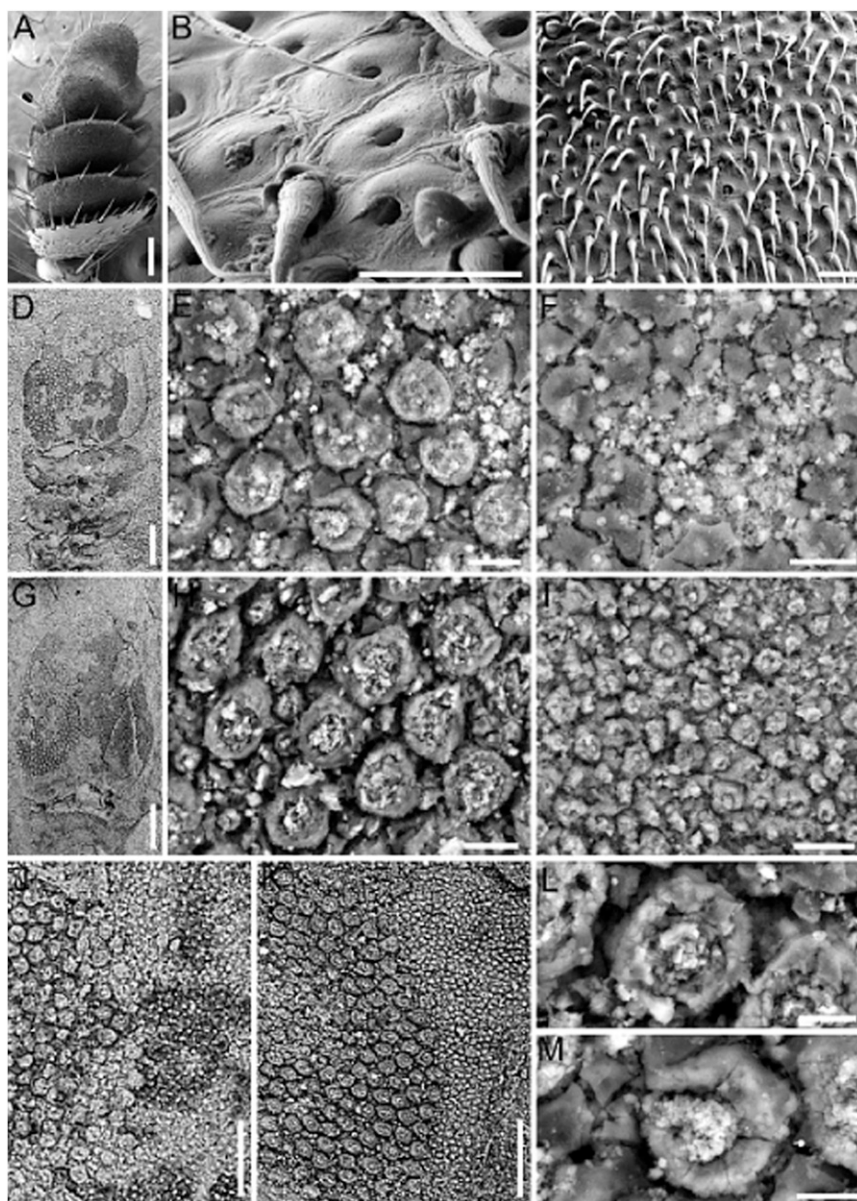


**Fig. S2.** Silphids from Daohugou; characterized by the apical three antennomeres being moderately to abruptly clubbed. (A) General habitus, mainly showing dorsal structures, 156147a. (B) 156147b, with mainly ventral structures shown. (C) 156146b, mainly showing ventral structure. (D) 156146a, mainly showing dorsal structures. (E) 157737a, mainly showing dorsal structure. (F) 157737b, mainly showing ventral structure. (G) 157738a, mainly showing dorsal structure. (H) 157738b, mainly showing ventral structure. (I) 157739, mainly showing ventral structure. (J) 156218, mainly showing dorsal structures. (K) 153700, mainly showing dorsal structures. (L) Enlargement of C, showing right antenna. (M) Enlargement of right antenna. (Scale bars: 5 mm in G and H; 2 mm in A–F, I–K; 500  $\mu$ m in L and M.)

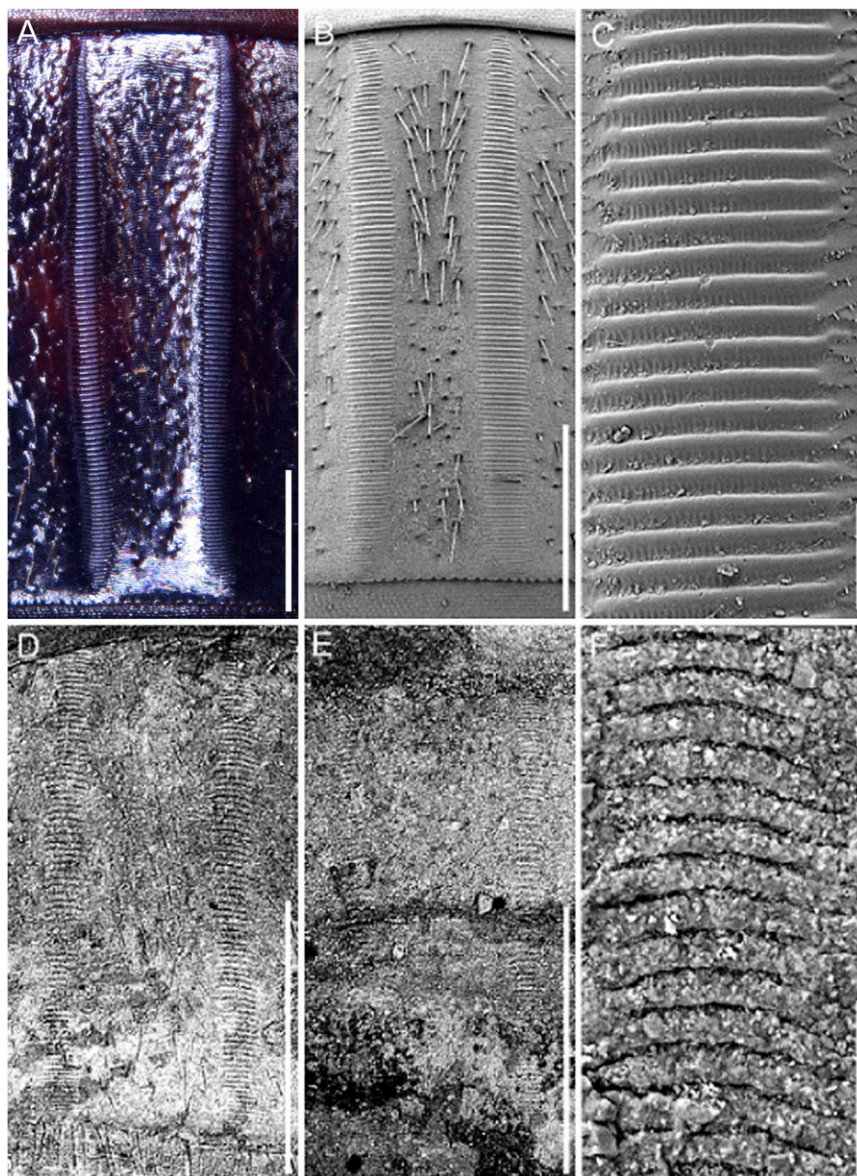


**Fig. S3.** Silphids from the Early Cretaceous of northeastern China. (A) 156152b, from Liutiaogou, Ningcheng County, Inner Mongolia, general habitus, mainly showing ventral structures. (B) 156152a, general habitus. (C) 156150a, from Huangbanjigou, Beipiao City, Liaoning Province, showing dorsal structures. (D) 156150b, showing ventral structures. (E) 156151, from Huangbanjigou, showing ventral structures. (F) 156153, from Huangbanjigou, showing ventral structures. (G) 156154, from Huangbanjigou, showing dorsal structures. (H) Enlargement of D, showing gradually widened left antenna. (I) Enlargement of C, showing right antenna. (J) Enlargement of E, left antenna, showing distinctly dilated apical four antennomeres. (K) Detail of 156150a, showing mandibles, exposed antennal insertions, straight epistomal sulcus, and Y-shaped gular sutures. (L) Enlargement of F, showing large compound eyes, mandibles, and Y-shaped gular sutures. (M) Detail of 156152a, showing robust spur, five-segmented protarsus. (N) Detail of 156152a, showing spur, truncate apex of tibia, five-segmented mesotarsus, and pretarsal claws. (O) Detail of 156152a, showing truncate apex of tibia, five-segmented metatarsus. (Scale bars: 2 mm in A–G; 500  $\mu$ m in H–O.)



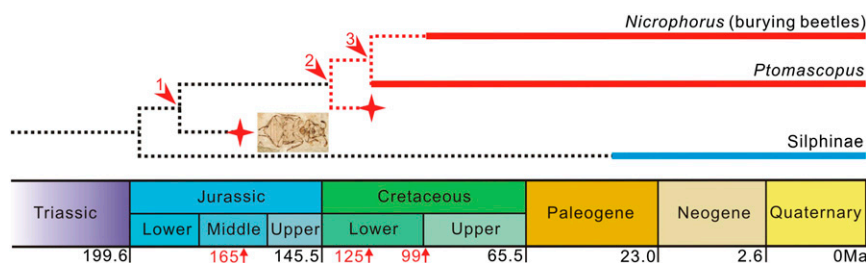


**Fig. 54.** Comparison of antennae and olfactory receptors between Jurassic and Recent silphids, scanning electron micrographs. (A) Enlargement of apical four antennomeres of a modern burying beetle (*Nicrophorus orbicollis* Say), showing densely setose apical three antennomeres, where olfactory receptors are located. (B) Enlargement of A, showing the pit-like sensilla coelosphaerica (*coel*). (C) Enlargement of A, showing the hair-like sensilla basiconica (*bas*). (D) Apical three antennomeres of Jurassic silphid, showing left antenna, 156144. (E) Enlargement of D, showing the pit-like *coel*. (F) Enlargement of D, showing hair-like *bas*, with only basal parts preserved. (G) Apical two antennomeres of Jurassic silphid, 156148b. (H) Enlargement of J, showing *coel*. (I) Enlargement of J, showing *bas*. (J) Enlargement of D, showing two different sensilla, *coel* and *bas*, located on each side of the apical antennomere along its axis. (K) Enlargement of G, showing *coel* and *bas*. (L) Enlargement of H, showing detail of *coel*. (M) Enlargement of E, showing detail of *coel*. (Scale bars: 200  $\mu$ m in A, D, and G; 100  $\mu$ m in J and K; 10  $\mu$ m in B, C, E, F, H, and I; 5  $\mu$ m in L and M.)



**Fig. S5.** Comparison of stridulatory files between Cretaceous and Recent microphorine silphids. (A) Stridulatory files in a modern burying beetle (*N. orbicollis* Say, 1825), under light microscope. (B) Stridulatory files of *N. orbicollis*, scanning electron micrograph. (C) Enlargement of B, showing details of stridulatory files. (D) Stridulatory files in a Cretaceous microphorine silphid, 156152a. (E) Stridulatory files in another Cretaceous microphorine silphid, 156154. (F) Enlargement of D, showing details of stridulatory files of a Cretaceous microphorine. (Scale bars: 500  $\mu\text{m}$  in A, B, D, and E; 50  $\mu\text{m}$  in C and F.)





**Fig. S6.** Phylogeny of Silphidae. Clade 1 is characterized by presence of epistomal sulcus, rounded pronotum with straight anterior margin, and truncate elytra. Clade 2, representing Nicrophorinae, is characterized by paired stridulatory files on tergite V and Y-shaped gular sutures. Clade 3, Nicrophorinae, is characterized by the greatly reduced second antennomere. The intriguing Jurassic silphids, sharing several features of modern nicrophorines and silphines, represent an offshoot of transitional forms between the two subfamilies.



**Fig. S7.** Diverse staphylinine rove beetles, potential predators of early nicrophorines from the Early Cretaceous Jehol biota of China. (A) *Thayeralinus* sp., 156155a, characterized by large body size, large head, prominent mandibles, transverse pronotum, and long abdomen. (B) Enlargement of A, showing prominent mandibles with two or three sharp preapical teeth. (C) Enlargement of D, showing prominent mandible with very sharp apex. (D) *Megolisthaerus minor* Cai and Huang, 153697a, characterized by moderate body size, prominent toothed mandibles and abdomen with a pair of basolateral ridges on tergites III to VI. (E) *Thayeralinus* sp., 156156a, showing large head and well-developed hind wings. (F) *Thayeralinus* sp., 156157. (G) *Thayeralinus* sp., 157735, showing slightly posteriorly-narrowed head, large mandibles and robust body. (Scale bars: 5 mm in A, E–G; 2 mm in D; 500  $\mu$ m in B and C.)





**Fig. S8.** Ecological reconstruction of early silphids from the Early Cretaceous of northeastern China. A pair of early necrophorines, feeding on the carcass of an early mammal, are guarding their larvae from potential predators or food competitors.