Blood-Feeding True Bugs in the Early Cretaceous

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Summary

Blood-feeding insects, as vectors of disease for humans and livestock alike, have garnered significant interest [1, 2], but our understanding of their early evolution is hindered by the scarcity of available material and the difficulty in distinguishing early hematothaphes from non-blood-feeding relatives. Here, we report a new family of true bugs including two new genera and species from the Early Cretaceous Yixian Formation in Northeastern China. By utilizing geochemical methods for determining their diets and combining morphological and taphonomic data, we demonstrate that these new species represent the earliest evidence of blood feeding among true bugs, extending the geological record of such lineages by approximately 30 million years. Remarkably, one of the bugs appears to have perished immediately following a blood meal, which may have been from coexisting mammals, birds, or avian-related dinosaurs. These records expand the phylogenetic and ecological diversity of blood-feeding insects in the Early Cretaceous, enriching our knowledge of paleoecological associations in these ancient environments.

Results

An extinct new family, Torirostratidae fam. nov., is described from the Early Cretaceous in China. We combine geochemical, morphological, and taphonomic data to demonstrate that the new species were hematophages, extending the geological record of such lineages by approximately 30 mega-annum (Ma). We found one individual that appears to have died immediately following a blood meal. These new bugs represent the earliest evidence of blood-feeding true bugs and likely played important ecological roles in the Jehol Biota. The new discovery suggests that free-living, blood-feeding insects had already appeared by the Early Cretaceous and may have been diverse. It also provides important clues about the evolutionary history of blood-feeding insects and their environmental changes and community succession.

Systematic Paleontology

Insecta Linnaeus, 1758.
Hemiptera Linnaeus, 1758.
Heteroptera Latreille, 1810.
Cimicomorpha Leston, Pendergrast, et Southwood, 1954.
Torirostratidae Yao, Cai, Shih, et Engel, fam. nov.

Diagnosis

Ocelli present; rostrum four-segmented, second segment longest with base swollen; antenna inserted ventrally on head, partially obscured by mandibular plates. Prosternum with depression for receipt of rostrum; apex of scutellum blunt, narrowed, or constricted in in apical half; a cross-vein on corium-membrane boundary not joined with claval suture, claval commissure absent; tarsi 3-3-3, basal tarsomeres of all legs longest and thickest, pulvilli present. Abdomen weakly sclerotized, with inner laterotergites, connexivum observable, ovipositor laciniate.

Torirostratus pilosus Yao, Shih, et Engel, gen. et sp. nov.

Etymology

Generic name is a combination of the Latin “torosus” (bulges) and “rostratus” (beaked), alluding to its predatory habits (gender of the name is masculine); specific epithet is from the Latin “pilosus” (referring to the dense setae).

Holotype

Male, CNU-HE-LB2006506PC, part and counterpart (Figure 1).

Horizon and Locality

Collected from the Early Cretaceous Yixian Formation (Early Aptian, 125 Ma) at Huangbanjingou, Chaomidian Village, Beipiao City, Dawangzhangzi Village, Lingyuan City, Liaoning Province; Liutiaogou Village, Dashuangmiao Township, Ningcheng County, Chifeng City, Inner Mongolia; and Shimen Village, Yangshuling Township, Pingquan County, Hebei Province.

Diagnosis for Genus and Species

Body length over 12 mm. Head width less than length, antennal portion longer than postocular; rostrum extending beyond procoxae; diameter of compound eyes dorsal view shorter than interocular space, interocellar space subequal to diameter of ocellus. Apex of corium fingerlike, cubitus situated along claval suture, contiguous to apex of clavaus. Abdominal subequal to pronotum in width, fourth segment widest.

Description, Dimensions, and Material

See Supplemental Information available online.

Flexicorpus acutirostratus Yao, Cai, et Engel, gen. et sp. nov.

Etymology

Generic name is a combination of the Latin “acuti” (sharp) and “rostratus” (beaked).

Holotype

Female, CNU-HE-LB2006435PC, part and counterpart (Figure 2).
Horizon and Locality
Same as those of T. pilosus.

Diagnosis for Genus and Species
Body length less than 10 mm. Head width greater than length; antecocular portion shorter than postocular; rostrum extending to procoxae; diameter of compound eye about 0.5 × as wide as interocular space; ocelli large, interocellar space slightly narrower than diameter of ocellus. Ovipositor extending through last two abdominal segments.

Description, Dimensions, and Material
See Supplemental Information available online.

Discussion
Blood feeding, or hematophagy, is a relatively uncommon feeding strategy among modern insects [1]. There are four primary orders from which critical hematophages have arisen [2], namely the Phthiraptera (lice), Siphonaptera (fleas), Diptera (true flies), and Heteroptera (true bugs), with only the latter three having documented records prior to the Cenozoic [3–7]. Indeed, the evolution of blood feeding has relied heavily on detective work due to the patchy nature of the insect fossil record as it pertains to such lineages [1], or on molecular
methods for elucidating the relationships of clades and timing of diversification events [8]. Unfortunately, paleontological evidence of ectoparasites is minimal, and unless preserved with sufficient fidelity, such as in amber or fine oil shales, much of the fine morphological details of the mouthparts are indiscernible.

Most extant true bugs (Heteroptera) are either entomophagous or phytophagous, but three families (Cimicidae, Reduviidae, and Polyctenidae) contain several blood-feeding species [9]. Indeed, these families include some of the most notorious blood feeders, including the common bed bug (Cimex lectularius) and kissing bugs (Reduviidae: Triatominae), many of which are vectors of Chagas disease throughout South America and southern North America. Up to now, only one species of fossil hematophagous bug, Quasicimex eilapinastes, has been described, from mid-Cretaceous (Albian-Cenomanian, 99–100 Ma) amber from Myanmar [3]. The inference of its blood-feeding habits was based on its phylogenetic position among basal Cimicidae and Polyctenidae, well-documented clades of blood feeders. Even among living species of Heteroptera, it is difficult to determine feeding habits solely from morphological characteristics such as traits of the rostrum, legs, and abdomen. In the absence of direct observation, this reality hinders our understanding of the early evolution
of blood-feeding behavior among Heteroptera. Recent work has used biogeochemical methods of ascertaining feeding habits, specifically looking for hemoglobin-related porphyrins or other biomolecular signatures indicative of blood meals in Paleogene Culicidae [10].

Blood-feeding insects receive a high iron load from their blood meals, and portions of the iron are incorporated into the tissues of the blood feeders [11–15]. Studies of trace elemental iron (Fe) in extant heteropterans have documented that iron content in blood-feeding bugs is significantly higher than that in phytophagous and predaceous species (Table S1). Accordingly, there may be geochemical signals preserved that document the feeding strategies of ancient insects, either in the form of diagenetic derivatives of macromolecules such as hemoglobin or in the selective concentration of iron.

Herein, we used energy-dispersive X-ray spectroscopy (EDS; see summary in Experimental Procedures) to analyze the geochemical composition of seven true bugs from the Early Cretaceous Yixian Formation in Northeastern China, including three specimens representing the two new genera and species, T. pilosus gen. et sp. nov. and F. acutirostratus gen. et sp. nov., and four specimens of other heteropterans from the same locality and horizon representing the phytophagous families Pachymeridiidae and Venicoridae and the predaceous families Reduviidae and Vetanthocoridae (Figures S1A, S1C, S1D, and S1F). The EDS data show trace levels of Fe, without any significant difference, among the shale matrices of all seven specimens (Figures 3B–3I and S2–S4; Tables 1 and S3). In contrast, the Fe contents of the insect bodies were significantly higher than those in the surrounding matrix (Figure 3B; Tables 1 and S3). More importantly, the relative iron contents (Fe content in the matrix was subtracted from the Fe content of the body) of T. pilosus gen. et sp. nov. (CNU-Het-LB2010044) and F. acutirostratus gen. et sp. nov. (CNU-Het-LB2006422

Figure 3. Geochemical Analyses for T. pilosus gen. et sp. nov., CNU-Het-LB2010044
(A) Light-microscopic image; red dots at the center of blue circles are areas of chemical analysis.
(B) Image of energy-dispersive spectrometry (EDS) mapping.
(C–I) Spot area analysis results by electron microprobe in EDS mode.
Scale bars represent 5 mm for (A); 400 μm for (B).
and CNU-Het-LB2006449) were significantly higher than those of the remaining species (Pachymeridiidae [CNU-Het-LB2006247], Venicoridae [CNU-Het-LB2012107], and Vetanthocoridae [CNU-Het-LB2006048]). There was no significant difference among those species representing pachymeridiids, reduviids, venicorids, and vetanthocorids. The iron contents of the fossils are consistent with those of modern Heteroptera. The geochemical analysis suggests that the two new species of true bugs had distinctly higher iron concentrations than those of other lineages, suggesting a concentrated source such as from a blood meal.

The open circulatory system of insects [16] means that hemolymph is distributed throughout the body and not concentrated within an individual organ system. Despite this, the iron detected is not evenly distributed throughout the body of the specimen CNU-Het-LB2010044 (T. pilosus gen. et sp. nov.). Instead, the heaviest iron concentrations are in the apex of the first segment of the rostrum and the abdomen (Figure 3C and 3E; Tables 1 and S3), significantly higher than those found in the antenna, thorax, legs, and elsewhere in the head (Figures 3D and 3G–3I; Tables 1 and S3). This concentration difference suggests that this true bug might have fed immediately prior to its death.

The blood-feeding habit of these new bugs is consistent with morphological and taphonomic evidence. Based on the collection of 3,827 fossil specimens of terrestrial Heteroptera at Capital Normal University (Beijing), we observed that 93.0% of vetanthocorids (predaceous bugs), 318 out of 342, are preserved with the rostra laterally oriented, extended position. For 368 specimens of venicorids, and 728 out of 749 rhopalids. The 1,809) have rostra appressed to their bodies [18–20]: 59 out of 59 primipentatomids, 672 out of 688 pachymeridiids, 309 out of 313 venicorids, and 728 out of 749 rohopalids. The different postures might be caused by the morphology of the rostra, which is loosely associated with the two different feeding habits. Mouthparts of 11 (38%) of the 29 specimens of Torirostratus gen. nov. are preserved with the rostra in a laterally stretched orientation and one (3.4%) in an anteriorly extended position. For the 368 specimens of Flexicorpus gen. nov., 115 are preserved with the rostra laterally oriented, while 23 (37.5%) are extended anteriorly. Generally, modern phytophagous bugs have a long and relatively slender rostrum, usually appressed to the body at rest, which is straight, with more or less parallel sides and/or uniform thickness, while predaceous or hematophagous bugs usually have stout, curving rostra, tapering from base to apex [21]. The rostra of the two new fossil taxa are stout with the basal segment swollen, the second segment longest and swollen at its base, and the fourth segment acute distally. The structure of the rostra and their preserved orientations suggest that these new species were predaceous or hematophagous. In addition, the large and broad abdomens were apparently weakly sclerotized and perhaps extensible (the boundaries of the abdominal segments for most of these specimens are not clearly preserved), with a broad connexivum and inner laterotergites present. The abdominal morphology of Torirostratus gen. nov. and Flexicorpus gen. nov. suggests that they could have ingested a large volume of liquid, as in many modern blood-feeding insects [22]. These data, when considered in conjunction with the distribution and selective concentrations of trace elemental iron, imply that the two species were hematophages.

Both taxa belong to the Cimicomorpha, and preliminary phylogenetic results place both as closely related and basal among the Reduvioida (Figures S5 and S6; Table S4), as evidenced by corium relatively small, almost 1/4 the area of the forewing; veins on corium raised and keel-like, with only three simple, almost straight longitudinal veins; apex of corium fingerlike; clavus clubbed, tapering from base to apex, claval commissure absent, and claval apices not concealed by the scutellum; connexivum completely exposed; and claws flattened, tapering from base to apex. These bugs had a relatively small corium that was not joined with the clavus. This, along with their relatively large body size, suggests that their flying capability was limited, meaning that they may have been vulnerable to detection by their putative hosts. It is possible that these species had biologies analogous to modern kissing bugs, which typically live on the periphery of their host’s habitat and venture into them during the night, when the host is resting. The fossil species may have similarly waited until a dormant phase in the host’s daily cycle and then crawled on to feed.

In the collection of Capital Normal University, the individual counts of Torirostratus gen. nov. and Flexicorpus gen. nov. are fairly high, 11% of all terrestrial true bugs in the Yixian Formation, well distributed in various localities across the Jehol Biota (see Supplemental Information). All modern terrestrial hematophagous heteropterans are free-living blood feeders that feed only on warm-blooded vertebrates, i.e., mammals and birds [9]. Certainly the Jehol Biota had a diversity of suitable hosts [23], including mammals, pterosaurs, birds, and avian-related dinosaurs. These bugs might have fed on the coexisting animals as hosts.

Hematophagous habits have evolved independently numerous times among arthropods [24, 25] and at least three times within the true bugs [9, 26, 27]. The new species presented here confirm this scenario (Figures S5B and S8) and represent the earliest evidence of such feeding behavior among the Heteroptera. It is likely that these species, and others like them, played a significant role in the ecology of the Jehol Biota, as evidenced by their relative abundance.

Table 1. Unnormalized Concentration, in Weight Percent, of Fe for Seven Specimens

<table>
<thead>
<tr>
<th>Examined</th>
<th>Rostrum</th>
<th>Antenna</th>
<th>Head</th>
<th>Thorax</th>
<th>Abdomen</th>
<th>Leg</th>
<th>Mean Value</th>
<th>Relative Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>F. acutirostratus</td>
<td>6.14</td>
<td>7.06</td>
<td>6.88</td>
<td>6.37</td>
<td>6.70</td>
<td>6.65</td>
<td>6.63</td>
<td>2.42</td>
</tr>
<tr>
<td>F. acutirostratus</td>
<td>6.34</td>
<td>6.38</td>
<td>6.28</td>
<td>6.19</td>
<td>7.10</td>
<td>6.47</td>
<td>6.46</td>
<td>2.28</td>
</tr>
<tr>
<td>T. pilosus (Torirostratidae, CNU-Het-LB2010044)</td>
<td>10.01</td>
<td>6.83</td>
<td>8.74</td>
<td>7.86</td>
<td>9.95</td>
<td>7.32</td>
<td>8.45</td>
<td>2.67</td>
</tr>
<tr>
<td>V. solari (Venicoridae, CNU-Het-LB2006541)</td>
<td>–</td>
<td>4.71</td>
<td>5.27</td>
<td>4.13</td>
<td>4.16</td>
<td>4.39</td>
<td>4.53</td>
<td>2.64</td>
</tr>
<tr>
<td>B. mirabilis (Pachymeridiidae, CNU-Het-LB2006247)</td>
<td>4.22</td>
<td>4.94</td>
<td>4.66</td>
<td>4.81</td>
<td>5.06</td>
<td>5.10</td>
<td>4.75</td>
<td>2.79</td>
</tr>
<tr>
<td>V. decorus (Vetanthocoridae, CNU-Het-LB2006048)</td>
<td>3.22</td>
<td>5.42</td>
<td>3.96</td>
<td>4.60</td>
<td>5.08</td>
<td>4.75</td>
<td>4.51</td>
<td>2.00</td>
</tr>
<tr>
<td>Undescribed specimens (Reduviidae, CNU-Het-LB2012107)</td>
<td>–</td>
<td>4.33</td>
<td>4.83</td>
<td>5.16</td>
<td>4.34</td>
<td>–</td>
<td>4.87</td>
<td>2.91</td>
</tr>
</tbody>
</table>

For Relative Value data, Fe in the shale matrix is subtracted from the mean.
It is increasingly clear that ectoparasites from diverse lineages were present in these ancient faunas, and that the use of vertebrate blood as a food source was well established by the Early Cretaceous [4–7, 26, 28]. Although the fossil record of ectoparasites remains sparse in comparison to that of other insect lineages, we are beginning to get glimpses into the diversity of these important groups and insights into their potential role in Mesozoic ecosystems. Blood feeders, as evidenced by Torirostrus, Flexicorpus, and early fleas reported from the same fauna, had diverse modes of interacting with their hosts, and it is interesting to speculate what impact they may have had on the health of individuals, particularly if feeding on immatures, subadults, or the already infirm. The degree to which such species negatively influenced the health of host individuals remains an unexplored, and perhaps impossible to determine, aspect of their ecology. In addition, it remains to be determined how long after the origin of blood feeding did associations with infectious agents evolve among a subset of hematophagous species, thereby enhancing their negative influence on their vertebrate hosts.

Experimental Procedures

All fossil specimens are deposited at the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University, Beijing. All extant specimens examined were obtained from the Entomological Museum of China Agricultural University, Beijing. All drawings were made using a camera lucida and binocular microscope. The photographs were taken with a Nikon D800E and processed with Adobe Photoshop CS2. Reconstructions were prepared with Autodesk Maya 2012 and Adobe Photoshop CS2. Inductively coupled plasma-mass spectrometry (Agilent 7500ce) was used for Fe analysis in extant samples. Geochemical analyses were performed with a Zeiss EVO LS 15 scanning electron microscope, using Bruker Nano XFlash Detector 5010 energy-dispersive spectrometry to examine the elements in the fossils. Standard statistical tests were performed using SPSS 18.0 for Windows.

See Supplemental Experimental Procedures for detailed materials and methods.

Supplemental Information

Supplemental Information includes six figures, five tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.06.045.

Author Contributions

Y.Y. and D.R. designed the research. Y.Y., W.C., and D.R. performed research. All authors contributed equally in analyses of data and writing of the manuscript.

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References


Supplemental Information

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Yunyun Zhao, and Dong Ren
Supplemental Data

i) Supplemental Figures

Figure S1. Six specimens for the geochemical analyses, Related to Figure 3 and Table 1. (A) *Bellicoris mirabilis* Yao, Cai e Ren, 2008 (Pachymeridiidae, CNU-Het-LB2006247). (B) *Flexicorpus acutirostratus* gen. et sp. nov. (Torirostratidae, CNU-Het-LB2006449). (C)
Undescribed specimens (Reduviidae, CNU-Het-LB2012107). (D) *Vetanthocoris decorus* Yao, Cai et Ren, 2006 (Vetanthocoridae, CNU-Het-LB2006048). (E) *Flexicorpus acutirostratus* gen. et sp. nov. (Torirostratidae, CNU-Het-LB2006422c). (F) *Venicoris solaris* Yao, Ren et Rider, 2012 (Venicoridae, CNU-Het-LB2006541). (All are photographs under ethanol). Red dots at the center of blue circles are areas of chemical analysis. Scale bar = 4mm.
Figure S2 SEM images with energy dispersive x-ray spectroscopy (EDS) data of *Flexicorpus acutirostratus* gen. et sp. nov. (Torirostratidae), Related to Figure 3 and Table 1. (A–G) CNU-Het-LB2006422. (H–N) CNU-Het-LB2006449. Red dots at the center of blue circles are areas of chemical analysis. Scale bars = 800 μm.

Figure S3 SEM images with energy dispersive x-ray spectroscopy (EDS) data, Related to
Figure 3 and Table 1. (A–F) *Venicoris solaris* Yao, Ren et Rider, 2012 (Venicoridae, CNU-Het-LB 2006541). (G–M) *Bellicoris mirabilis* Yao, Cai et Ren, 2008 (Pachymeridiidae, CNU-Het-LB2006247). Red dots at the center of blue circles are areas of chemical analysis. Scale bars = 800 μm.

Figure S4. SEM images with energy dispersive x-ray spectroscopy (EDS) data, Related to Figure 3 and Table 1. (A–G) *Vetanthocoris decorus* Yao, Cai et Ren, 2006 (Vetanthocoridae, CNU-Het-LB2006048). (H–L) Undescribed specimens (Reduviidae, CNU-Het-LB2012107). Red dots at the center of blue circles are areas of chemical analysis. Scale bars = 800 μm.
Figure S5. Related to Figure 1 and 2. (A) The strict consensus tree of 8 most parsimonious trees with Bremer support values (near branch nodes), (●) Nonhomoplasious; (○) homoplasious. (B) Nutritional mode of terminal taxa mapped onto the strict consensus tree using Mesquite parsimony (P) model. Branches are color coded to represent different feeding habits (see color legends).
Figure S6. Major groups of terrestrial bugs and their putative phylogenetic relationships, Related to Figure 1 and 2. Phylogenetic relationships and ancestral state reconstructions of diet derived from phylogenetic analysis (Table S4; Figure S5). At left are geologic periods calibrated to a time scale in millions of years; localities at the far left are indicated deposits from which the earliest confirmed fossil occurrence of each family is known (Table S5). Ghost ranges are indicated as thin lines and merely depict phylogenetic relationships but do not establish ultimate ages for individual clades.
### ii) Supplemental Tables

<table>
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<th>Feeding habits</th>
<th>Examined</th>
<th>Specimen</th>
<th>Collecting date</th>
<th>Weight (g)</th>
<th>Content (Fe) (ng/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>blood feeding</td>
<td>Cimex lectularius Linnaeus, 1758 (Cimicidae)</td>
<td>China, Beijing/wild</td>
<td>2012-IV-25</td>
<td>0.0024</td>
<td>1.28E+06</td>
</tr>
<tr>
<td>Triatoma melanosoma Martinez, Olmedo &amp; Carvavallo, 1987 (Triatominae)</td>
<td>Beasil/artificial rearing</td>
<td>1995-III-18</td>
<td>0.0170</td>
<td>8.64E+05</td>
<td></td>
</tr>
<tr>
<td>Triatoma rubrofasciata De Geer, 1773 (Triatominae)</td>
<td>China, Hainan/wild</td>
<td>2008-X-25</td>
<td>0.0365</td>
<td>7.78E+05</td>
<td></td>
</tr>
<tr>
<td>Lisarda rhypara Stål, 1859 (Reduviidae)</td>
<td>China, Yunnan/wild</td>
<td>2012-V-22</td>
<td>0.0193</td>
<td>2.19E+05</td>
<td></td>
</tr>
<tr>
<td>predaceous</td>
<td>Liscocoris sinensis Kormilev, 1957 (Reduviidae)</td>
<td>China, Shanxi/wild</td>
<td>2012-VII-26</td>
<td>0.0090</td>
<td>3.32E+05</td>
</tr>
<tr>
<td>Platymeris biguttatus (Linnaeus, 1767) (Reduviidae)</td>
<td>China, Beijing/artificial rearing</td>
<td>2012-VI-29</td>
<td>0.0875</td>
<td>2.029E+05</td>
<td></td>
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<tr>
<td>Prionolomia gigas Distant, 1870 (Coreidae)</td>
<td>China, Yunnan/wild</td>
<td>2012-V-22</td>
<td>0.1086</td>
<td>1.15E+05</td>
<td></td>
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<td>phytophagous</td>
<td>Palomena viridissima (Poda, 1761, Coreidae)</td>
<td>China, Shanxi/wild</td>
<td>2012-VII-26</td>
<td>0.0542</td>
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<td>Erthesina fullo (Thunberg, 1783, Pentatomidae)</td>
<td>China, Shanxi/wild</td>
<td>2012-VII-26</td>
<td>0.0861</td>
<td>2.029E+05</td>
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<tr>
<td>Riptortus pedestris (Fabricius, 1775, Alydidae)</td>
<td>China, Shanxi/wild</td>
<td>2012-VII-26</td>
<td>0.0301</td>
<td>2.46E+05</td>
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### Table S2. Operating Conditions for the ICP-MS, Related to Table1. (Rf Power = radio frequency power).

<table>
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<tr>
<th>Parameter</th>
<th>Value</th>
<th>Parameter</th>
<th>Value</th>
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</thead>
<tbody>
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<td>Rf Power</td>
<td>1550W</td>
<td>Orifice of sampling cone</td>
<td>1.0 mm</td>
</tr>
<tr>
<td>Cool gas</td>
<td>15.0 L·min⁻¹</td>
<td>Orifice of skimmer cone</td>
<td>0.4 mm</td>
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<tr>
<td>Auxiliary gas</td>
<td>1.0 L·min⁻¹</td>
<td>Data Acquisition mode</td>
<td>Quantity Analysis</td>
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<tr>
<td>Carrier gas</td>
<td>1.12 L·min⁻¹</td>
<td>Integration time</td>
<td>0.3 s</td>
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<tr>
<td>Sampling rate</td>
<td>1.0 mL·min⁻¹</td>
<td>Oxide</td>
<td>&lt;0.5 %</td>
</tr>
<tr>
<td>Sampling depth</td>
<td>8 mm</td>
<td>Doubly charge</td>
<td>&lt;2 %</td>
</tr>
</tbody>
</table>
Table S3. Atom.C [at.%] of Fe for seven specimens, Related to Figure 3 and Table1. (Atom.c [at.%] = percentage of atom quantity. relative value*= Fe in shale matrixes is subtracted from mean).

<table>
<thead>
<tr>
<th>Examined</th>
<th>rostrum</th>
<th>antenna</th>
<th>head</th>
<th>thorax</th>
<th>abdomen</th>
<th>leg</th>
<th>mean</th>
<th>shale matrix</th>
<th>relative value*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>F. acutirostratus</em> (Torirostratidae, CNU-Het-LB2006422)</td>
<td>2.42</td>
<td>3.20</td>
<td>2.60</td>
<td>2.38</td>
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<td>2.78</td>
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<td>2.53</td>
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<td>2.85</td>
<td>2.20</td>
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<td>2.36</td>
<td>2.98</td>
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<td><em>V. solaris</em> (Venicoridae, CNU-Het-LB2006541)</td>
<td>-</td>
<td>1.99</td>
<td>2.16</td>
<td>1.60</td>
<td>1.74</td>
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<td>1.86</td>
<td>1.09</td>
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<td>2.05</td>
<td>1.82</td>
<td>1.96</td>
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<td>2.06</td>
<td>1.92</td>
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<td><em>V. decorus</em> (Vetanthocoridae, CNU-Het-LB2006048)</td>
<td>1.53</td>
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<td>1.72</td>
<td>2.04</td>
<td>2.13</td>
<td>2.13</td>
<td>2.00</td>
<td>0.82</td>
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<td>Undescribed specimens (Reduviidae, CNU-Het-LB2012107)</td>
<td>-</td>
<td>1.62</td>
<td>1.93</td>
<td>2.27</td>
<td>1.65</td>
<td>-</td>
<td>1.87</td>
<td>1.43</td>
<td>0.44</td>
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Table S4. Character matrix of 81 characters for the 45 taxa included in this study, character 82 is for the nutritional mode reconstruction. (*denotes a fossil species)

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<td>Scotomeles alienus Distant, 1904 (Velocipedidae) 2111010100 0001021001 0001111101 0001000001 1002010010 0010030000 1000011101 0000111102 01</td>
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Table S5. Geographical and stratigraphic distribution of the oldest fossil confirmed occurrence in each family of Pentatomomorpha and Cimicomorpha, Related to Figure 1 and 2.

<table>
<thead>
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<th>Formation</th>
<th>Locality</th>
<th>Reference</th>
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<td>Early Cretaceous</td>
<td>Gurvan-Eren</td>
<td>Mongolia</td>
<td>[S1]</td>
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<td>Kobdocoridae</td>
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<td>Gurvan-Eren</td>
<td>Mongolia</td>
<td>[S2]</td>
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<td>Pachymeridiidae</td>
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<td>Charmouth</td>
<td>England</td>
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<tr>
<td>Piesmatidae</td>
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<tr>
<td>Coreidae</td>
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<td>Huangshanjie</td>
<td>China</td>
<td>[S5]</td>
</tr>
<tr>
<td>Alydidae</td>
<td>Late Jurassic</td>
<td>Karatau</td>
<td>Kazakhstan</td>
<td>[S6]</td>
</tr>
<tr>
<td>Rhopalidae</td>
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<td>Jiulongshan</td>
<td>China</td>
<td>[S7]</td>
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<td>Cydnidae</td>
<td>Early Cretaceous</td>
<td>Yixian</td>
<td>China</td>
<td>[S8]</td>
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<tr>
<td>Acanthosomatidae</td>
<td>Oligocene</td>
<td>France</td>
<td></td>
<td>[S9]</td>
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<tr>
<td>Scutellerida</td>
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<td>France</td>
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<td>China</td>
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<td>Pentatomidae</td>
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<td>Tingidae</td>
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<td>Thaumastocoridae</td>
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<td>China</td>
<td>Undescribed specimens</td>
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</tbody>
</table>

iv) Materials and methods

Background of the localities

The Yixian Formation, located below the Jiufotang Formation and considered as an important component of the Jehol Entomofauna, is a Mesozoic non-marine sedimentary stratum that outcrops in northeastern China [S20, S21]. This formation generally contains 24 beds situated in six regions of the western Liaoning Province, northern Hebei Province, and eastern Inner Mongolia. Huangbanjigou and Dawangzhangzi Villages are two very important sections of the Yixian Formation. Fossil insects and accompanying animals and plants from the Yixian Formation are
mainly collected from these two localities, especially Huangbanjigou. Huangbanjigou Village is situated in Shangyuan District, 28 km southeast of Beipiao City, while Dawangzhangzi Village is situated 12 km southwest of Lingyuan City, Liaoning Province. In addition, we also have collected three specimens from Liutiaogou Village, Dashuangmiao Town, Ningcheng County, Chifeng City, Inner Mongolia and two specimens from Shimen Village, Yangshuling Township, Pingquan County, Hebei Province.

The geological age of the Yixian Formation is considered as the Early Cretaceous (about 125.2 to 122.1 Ma). So far, 468 species and 328 genera belonging to 144 families and 16 orders (Ephemeroptera, Odonata, Plecoptera, Blattodea, Dermaptera, Orthoptera, Phasmatodea, Homoptera, Heteroptera, Raphidioptera, Neuroptera, Coleoptera, Mecoptera, Diptera, Trichoptera, and Hymenoptera) of insects have been recorded from fossils recovered in the Yixian Formation [S22–S25], and these are important materials for studying the structure and palaeoecology of the Jehol Biota. Coleoptera (28 families and 78 genera) is thus far understood to be the dominant group of the Jehol entomofauna, followed by Hymenoptera (23 families and 56 genera). There have been recorded 13 families, 32 genera, and 37 species belonging to Heteroptera [17, 19,20, S26–S34].

Examined taxa and terminology

Our material consists of 399 well-preserved fossil specimens, including 42 parts and counterparts, from the Jianshangou Bed in the lower part of the Yixian Formation at Chaomidian Village near Shangyuan Village, Beipiao City, Liaoning; Dawangzhangzi Village, Lingyuan City, Liaoning; Liutiaogou Village, Dashuangmiao Town, Ningcheng County, Chifeng City, Inner Mongolia; and Shimen Village, Yangshuling Township, Pingquan County, Hebei Province China. These specimens are common among the collection of the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University (CNU), and account for 11% of all terrestrial true bugs collected from the Yixian Formation. Among them, there are many complete specimens, including well-preserved antennae, rostra, ocelli, compound eyes, mesoscutella, pronota, wings, legs, abdomens, and ovipositors. Due
to lack of discernible mouthpart structures, two out of 399 specimens were not used in
the study of orientation and position of the rostra. Morphological terminology mainly
follows Schuh and Slater [21]. All measurements are in millimeters.

v) Supplemental description, material and measurements of the
characters present in the two new taxa

_Torirostratus pilosus_ Yao, Shih, et Engel, _gen. et sp. nov._ (Figure 1)

**Description:** Body about 3 times as long as wide; head shorter than wide; second
antennal segment about 3 times as long as first and 1.4 times as long as third and
fourth, basal 1/6 of third segment paler; rostrum short, first segment thickest, 0.5
times as long as second, basal 1/5 of second segment thicker, apex of second and third
segments nearly of same thickness, third segment 0.5 times as long as second, fourth
thinnest, tapering, 0.7 times as long as third. Mesoscutellum 0.6 times as long as
pronotum at midline, 1.1 times as wide as long; femora stout, about 2 times as thick as
Corresponding tibiae, basal 1/4 of first tarsomere paler, pro- and mesofemora slightly
shorter than corresponding tibiae, tarsus elongate, over 0.5 times as long as
corresponding tibia, basal tarsomere 3.5 times as long as second and 1.4 times as long
as third; hind legs distinctly longer than fore- and mid-legs, metatibia almost 1.2 times
as long as metafemur, metatarsus similar to pro- and mesotarsi, 0.4 times as long as
metatibia, basal tarsomere 2.5 times as long as second and 1.7 times as long as third;
hemelytron 3.3 times as long as wide, corium over half of hemelytron in length,
membrane with two black markings, outside marking largest. Abdomen oval, with 8
visible segments, longer than wide, connexivum broad, with black square markings at
posterior angles of segments III–V and a cuneiform marking between segments VI
and VII.

**Dimensions (in mm):** Body length 13.72–15.04 (♂), 11.87–15.00 (♀); maximal
width of body 4.08–4.59 (♂), 3.98–5.11 (♀); head length 1.83–2.16 (♂), 1.79–2.11
(♀), width 1.95–2.21 (♂), 1.87–2.31 (♀); antennal segments length I–IV: 0.65–0.79,
1.98–2.30, 1.39–1.41, 1.37–1.41 (♂), 0.61–0.79, 1.95–2.07, 1.38–1.42, 1.37–2.11 (♀);
rostral segments length I–IV: 0.88–1.0, 1.61–1.7, 0.79–1.0, 0.66–0.70 (♂), 0.78–0.93, 1.41–1.7, 0.89–1.0, 0.61–0.75 (♀); pronotum length 2.66–2.90 (♂), 2.45–2.86 (♀), width 3.71–3.99 (♂), 3.88–4.01 (♀); mesoscutellum length 1.71–1.80 (♂), 1.65–1.89 (♀), width 1.81–1.90 (♂), 1.69–1.83 (♀); hemelytron length 8.80–9.45 (♂), 8.43–9.37 (♀), width 2.86–3.02 (♂), 2.91–3.10 (♀), length of anterior margin of corium 5.16–5.55 (♂), 5.23–5.50 (♀); fore-leg length: profemur 2.12–2.47 (♂), 2.09–2.38 (♀), protibia 2.41–2.71 (♂), 2.48–2.73 (♀), protarsomeres I–III: 0.71–0.78, 0.21–0.30, 0.44–0.51 (♂), 0.69–0.75, 0.24–0.31, 0.39–0.50 (♀); mid-leg length: mesofemur 2.56–2.69 (♂), 2.57–2.73 (♀), mesotibia 2.90–3.12 (♂), 2.92–3.15 (♀), mesotarsomeres I–III: 0.81–0.97, 0.28–0.33, 0.59–0.64 (♂), 0.75–0.93, 0.23–0.31, 0.42–0.53 (♀); hind leg length: metafemur 3.51–3.78 (♂), 3.43–3.66 (♀), metatibia 4.32–4.50 (♂), 4.47–4.61 (♀), metatarsomeres I–III: 0.88–1.00, 0.31–0.43, 0.55–0.61 (♂), 0.88–0.97, 0.031–0.40, 0.50–0.55 (♀); ovipositor length 1.99–2.14.


*Flexicorpus acutirostratus* Yao, Cai, et Engel, gen. et sp. nov. (Figure 2)

**Description:** Body about 2.8 times as long as wide. Head shorter than wide; compound eyes prominent, diameter about 0.5 times as wide as interocular space, ocellus large, between ocellus and compound eye as wide as interocellar space; antenna 0.4 as long as body, second segment 3.7 times as long as first and 1.5 times as long as third; rostrum short, first segment thickest, 0.6 times as long as second, basal 1/5 of second thicker, apex of second and third nearly of same thickness, third segment 0.6 times as long as second, fourth thinnest, tapering, 0.6 times as long as third; mesoscutellum 0.7 times as long as pronotum at midline, as wide as long; femora stout, about 2 times as thick as corresponding tibiae, pro- and mesofemora
slightly shorter than corresponding tibiae, mesotarsus elongate, over 0.5 times as long as corresponding tibia, mesobasitarsus 2.5 times as long as second and 1.4 times as long as third mesotarsomeres; hind legs distinctly longer than fore- and mid-legs, metatibia almost 1.1 times as long as metafemur, metatarsus similar to pro- and mesotarsi, 0.5 times as long as metatibia, metabasitarsus 2.6 times as long as second and 1.7 times as long as third metatarsomeres; hemelytron 2.5 times as long as wide, corium 0.7 times as long as hemelytron, costal margin with two dark markings; clavus slightly longer than lateral margin of mesoscutellum, sticklike, 0.4 times as long as hemelytron, membrane with a black marking near apex of corium. Abdomen oval, with 8 visible segments, longer than wide, connexivum broad, with a black square marking at posterior angle of each segment.

**Dimensions (in mm):**

- Body length: 8.69–10.12 (♂), 9.21–9.46 (♀);
- Maximal width of body: 3.50–3.81 (♂), 3.21–3.35 (♀);
- Head length: 1.16–1.43 (♂), 1.17–1.20 (♀);
- Antennal segments length I–IV: 0.37–0.44, 1.35–1.41, 0.89–0.97, 0.91–1.01 (♂), 0.40–0.48, 1.46–1.53, 0.91–1.01, 0.90–1.11 (♀);
- Rostral segments length I–IV: 0.63–0.79, 1.12–1.23, 0.68–0.79, 0.39–0.50 (♂), 0.61–0.85, 1.07–1.26, 0.65–0.72, 0.34–0.46 (♀);
- Pronotum length: 1.91–2.15 (♂), 1.95–2.14 (♀);
- Mesoscutellum length: 1.43–1.55 (♂), 1.39–1.56 (♀);
- Hemelytron length: 5.43–6.09 (♂), 5.98–6.24 (♀);
- Length of anterior margin of corium: 3.00–3.41 (♂), 3.45–3.63(♀);
- Fore-leg length: profemur 1.60–1.76 (♂), 1.59–1.72 (♀), protibia 1.79–2.06 (♂), 1.80–2.01 (♀), protarsomeres I–III: 0.54–0.63, 0.21–0.23, 0.37–0.40 (♂), 0.50–0.62, 0.21–0.26, 0.34–0.41 (♀);
- Mid-leg length: mesofemur 1.74–1.94 (♂), 1.88–1.98 (♀), mesotibia 2.08–2.19 (♂), 2.03–2.15 (♀), mesotarsomeres I–III: 0.53–0.67, 0.24–0.33, 0.37–0.41 (♂), 0.54–0.69, 0.21–0.26, 0.31–0.36 (♀); hind leg length: metafemur 2.48–2.73 (♂), 2.53–2.69 (♀), metatibia 3.11–3.27 (♂), 3.10–3.24 (♀), metatarsomeres I–III: 0.64–0.81, 0.29–0.34, 0.40–0.45 (♂), 0.64–0.83, 0.27–0.31, 0.41–0.50 (♀); ovipositor length: 0.77–0.91.

**Material:** Holotype, ♂, CNU-Het-LB2006435pc (part and counterpart); paratypes, 146 ♂: CNU-Het-LB2006331pc/418pc/443pc/406pc, ♂, CNU-Het-LB2010115pc/
vi) Determination of trace element Iron (Fe) in extant Heteroptera by Inductively Coupled Plasma-Mass Spectrometry (ICP-MS)

Instruments and reagents
Inductively Coupled Plasma-Mass Spectrometry (Agilent7500ce, Agilent Technologies Co. Ltd., USA) was used for sample analysis. A micro-wave sample preparation system equipped with up to 40 vessels (CEM MARSX press, USA) was employed for sample digestion.

All chemical reagents were of guarantee reagent. HNO₃ (65%, Merck); H₂O₂ (30%, v/v) was obtained from the chemical industry (Beijing, China). Working analytical solutions for B were prepared immediately before use by serial dilution of stock reference solutions containing 1000 mg L⁻¹ of Fe (National Research Center for Reference Materials, Beijing, China), with 5% HNO₃ in a gradient as necessary. Milli-Q water (18.2 MΩ cm) was used to prepare all solutions throughout the work.

**Sample Digestion and Detection.**

Ten extant species including three blood-feeding bugs, three predaceous bugs, and four phytophagous bugs were used in the study (Table S1). Samples were flushed with tap water to remove impurities such as sands, then rinsed clean using deionized water, dried to constant weight in a drying oven at 70–80°C, ground in agate mortars, and finally weighed. The samples were added to the digester and followed by 5mL of HNO₃ and 1mL of H₂O₂, respectively. The mixture was shaken gently and then incubated for 10 min at room temperature. The digester was sealed tightly and placed in the container. The microwave energy program used for digestion was set as the pre-setting procedure. The volume of the digests was adjusted to 25mL with Milli-Q water after sample digestion. Under the working conditions of the instruments described in Table S2, the standard, sample, and calibration blank solutions were determined by ICP-MS. All results were calculated automatically by software after working curves were plotted.

**Results**

The results of determination of trace element iron (Fe) in Heteroptera by ICP-MS are in Table S1.

**Statistical Analysis**

Comparisons between groups were performed by one-way analysis of variance (ANOVA) and followed by Student’s t test. All standard statistical tests were performed using SPSS 18.0 for Windows software. A probability value of less than
0.05 was considered statistically significant. One-way ANOVA demonstrated significant differences in among three diagnostic groups in Table S1 (F=23.276, df=9; p=0.001<0.05). Results of Student’s t test show that there was no significant difference in the iron (Fe) content between predaceous and phytophagous groups (p=0.599), but differences between the blood-feeding group and predaceous group and between the blood-feeding group and phytophagous group were significant (p=0.011 and 0.003<0.05). Consequently, we have reasons to believe that the iron content in blood-feeding bugs is significantly higher than those in phytophagous and predaceous bugs.

vii) Geochemical analyses

We examined seven fossil heteropterans specimens (Figures 3 and S1) for geochemical data that could reveal the underlying geochemical composition of antennae, mouthparts, legs, heads, thoraces, and abdomens. These seven specimens, collected from the same locality and horizon (at Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province), represent five families (Table 1): Torirostratidae fam. nov. (CNU-Het-LB2006422c/449/2010044), Pachymeridiidae (phytophagous, CNU-Het-LB2006247), Venicoridae (phytophagous, CNU-Het-LB2006541), Reduviidae (predaceous, CNU-Het-LB2012107), and Vetanthocoridae (predaceous, CNU-Het-LB2006048). Fossil matrices with specimens were cut to the appropriate size, and their undersurfaces were polished (topside of samples should not be polished in order to avoid any disturbance of fossil specimens). These samples were then cleaned with pure alcohol (99%), and dried in the laboratory environment.

Geochemical analyses were performed on uncoated samples with a Zeiss EVO/LS 15 Scanning Electron Microscope (SEM), using Bruker Nano XFlash Detector 5010 energy dispersive spectrometry (EDS) to examine small areas (size of each analyzed area is 22.5×28.9 μm) for elemental analyses. This collection of Backscattered Electron Imaging (BSEI) images and spot area analysis results by electron microprobe in EDS, were acquired under low vacuum at 20 kilovolts (kv), a beam current of
about 0.1 milliamperes (mA), and a pressure of 40 pascal (Pa) in the sample chamber. The pulse for the EDS detector was between 6.69 and 15.03 kilo-counts per second (kcps).

Geochemical data yields from seven specimens demonstrated that the content of elemental iron (Fe) was of particular interest. The results obtained from elemental analyses of the seven specimen indicate that iron (Fe) is present even within the shale matrix (Figures 3 and S2–S4; Tables 1 and S3), but the content is quite low and at trace levels. The differences of iron content are shown in Tables 1, 2. We made a statistical analysis for the unnormalized concentration [wt.%] (Table 1) of iron content in the matrix and insect bodies. In the matrix, a one-way analysis of variance yielded a p value = 0.706>0.05, and showed no significant differences among the three groups. In the bodies, results of Student’s t test show that there was no significant difference in the iron (Fe) content among those species representing pachymeridiids, reduviids, venicorids, and ventanthocorids (p = 0.633). However, there are significant differences between torirostratids [T. pilosus gen. et sp. nov. (CNU-Het-LB2010044) and F. acutirostratus gen. et sp. nov. (CNU-Het-LB2006422 and CNU-Het-LB2006449)] and the remaining specimens [(Pachymeridiidae (CNU-Het-LB2006247), Venicoridae (CNU-Het-LB2006541), Reduviidae (CNU-Het-LB2012107), and Vetanthocoridae (CNU-Het-LB2006048)] (p = 0.026 and 0.039<0.05). An analysis of one-way ANOVA also shows significant differences among torirostratids and the remaining specimens (F = 12.741; df = 6; p = 0.018<0.05).

viii) Phylogenetic analyses

Methods

We carried out phylogenetic analyses for Geocorisae (including Pentatodomomorpha and Cimicomorpha) to clarify and confirm the position of our new taxa. According to previous studies [S35–S42], we chose Megochterus occidentalis Baehr, 1990 [Ochteridae, S43], and Lycorma delicatula White, 1845 (Fulgoridae) as
our outgroup taxa. The 43 ingroup terminal taxa include five fossil taxa and 38 extant taxa. A complete list of the taxa used in the phylogenetic analyses is given in Table S4.

A total of 81 characters (including 79 morphological characters) were used in the analyses, 52 of these are binary and 29 are multistate. All the characters are unordered and with equal weight, the missing data were scored as unknown, the inapplicable data were scored as hyphens. For Medocostidae we coded their character states according to the relevant literature as material was not available [S44]. The character matrix is provided in Table S4. Analysis of the character matrix was performed in NONA version 2.0 [S45] and using the WinClada version 1.00.08 interface [S46]. Runs were conducted using the following commands: multiple TBR+TBR search strategy, Maximum trees to keep (hold) = 10000; number of replications (mult*N) = 1000; starting trees per rep (hold/=100. Bremer support values were obtained using command files composed by TreeRot V3 [S47] in conjunction with the heuristic search algorithm in PAUP v4.0b10 [S48]. Ancestral character state reconstruction of diet was conducted using equally-weighted parsimony methods in Mesquite 2.75 [S49]. We coded the data for diet of terminal taxa based on biological data from the corresponding species (Table S4, character 82).

**Phylogenetic Results**

Analyses of the character matrix yielded eight most parsimonious trees (tree length = 289, consistency index (CI) = 0.39, retention index (RI) = 0.75). The strict consensus is shown in Figure S5A. Pertinent results of the phylogenetic analysis include: Pentatomomorpha and Cimicomorpha were recovered as monophyletic; the Reduvioida with our new fossil complex being the sister-group of the Cimiciformes; these fossils represent a new family, treated as the sister group of Reduvioida; Mirioidea (Miriidae, Tingidae, and Thaumastocoridae) were located at the base of the Cimicomorpha; the Cimicoidea, Reduvioida, and our fossil taxa were supported as monophyletic. These results are simplified as follows: (Aradoidea+(Coreoidea (sensu lato) +Pentatomomorpha)) + (Mirioidea + (Cimiciformes + (Reduvioida + Torirostratidae fam. nov.))).
Conclusions

Cimicomorpha

The monophyly of Cimicomorpha is well supported by four synapomorphic characters in the present analysis: abdominal spiracle 1 absent (character 70:1), spermatheca nonfunctional (character 76:1), fertilization via lateral oviducts or ovarial pedicels (character 77:1), and eggs have a well-developed operculum (character 80:2).

Torirostratidae fam. nov.

We carried out a phylogenetic analysis for Pentatomomorpha and Cimicomorpha to clarify and confirm the position of our new taxa. According to our results, the new taxa belong to Cimicomorpha and are best considered as a new family, here treated as the sister group of Reduvioidea. In the best-supported cladogram (Figures S5A and S6), the lineages of Torirostratidae fam. nov. strongly support monophyly, with a series of characters, e.g., surface of body smooth, without punctures (character 3:0), ocelli closer to each other than to compound eyes (character 13:1), antennal segment I very short, stout, barrel-shaped, shorter than half of the head in length (character 20:0), base on second segment of rostrum thickened, like a small segment (character 27:2), mesoscutellum subtriangular, apex blunt, narrowed or constricted in apical half (character 39:1), a crossvein on corium-membrane boundary not joined with claval suture (character 51:1), and connexivum on segment VII present (character 67:0). Among the above characters, characters 27, 39, and 51 are synapomorphic, which are shared only by these taxa and support the monophyly of the family.

Although Torirostratidae have some characteristics of the Pentatomomorpha, such as an enlarged pulvillus and the overall shape of the antenna, but according to our analysis they have more derived features in common with the Reduvioidea such as the unique corium, veins on the corium, and clavus. In addition, the completely exposed connexivum, presence of ventral laterotergites, and the blood-feeding habits (Figures 1C, E, F–H; 2B, K) also support Torirostratidae as a member of the Cimicomorpha.

Reduvioidea
Reduviioidea and the fossil family Torirostratidae are combined as a monophyletic group by the relatively small corium, almost 1/4 area of forewing (character 42:1), veins on corium well-developed, raised, and keel-like, 3 simple longitudinal veins, veins almost straight, not connecting to each other (character 44:1), apex of corium fingerlike (character 50:1), clavus narrow, clubbed, tapering from base to apex (character 52:1), claval commissure absent, claval apices not concealed by mesoscutellum (character 53:3), connexivum completely exposed (character 54:2), and pretarsal claws flattened, tapering from base to apex (character 62:1). Within these aforementioned characters, characters 42 and 44 are putatively synapomorphic for this clade. As in the results of a previous study [S50], the monophyly of Reduviioidea once again has been confirmed. Its monophyly was supported by antennae filiform, third and fourth antennal segments slender, distinctly thinner than second (character 16:2), antenniferous tubercles base arising above level of compound eye, completely visible in dorsal view (character 17:1), prepedicellite present (character 21:1), clavus obly with 1A vein (character 49:1), fossula spongiosa present (character 58:1), sternite VIII concealed by segment VII in males (character 69:1), and ovipositor platelike (character 75:1).

Cimiciformes

The monophyly of the Cimiciformes, which was called the nabid-cimicoid lineage in the system of Carayon [S51], was supported by two characters: labial groove on thoracic sternum absent (character 32:0) and paramere orientation not backward (character 74:1). Here, Cimiciformes includes the Joppeicidae, Microphysidae, Velocipedidae, Cimicoidea, and Naboidea, as proposed by Schuh et al. [S39]. Although it was not supported strongly, Naboidea is considered the sister group of Cimicoidea as proposed by Schuh and Štys [S35] and Tian et al. [S37].

Miroidea

The present analysis did not support monophyly of the Miroidea. Our result substantiates the findings proposed by Kerzhner [S52] and Tian et al. [S37]. In Schuh et al. [S39], the monophyly of the Miroidea had only limited support in the combined morphology and molecular analysis. Our result did not corroborate the basal position
of Reduviidae in Cimicomorpha as proposed by Schuh and Štys [S35] and Schuh et al. [S39]. In our topologies Tingidae, Thaumastocoridae, and Miridae were placed more basal among the Cimicomorpha, which is in agreement with the views of Kerzhner [S52] and Tian et al. [S37]; Thaumastocoridae, Miridae, and Tingidae are obviously closely related but have an ambiguous relationship among them that requires further investigation.

**Pentatomomorpha**

Pentatomomorpha was well supported as monophyletic by three characters: connexivum partially covered by forewing; (character 54:1), distal sector of R+M in hind wing branching (character 56:1), and endosoma with ejaculatory reservoir (character 72:1). Our results reaffirm Pentatomomorpha as monophyletic and the sister-group of the Cimicomorpha as indicated in previous studies [21, S53].

**Pentatomoidea**

The family Urostylididae as the basal grouping within Pentatomoidea was supported by our study; this is similar to the findings of Gapud [S54] and Grazia et al. [S55]. Pentatomoidea was well supported as monophyletic by the following: laterally head dorso-ventrally flattened, laterally carinate (character 5:1), antenna 5-segmented (character 18:1), pretarsal claws flattened, tapering from base to apex (character 62:1), sternite VIII in males concealed by segment VII (character 69:1), and abdominal sterna 3–7 with 1–2 trichobothrium on either side of midline (character 78:1).

**Coreoidea (sensu lato)**

According to the present result, the monophyly of the Coreoidea (sensu lato) was not supported. All families in the Coreoidea (sensu lato) apparently are closely related but have an ambiguous relationship among them, and may form a grade to Pentatomoidea. Resolving these relationships is beyond the scope of this paper and will require more evidence from living and fossil representatives.

**Ancestral state reconstructions of diet**

Our reconstruction of diet shows that the phytophagous feeding strategy is ancestral for terrestrial true bugs (Cimicomorpha + Pentatomomorpha). A hematophagous life-style appeared at least thrice independently among the
Cimicomorpha — Triatominae (*Triatoma*), Torirostratidae, and Cimicidae + Polycetenidae (Figure S5B).

**Character descriptions**

(List of characters 1–81 used in phylogenetic analyses, character 82 for diet reconstruction. All terminal taxa are species, all characters for each terminal are coded directly from specimens.)

1. General outline of the body: (0) elongate, but length less than 4 times as long as maximum pronotal width; (1) much longer than wide, length at least 6 times maximum pronotal width; (2) ovoid, at most, slightly longer than wide; (3) spheroid, not quite as long as wide. 【Among our taxa, the general outline of the body is often ovoid (e.g., most Pentatomoidea) or elongate (e.g., most Coreoidea, Pyrrhocoroidea and Lygaeoidea). Having a very slender body, (length at least 6 times maximum pronotal width) is an uncommon condition within ingroup, and is only found in some Alydidae, Berytidae and Colobathristidae. A spheroid body shape is only found in the Plataspididae.】

2. Body: (0) columniform or slightly dorsoventrally flattened habitus, (1) body dorsoventrally flattened, but not extremely flattened dorsoventrally; (2) extremely flattened dorsoventrally. 【The grade of ‘Homoptera’ usually have a slightly dorsoventrally-flattened habitus, the dorsoventrally extremely-flattened body shape occurs in Aradidae.】

3. Surface of body: (0) smooth, without punctures; (1) sparsely punctuate; (2) densely punctuate. 【The sparsely punctured pronotum and scutellum is the common condition in most of the families of the Heteroptera. Members of the Piesmatidae and Malcidae are densely punctate (i.e. the diameter of the punctures are as wide as the space between the punctures, usually areolate.】

**Head**

4. Anterior area of head: (0) preclypsyus and mandibular plates declivent strongly from the base of antenna, partly or not visible in dorsal view; (1) head porrect, preclypsyus and mandibular plates completely visible in dorsal view. 【Preclypsyus and mandibular plates declivent strongly from the base of antenna is found in
Colobathristidae, Malcidae and outgroup.

5. Laterally head: (0) conical or sub-conical; (1) dorso-ventrally flattened, laterally carinate. [Grazia et al. [S55] considered the head dorso-ventrally flattened and laterally carinate is the condition found in Pentatomoidea (character 2). We follow their description to check our ingroup and coded them. In our fossils, some specimens of them are laterally compressed, we didn’t find any grooves or carinae on the heads. Here we coded the fossil as 0.]

6. Base of head: (0) not forming a ‘neck’; (1) forming a ‘neck’. [This character and the next character were changed from “character 6” of Grazia et al. [S55]. In the grade of ‘Homoptera’ most taxa lack a ‘neck’ and the anterior margin of the pronotum is almost adjacent to the compound eyes, and the same is true for the water bugs.]

7. Base of head: (0) anterior margins of pronotum almost adjacent to compound eyes; (1) anterior margin of pronotum distant from compound eyes.

8. Mandibular plates: (0) short, not extending to apex of clypeus; (1) slightly elongate, extending to apex of clypeus. [Mandibular plates lengthened, extending to apex of clypeus is found in most Pentatomoidea, Thaumastocoridae, and Aradidae. The exceptions occur in the family Urostylididae. Our new fossil has small mandibular plates.]

9. Clypeus: (0) posteriorly orientated, swollen; (1) porrect, usually narrow; (2) porrect, dilated, broad. [Clypeus porrect, usually narrow is relatively common in all extant terrestrial true bugs.]

10. Bucculae length: (0) short or reduced; (1) long, narrow, extending half the length of head or more. [This coding is derived from Cassic & Schuh [S40], character 18, Henry [S56], character 5 and Grazia et al. [S55], character 11.]

11. Compound eyes: (0) present; (1) absent. [State (1) occurs only in Polyc tenidae.]

12. Ocelli: (0) present; (1) absent. Henry [S56] coded the Piesmatidae as ocelli absent. We checked some specimens of Piesmatidae and they actually have ocelli, but they are often hidden under the anterior margin of the pronotum. Here we coded
Piesmatidae as having ocelli.

13. Distance between ocelli and compound eyes: (0) ocelli closer to compound eyes than to each other; (1) ocelli closer to each other than to compound eyes. Ocelli closer to compound eyes than to each other is the common condition among extant Heteroptera, and also is found in the outgroup Fulgoridae; while state (1) occurs in the new fossil taxa, Ochteridae, Coreidae, Alydidae, Malcidae, and Urostylididae.

14. Post-ocular tubercles: (0) present; (1) absent. This coding was derived from Grazia et al. [S55], character 5.

15. Sutures between ocelli and compound eyes: (0) absent; (1) strongly developed. This coding was derived from Henry [S56], character 3.

16. Antennae: (0) setaceous; (1) filiform, second, third, and fourth antennal segments of almost same thickness; (2) filiform, third and fourth antennal segments slender, distinctly thinner than second. In Cicadomorpha, phytophagous Miridae, Thaumastocoridae and Tingidae have the same shape of antennae with Pentatomomorpha. State (2) only occurs in all predaceous or bloodsucking Cicadomorpha.

17. Antenniferous tubercles: (0) base arising below level of eye, partially obscured by mandibular plates; (1) base arising above level of eye, completely visible in dorsal view; (2) ventral on head, completely covered by mandibular plates. This coding is derived from Henry [S56] character 7, and Grazia et al. [S55], character 7.

18. Number of antennal segments: (0) four; (1) five, pedicel subdivided. Antennae five segments is only found in the Pentatomoidea.

19. Length of antenna: (0) short than head; (1) short than body; (2) antennae threadlike, longer than body. Antennae short than body is found in most true bugs. The exceptions occur in the two families Berytidae and Colobathristidae, the antenna very long, threadlike.

20. Antennal segment I: (0) short, stout, barrel shaped, short than half of the head in length; (1) slender, usually longer than head in length; (2) very long, slender,
longest of four segments. A very long first antennal segment occurs only in the Berytidae. In the Mesozoic fossil record, almost all taxa have a short first antennal segment which short than head in length and usually does not attain the apex of the head. So we believe the very short first segment antenna is a primitive trait in Heteroptera.

21. Prepedicellate: (0) absent; (1) present. This coding is derived from Schuh et al. [S39] character 11.

22. Antennal segment II: (0) uniformly slender or gradually widened over entire length; (1) clavate apically. Antennal segment II clavate apically found only in the Berytidae and Malcidae.

23. Antennal last segment: (0) slender, not modified or clubbed, similar to segments II or III; (1) clubbed, thickened and fusiform, or globose. This coding is derived from Henry [S56], character 10.

24. Rostrum: (0) the rostrum originates from the posterior region of the head, near to the occiput; (1) rostrum inserted distally on head.

25. Shape of labium: (0) slender, elongate, more-or-less parallel sided or uniform thickness; (1) stout, tapering from base to apex. State (1) only occurs in all predaceous or blood-feeding true bugs.

26. Ultimate labial segment: (0) long and relatively slender; (1) short and distinctly dilated; (2) absent. Schuh et al. [S39] believed that the first labial segment was short and distinctly dilated in Thaumastocoridae, in fact, in Thaumastocoridae the second labial segment is sometimes shorter than the first and is different from that in Velocipedidae. Here, we have treated Thaumastocoridae as having state 0.

27. Second segment of labium: (0) uniform thickness; (1) gradually contracted over entire length; (2) base thickened, like a small segment. State (1) occurs only in the new fossils. This character is regarded as a synapomorphy for this group.

28. Labium segment 3: (0) not longest, if longest, just slightly longer than second or forth segment; (1) extremely long. Labium segment 3 extremely long only found in Ochteridae, Velocipedidae, and most flower bugs.

Thorax
29. Pronotum: (0) trapezoidal; (1) hexagon, semicircular or other.  
   The trapezoidal pronotum is the common condition in Heteroptera. It’s also found in all Mesozoic fossil bugs. Hexagon pronotum is found in most Pentatomoidea. Shape of pronotum in the Aradidae have both. Here the Aradidae (Alychus calcaratus) with hexagon pronotum, so we coded Arididae as 0.

30. Pronotum: (0) without a distinct collar; (1) with a distinct collar.  
   In Cimicomorpha, only Miroidea, Cimicidae and Polycenetidae have Pronotum without a distinct collar.

31. Pronotum: (0) not laterally reflexed; (1) laterally reflexed.  
   In our taxon, pronotum laterally reflexed is only found in Pyrrhopeplus carduelis (Pyrrhocororidae).

32. Labial groove on thoracic sternum: (0) without sulcus to moderately sulcate; (1) deeply sulcate.  
   This coding was derived from Henry [S56], character 14, and Cassis & Schuh [S40], character 29.

33. Carina on thoracic sternum: (0) carina absent or moderately carinate; (1) strongly carinate.  
   This coding was derived from Henry [S56], character 13.

34. Prosternal stridulatory groove: (0) absent; (1) present.  
   Prosternum usually with a transversely striate stridulatory groove is only found in the Reduviidae.

35. Metathoracic scent gland: (0) primordial absent; (1) present or secondary absent.  
   State (1) only occurs in Heteroptera. This trait is regarded as a synapomorphy for Heteroptera.

36. Scent gland: (0) omphalian type; (1) diastomian type.  
   Scent glands of a diastomian type are found in Cimicomomorpha and Pentatomomorpha.

37. Metathoracic scent-gland evaporatory structures: (0) evaporatorium and peritreme present; (1) only peritreme present; (2) both evaporatorium and peritreme lacking.  
   Our coding of this character is often based on references [21, S57, S58], not always on original observations. Openings of the metathoracic scent-gland present is the condition found in all Pentatomomorpha, except in the Pyrrhocoroidea, Rhopalidae, and Piesmatidae. In the Cimicomorpha, only Reduviidae have a strongly reduced metathoracic scent gland.

38. Armature on scutellum: (0) absent; (1) armed with median carinae, conical or
globose tubercle, or slender spine.【This coding was derived from Henry [S56], character 18.】

39. Mesoscutellum: (0) triangle, sharp-pointed; (1) subtriangular, apex blunt, constricted half of apex region; (2) tongue-shaped.【The tongue-shaped mesoscutellum is a relatively common condition in the Pentatomoidea (except Urostylididae) and Aradidae. State (1) occurs only in our new fossil taxa.】

40. Mesoscutellum (size): (0) smaller than one-tenth length of body; (1) longer than one-tenth length of body and shorter than one-fourth length of body; (2) very large, longer than one-fourth length of body.【Cicadidae, Fulgoridae, Tingidae, Cimicidae, Polycytenidae, Piesmatidae, Berytidae and Colobathristidae the mesoscutella are very small, usually smaller than one-tenth length of body. Mesoscutellum longer than than one-third length of hemelytron is found in all Pentatomoidea. The exceptions occur in the Urostylididae, the mesoscutellum triangle and shorter than one-third length of hemelytron.】

41. Forewing: (0) usually held roof-wise over abdomen, without sharp differentiation into a coriaceous base and a membranous apical area; (1) usually held flat over abdomen when at rest, often in the form of hemelytra.【State (1) only occurs in Heteroptera. This trait is regarded as a synapomorphy for Heteroptera.】

42. Corium (in size): (0) area of corium larger than area of forewing; (1) corium relatively small, almost 1/4 area of forewing; (2) absent.【Our new fossils are similar to Reduviidae are in the size of the corium.】

43. Corial margin of forewing: (0) convex or nearly straight, without base of abdomen constricted; (1) narrowed, corial margin concave, with base of abdomen constricted.【Corial margin of forewing convex or nearly straight is the common condition in most of the families of the Heteroptera. In the families, Alydidae, Berytidae, Colobathristidae and Malcidae, the forewing is narrowed, the corial margin is concave, with the base of the abdomen constricted.】

44. Veins on corium: (0) well-developed, raised and keel-like, usually Veins connecting to each other and formed 2–5 closed cells; (1) well-developed, raised
and keel-like, 3 simple longitudinal veins, veins almost straight, not connecting
to each other; (2) reduced, usually just 1–2 veins.

45. Sc, R, M veins: (0) not diverging at a single point; (1) diverging at a single point.
   【Sc, R, M veins diverging at a single point is only found in two families, Idiostolidae and Pachymeridiidae.】

46. Costal fracture: (0) absent; (1) parallel to apex margin of corium; (2) vertical to
   anterior margin of corium. 【This character and next character was changed basal
   on “character 31” of Schuh et al. [S39]. Costal fracture appears in two different
   forms: parallel to apical margin of corium, such as Salidae, Ochteridae, and
   Pachymeridiidae (a Mesozoic family); and, usually vertical to anterior margin of
   corium, such as Miridae and Anthocoridae. Only the latter has strictly a formed
   cuneus. Thus, we believe the costal fracture and cuneus are two different
   characteristics.】

47. Cuneus: (0) absent; (1) present. 【Cuneus occurs only in Microphysidae, Miridae,
   and flower bugs.】

48. Medial fracture in forewing: (0) well developed and in combination with costal
   fracture; (1) absent. 【Forewing with distinctly medial fracture is only found in
   Ochteridae, Velocipedidae, Microphysidae, Miridae, Miridae, and all flower
   bugs.】

49. Veins on Clavus: (0) 1A and 2A present; (1) 1A present, 2A absent; (2) both 1A
   and 2A absent. 【Clavus with 1A and 2A veins is only found in four families,
   Fulgoridae, Tingidae, Idiostolidae, and Pachymeridiidae.】

50. Apex of corium: (0) not formed fingerlike; (1) fingerlike. 【State (1) only occurs
   in Reduviidae, Alydidae, Berytidae, Colobathristidae, and the new fossils.】

51. The end of corium: (0) joined with claval suture; (1) a crossvein on
   corium-membrane boundary not joined with claval suture. 【A crossvein on the
   corium-membrane boundary not joined with the claval suture is a peculiar
   feature among bugs. Previously we were not aware of its occurrence among
   terrestrial true bugs, only some aquatic bugs were known to have this state, e.g.,
Mesoveliidae or Gerridae.

52. Clavus (form): (0) broad, usually claval suture and inner side of clavus subparallel; (1) narrow, clubbed, tapering from base to apex. The narrow, clubbed, tapering from base to apex occurs in Pentatomoidea, Reduviidae, and the new fossils.

53. Claval commissure: (0) well developed, distinct longer than mesoscutellum, even close two times of length of mesoscutellum; (1) developed, usually shorter than mesoscutellum in length; (2) absent, claval apices concealed by mesoscutellum; (3) absent, claval apices not concealed by mesoscutellum. Within the Piesmatidae the claval commissure is very long. Claval commissures are absent in the Pentatomidae, Aradidae, Reduviidae, and Torirostratidae, but when present there are two different conditions—one is the mesoscutellum very large, concealing claval apices in repose (Pentatomidae and Aradidae), the other is the mesoscutellum small, not concealed by the claval apices in repose (Reduviidae and Torirostratidae).

54. Connexivum: (0) completely covered by forewing or scutellum; (1) partially covered by forewing; (2) completely exposed. The connexivum completely or partially covered by the forewing or mesoscutellum is the common condition in most Pentatommomorpha. The completely exposed connexivum is only found in Reduviidae and the new fossils.

55. Veins on hemelytral membrane: (0) 4 or 5 closed cells; (1) 1 to 3 closed cells; (2) reticulate venation; (3) 6~8 or more simple longitudinal veins; (4) only 3~4 simple longitudinal veins. The veins including emanating from closed cells in distal part of membrane.

56. Distal sector of R+M in hindwing: (0) not branching; (1) branching. Distal sector of R+M in hindwing branching is found in all Pentatomomorpha and lost in the outgroups and Cimicomorpha.

57. Legs: (0) normal; (1) legs threadlike, long. Legs very slender, threadlike, long is only found in Berytidae and Malcidae.

58. Fossula spongiosa: (0) never present; (1) often present on 1 or more pairs of legs.
(at least vestigially). In Polyctenidae we didn’t find fossula spongiosa. Schuh and Slater [21] also recorded that they do not have fossula spongiosa. The original coding [S39] and our own observations contradict this assertion. According to Carpintero and DellaPé’s (original Figures 4, 5) original description [S59], pro- and mesotibiae of Thaumastocoridae have three subapical dark teeth and setae on the inner margin arranged in a triangle, so we coded Thaumastocoridae as without fossula spongiosa.

59. Articulation of metacoxae: (0) directed laterally; (1) directed posterolaterally. This coding is derived from Henry [S56], character 31.

60. Tarsal formula: (0) 3-3-3; (1) 2-2-2; (2) 3-4-4; (3) 2-2-3. Tarsi three-segmented is the common condition in Heteroptera.

61. Pulvillus: (0) developed, usually differentiated into basi- and distipulvillus; (1) pulvillus obsolete or absent. This coding was derived from Grazia et al. [S55], character 32 and Cassic and Schuh [S40], character 51.

62. Pretarsal claws (form): (0) cylindrical; (1) flattened, tapering from base to apex. This coding was derived from Grazia et al. [S55], character 30.

Abdomen and genitalia

63. Segmental sutures: (0) all complete; (1) sutures 4 and 5 incomplete. A curved suture between abdominal sterna 4 and 5 not attaining the dorsal margin has been found in Pyrrhocoridae and Largidae.

64. Sternite II at middle: (0) not concealed by metasternum; (1) concealed by metasternum. This coding is derived from Grazia et al. [S55], character 38. They recorded almost all Pentatomoidea with abdominal sternite II concealed by the metasternum, except Urostylididae. We follow their codings and found in Aradidae, Corioidea (sensu lato), all Cicadomorpha, and outgroups abdominal sternite II is exposed.

65. Dorsal laterotergites: (0) not fused with mediotergites; (1) fused with mediotergites. Schuh et al. [S39] asserted that the Microphysidae without possesses dorsal laterotergites. But in Štys’s paper (original Figure 26), dorsal laterotergites of abdomen is present [S25]. Here, we have coded Microphysidae
as dorsal laterotergites not fused with mediotergites.

66. Ventral laterotergites: (0) present; (1) not visible and fused with sternum. [This coding was derived from Cassic & Schuh [S40], character 57, Henry [S56], character 27 and Schuh et al. [S39], character 41.]

67. Connexivum on segment VII: (0) present; (1) absent. [This coding is derived from Henry [S56], character 29.]

68. Sternite VII: (0) sternite VII split by ovipositor; (1) sternite VII not split by ovipositor, entire. [This coding was derived from Cassis & Schuh [S21], character 59 and Henry [S56], character 35.]

69. Sternite VIII in males: (0) not or partially covered by segment VII; (1) concealed by segment VII. [This coding was derived from Grazia et al. [S55], character 40 and Schuh et al. [S39], character 53.]

70. Abdominal spiracle 1: (0) present; (1) absent. [This coding was derived from Schuh et al. [S39], character 43 and Schuh & Slater [21].]

71. Position of spiracles: (0) all ventral; (1) only II dorsal, remainder ventral; (2) II, III, and IV dorsal; (3) all dorsal. [This coding was derived from Henry [S56], character 23 and Schuh & Slater [21].]

72. Endosoma: (0) without ejaculatory reservoir; (1) ejaculatory reservoir present. [State (1) occurs only in Pentatomomorpha.]

73. Male genitalia: (0) symmetrical; (1) asymmetrical. [This coding is derived from Schuh and Štys [S35]), character 37, Cassis and Schuh [S40], character 63 and Schuh et al. [S39], character 57.]

74. Paramere orientation: (0) backward; (1) forward or transverse. [This coding is derived from Schuh et al. [S39], character 58.]

75. Type of ovipositor: (0) lanceolate; (1) platelike; (2) ovipositor greatly reduced or absent. [This coding is derived from Schuh & Slater [21]. In the Mesozoic fossil records all taxa have a lanceolate ovipositor.]

76. Spermatheca: (0) present and functional; (1) nonfunctional, transformed into a vermiform gland; (2) absent. [State (1) and (2) occurs only in Cimicomorpha.]

77. Fertilization location: (0) in ectodermal portion of reproductive tract; (1) in lateral
oviducts or ovarian pedicels; (2) in vitellarium. 【This coding is derived from Schuh et al. [S39], character 68.】

78. Abdominal trichobothria number per segment: (0) absent; (1) sterna 3–7 with 1–2 trichobothrium on either side of midline; (2) sterna 3–7 with more than 2 trichobothrium on either side of midline. 【This coding was derived from Grazia et al. [S55], character 34 and Schuh et al. [S39], character 45.】

**Eggs and habits**

79. Mode of insemination: (0) no traumatic insemination; (1) traumatic insemination. 【State (1) occurs only in Cimicoidea.】

80. Eggs: (0) without operculum; (1) reduced; (2) well developed operculum. 【This coding was derived from Schuh & Slater [21]. Eggs with well developed operculum only found in Cimicomorpha.】

81. Living habits: (0) free living, living along the shores of ponds or streams; (1) free living, terrestrial habitats; (2) ectoparasitic. 【This coding was derived from Schuh & Slater [21]. In Heteroptera only Cimicidae and Polyctenidae are wholly ectoparasitic.】

82. Feeding habits: (0) phytophagous; (1) predaceous; (2) fungivorous; (3) feeding on vertebrate blood. 【Most Pentatomomorpha are phytophagous. Aradidae are usually considered to be fungivorous.】
viii) References for Supplementary Information


Fossil Treasures from Dinosaur Era of the Northeastern China. (Science Press, Beijing).


