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A specialized prey-capture apparatus in mid-Cretaceous rove beetles

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The hyperdiverse rove-beetle genus *Stenus* is characterized by one of the most specialized prey-capture structures known from extant arthropods [1,2]. The harpoon-like apparatus is formed by an elongated protrusible labium with terminal sticky cushions called paraglossae (Figure 1A) and a haemolymph pressure mechanism that enables the beetle to catch fast-fleeing prey within a few milliseconds [1–5]. Living in various microhabitats, extant *Stenus* species prey on fast-fleeing springtails (Collembola) and other small animals [1–3]. *Stenus* have been observed to secrete an adhesive during prey capture [5], and the morphology of the cushions accounts for variation in adhesive performance among species and between prey types [1,4,5]. Fossils with an exposed prey-capture apparatus are exceedingly rare, the oldest being from Eocene Baltic amber (approximately 45 million years old) [6]. Mesozoic stenines are therefore significant for elucidating the early evolution of the group and have been documented from middle–late Cretaceous deposits in France, Myanmar and Russia [6]. However, direct evidence of the exposed prey-capture apparatus is lacking. Here we confirm the Mesozoic antiquity of this possible key innovation in two species of the extinct genus *Festenus*, which was recently described [6] from mid-Cretaceous Burmese amber (approximately 99 million years old) and represents one of the earliest members of Steninae. We therefore provide critical information about the origin and early evolution of both the novel predatory structure and the subfamily Steninae.

Steninae include three extant genera: the widespread *Stenus* (~3000 species), the Holarctic *Dianous* (~220 species), and a new genus from Australia comprised of three new species [7]. We examined over 120 individuals of Steninae among 23,000 fossiliferous Burmese amber pieces, only two of which preserved an exposed prey-capture apparatus (Supplemental Information). One is *Festenus gracilis* (NIGP168835; Figure 1B) [6] as supported by the body shape and the characteristic bicolored elytra (modified forewings forming hardened wing covers). The other represents a new species of *Festenus* (NIGP168836; Figure 1E). The prey-capture apparatus in NIGP168835 is partly protruded showing completely preserved apical adhesive paraglossae (Figure 1C), whereas in NIGP168836 it is disassociated from the head and the adhesive paraglossae are not preserved (Figure 1F).

As in *Stenus* and the Australian genus [1,7], the prey-capture apparatus in NIGP168835 is formed by the extended labium (Figure 1C). The labial palpi are three-segmented with an elongated palpomere 1, a dilated and sparsely setose palpomere 2, and an acicular palpomere 3. The prementum is slightly widened toward its apex, bearing a pair of anterolateral paraglossae. As in most extant *Stenus*, these paraglossae form ellipsoid cushions with dense terminal ramifications (Figure 1C, D) that increase the chance of successful adhesion [4–5]. A shiny film appears to cover these ramifications (Figure 1D),

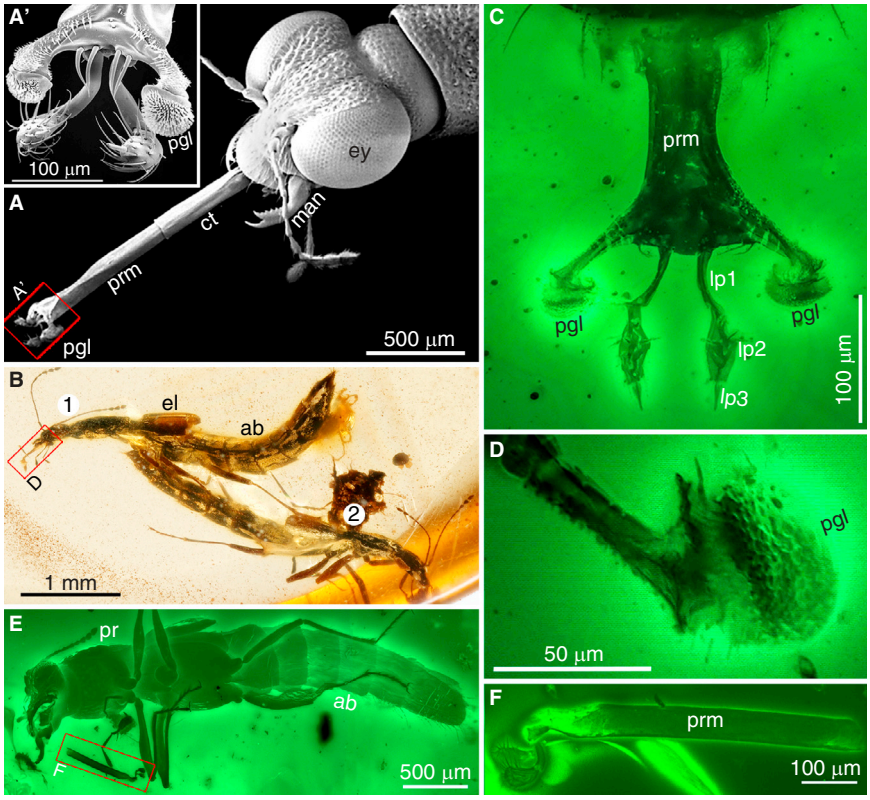

Figure 1. Specialized prey-capture apparatus in extant and mid-Cretaceous stenine rove beetles. (A) Scanning electron microscope image of the prey-capture apparatus of extant *Stenus comma*, adapted from Bauer and Pfeiffer [3] and reproduced with permission. (A') Enlargement of (A), highlighting details of the sticky cushions (paraglossae). (B) Two individuals of *Festenus gracilis* in Burmese amber; the upper one ('1', NIGP168835) with prey-capture apparatus partly exposed, under reflected light. (C) Frontal view of NIGP168835, showing prey-capture apparatus. (D) Lateral view of paraglossa, with outgrowths apparently immersed within adhesive secretion, under epifluorescence. (E) Ventral view of *Festenus* sp. (NIGP168836), showing disarticulated prey-capture apparatus, under epifluorescence. (F) Enlargement of (E), showing prementum and labial palpi, under confocal microscopy. Abbreviations: ab, abdomen; ct, membranous connecting tube; el, elytron; ey, eye; lp1, lp2, lp3, labial palpomeres 1, 2 and 3; man, mandible; pgl, paraglossa; pr, pronotum; prm, prementum.

suggesting that the outgrowths were probably covered with an adhesive secretion. The paraglossae display a generalized form (as in *S. comma*), which may have been modified in various ways during the evolutionary history of stenines [4]. The visible part of the prementum is short, but it is only partly extended and the connecting tube is still hidden within the head. In NIGP168836, however, the prey-capture apparatus is disarticulated from the mouthparts, and although only residual parts of the paraglossae were preserved (Figure 1F), the prementum is approximately two times the length of the head, similar to many extant species of *Stenus* (for example, *S. bimaculatus*, *S. bipunctatus* and *S. comma*). Thus, because the connecting tube is about as long as the prementum, in NIGP168836 the adhesive paraglossae could be hurled a maximum distance of approximately four times the head length to catch prey. Collectively, the comparison of these fossils with extant species confirms that the labium of *Festenus* species was protrusible and could be withdrawn back into the head when not in use. Therefore, the fossil species with large modified cushions and possible adhesive secretions may represent an active and efficient predator in the ancient forest, a notion that is also supported by its large globular eyes and long slender legs. Springtails in Burmese amber are very abundant and diverse, and may have been preyed upon by at least a coeval lineage of specialized ant-like stone beetles (Staphylinidae: Scydmaeninae) [8]. Despite the effective escape mechanism of springtails [8], Cretaceous stenines were likely able to catch them and other microarthropods using their sticky harpoons.

Our discovery of direct evidence of a protrusible prey-capture apparatus in one of the earliest known stenine beetles from the mid-Cretaceous illuminates their early evolution and confirms an ancient origin for their derived predatory behavior. Among extant stenines, the sticky harpoon mechanism is well developed in many species of *Stenus* and in the Australian genus (Supplemental Information), but absent in *Dianous* [1,7]. It is challenging to reconstruct the phylogenetic tree of Steninae [6,9] due to insufficient sampling of this hyperdiverse group, which usually defies species-level identification. Molecular phylogenetic studies of selected species of *Stenus* and *Dianous* indicated an evolutionary origin of *Dianous* within *Stenus*, suggesting a secondary loss of the harpoon apparatus [9]. This hypothesis is further reinforced by another phylogenetic result — that the Australian genus, which possesses a prey-capture apparatus homologous to that of *Stenus*, is a sister group to *Stenus* + *Dianous* (all sampled genera represented by one species) [10]. The presence of a protrusible prey-capture apparatus has been considered the most prominent apomorphic character for *Stenus* [1], but this assumption is not supported by recent discoveries of extant and extinct Steninae. Additionally, the ellipsoid cushions can be found in *Festenus*, the Australian genus, and most studied *Stenus* species, suggesting that this common form is the most likely ground plan for structure and function of the adhesive paraglossae in Steninae.

Steninae are recovered as the sister group of Euaesthetinae in morphological and molecular phylogenies [6,7,10]. Interestingly, the euaesthetine genus *Tyrannomastax* (Madagascar) has an elongated protrusible labium that may also function as a prey-capture apparatus [7]. However, in contrast to Steninae with a protrusible labium, the *Tyrannomastax* labium elongation is lesser and the paraglossae and other mouthpart structures are differently modified. It is therefore likely that this similar elongation of the labium resulted from a convergent predatory lifestyle in the forest litter layer.

SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental methods, one figure and supplemental references, and can be found with this article online at https://doi.org/10.1016/j.cub.2019.01.002.

ACKNOWLEDGMENTS

We are grateful to Dr. Oliver Betz (Universität Tübingen, Germany) for providing Figure 1A. Financial support was provided by the Strategic Priority Research Program (B) (XDB26000000, XDB18000000) of the Chinese Academy of Sciences, the National Natural Science Foundation of China (41688103 and 91514302), the Natural Science Foundation of Jiangsu Province (BK20161091), and the Youth Innovation Promotion Association of the CAS (2018347).

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