

A new pygmy mole cricket in Cretaceous amber from Burma (Orthoptera: Tridactylidae)

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Abstract: A new genus and species of Tridactylidae (Orthoptera: Caelifera: Tridactyloidea) is described from mid-Cretaceous Burmese amber. *Burmadactylus grimaldii* gen. et sp. nov. is the first tridactylid to be formally described from a Cretaceous amber and is assigned to the extant subfamily Dentractylinae. The new genus is distinguished from all other Dentractylinae by unusually small male paraproctal lobes and represents the first record of an extant tridactylid subfamily from the Mesozoic. A key to the genera of Dentractylinae is also provided.

Key words: Tridactyloidea, Tridactylidae, Dentractylinae, burmite, Myanmar.

Santrauka: Remiantis vidurinis kriedos Birmos (Myanmaro) gintaru aprašoma nauja šeimos Tridactylidae (Orthoptera: Caelifera: Tridactyloidea) gentis ir nauja rūšis. *Burmadactylus grimaldii* gen. et sp. nov. yra pirmoji Tridactylidae rūšis apibdinama pagal Kriedos gintarų. Ji priskiriama dabartiniui metu egzistuojančiai Dentractylinae pošeimiui. Kartu tai pirmas atvejis, kai dabartinio Tridactylidae pošeimio rūšis randama mezozojuje. Nauja gentis nuo visų kitų Dentractylinae skiriasi ne paprastai mažomis patinų paraproktalinėmis skiautėmis (paraproctal lobes). Taip pat pateikiamas Dentractylinae genčių apibdinimo raktas.

Raktiniai žodžiai: Tridactyloidea, Tridactylidae, Dentractylinae, birmitas, Myanmaras.

Introduction

In terms of its biotic diversity, Burmese amber is by far the richest Cretaceous amber in the world. The abundance, diversity and exquisite preservation of its biological inclusions have made Burmese amber the subject of intense scientific scrutiny in recent years¹ (GRIMALDI 1996; ZHERIKHIN & ROSS 2000; GRIMALDI et al. 2002; GRIMALDI & ENGEL 2005). To date, over 300 species representing some 130 families in 27 hexapod orders have been recorded, amongst which are the oldest Strepsiptera (GRIMALDI & ENGEL 2005) as well as the only Mesozoic Zoraptera (ENGEL & GRIMALDI 2002) and Embiidea (ENGEL & GRIMALDI 2006). In addition to hexapods, the amber has also yielded other organisms including bryophytes and higher plants (an angiosperm flower), nematode worms, pulmonate gastropods, a remarkable peripatid onychophoran, myriapods, numerous arachnids, a feather and fragments of reptili-

an skin (GRIMALDI et al. 2002). This incredibly diverse microbiota and a probable Turonian-Cenomanian age combine to make Burmese amber one of the most significant Cretaceous ambers in the world (GRIMALDI & ENGEL 2005), though study of this extraordinary resource is still in its infancy.

Orthoptera are rare in amber, so it is perhaps not surprising that the study of orthopteran inclusions has lagged far behind that of other insect groups. Only eight specimens were recorded from Burmese amber by GRIMALDI et al. (2002), all of which are small ensiferan nymphs. Indeed, adult orthopterans are extremely scarce in amber as they are usually large enough to free themselves from resin traps. This complicates the study of amber Orthoptera considerably as little can be gleaned from immature specimens beyond basic identification to family-group. Nevertheless, POINAR et al. (2007) recently described *Longioculus burmensis* (Elcanidae) from a small adult specimen previously figured by POINAR et al. (2005). Here, I describe a new genus and species of Tridactylidae from Burmese amber, representing the first Mesozoic record of the extant subfamily Dentractylinae. AZAR & NEL (2008) described the dentractyline *Guntheridactylus* from Eocene French amber and additional tridactylids are known from both Dominican (HEADS 2009, this volume) and Arch-

¹ Burmese amber, or "Burmite", was exported to China as early as the first century AD and was highly sought after for use in jewellery or as a medium for sculptors (GRIMALDI et al. 2002). However, mining ceased abruptly in the mid-twentieth century and it was not until comparatively recently (1999/2000) that interest from the Leeward Capital Corporation led to renewed mining and exploitation efforts. Important collections of Burmese amber inclusions are held at the American Museum of Natural History in New York and the Natural History Museum in London, and were summarised by GRIMALDI et al. (2002).

geay ambers (PERRICHOT 2004). However, the current paper constitutes the first record of an extant tridactylid subfamily from the Mesozoic.

The specimen described here is deposited in the amber collection of the Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York (AMNH) and was studied using a Zeiss stereomicroscope. Drawings were made with the aid of a camera lucida and photomicrographs produced using a scope-mounted Olympus digital camera. The age and biotic diversity of Burmese amber are reviewed in detail by ZHERIKHIN & ROSS (2000), ROSS & YORK (2000), RASNITSYN & ROSS (2000) and GRIMALDI et al. (2002).

Systematic account

Superfamily Tridactyloidea

The superfamily Tridactyloidea comprises three families: Tridactylidae BLANCHARD, 1845, Rhipipterygidae ANDER, 1939 and Cyldrachetidae GIGLIO-TOS, 1914. The Rhipipterygidae² are very closely related to Tridactylidae and have at times been considered a subfamily of the latter (e.g. CHOPARD 1949; RAGGE 1955). They are nevertheless distinct from the tridactylids in having elongate mesotibia with parallel or near-parallel margins and males with one-segmented cerci. Cyldrachetidae (sand goppers) are a peculiar group of fossorial insects known only from Patagonia, Australia and New Guinea. Monophyly of Tridactyloidea is supported by a number of morphological characters: [1] the prosternum connected directly to the pronotum by means of a precoxal bridge; [2] protarsus with two tarsomeres, inserted on the inner surface of the protibia [3] mesotarsus with two tarsomeres; [4] metatarsus always reduced to only one tarsomere; [5] arolia entirely absent; [6] abdomen with nine fully sclerotised sterna in both sexes, the ninth forming a simple subgenital plate lacking styli; [7] abdominal repugnatorial glands; and [8] male paraproct with distinctive sclerotised hooks. Members of the superfamily superficially resemble certain Grylloidea (Ensifera) with tridactylids and rhipipterygids approximating true crickets (Gryllidae) and cyldrachetids remarkably convergent on mole crickets (Gryllotalpidae). Indeed, the tridactyloid families have in the past been classified along with the Grylloidea (TINDALE 1928) though their caeliferan identity has now been confirmed beyond doubt (ANDER 1934).

² Rhipipterygidae is commonly misspelled as "Rhipipterygidae". This is due to an early misspelling of the genus-group name *Rhipipteryx* NEWMAN, 1834 by AUDINET-SERVILLE (1838). This error was repeated by SAUSSURE (1859) and gained wide usage during the first half of the 20th century. Indeed, ANDER (1939) used this incorrect spelling when forming the combining stem of the family-group name (i.e. Rhipipteryg-). GÜNTHER (1994) subsequently recognised *Rhipipteryx* AUDINET-SERVILLE, 1838 as a junior synonym of *Rhipipteryx* NEWMAN, 1834 and was followed by OTTE (1997), though misspelling of both the genus-group and family-group names is still widespread.

Tridactyloidea are an ancient group, though fossil representatives are extremely rare. The earliest definitive tridactylids are known from the Early Cretaceous of Central Asia (Transbaikalia and Mongolia), Brazil and southern England (SHAROV 1968; MARTINS-NETO 1990; GOROCHOV 1992; GOROCHOV et al. 2006) though the precise relationships of these primitive taxa remains uncertain. GOROCHOV et al. (2006) place all the Cretaceous genera in the extinct tridactylid subfamily Mongoloxiinae GOROCHOV, 1992. However, this subfamily is defined solely on the basis of plesiomorphic tegminal venation and is almost certainly paraphyletic. Moreover, it is still unclear as to whether the Cretaceous genera represent stem-group Tridactylidae sensu stricto or are the stem-group to a clade comprising Tridactylidae and Rhipipterygidae. Tridactylidae were also reported from the Early Cretaceous Archingey amber of southwest France by PERRICHOT (2004) though they were not figured and remain undescribed. *Gunteridactylus grimaulti* AZAR & NEL is the only tridactylid described so far from the Cenozoic, though undescribed species of *Ellices* (Tridactylidae) and *Rhipipteryx* (Rhipipterygidae) are present in Miocene amber from the Dominican Republic and will be described elsewhere (HEADS in prep.). Cyldrachetidae are at least as old as the Tridactylidae-Rhipipterygidae clade and although they are entirely unknown as fossils, their disjunct austral distribution supports a Mesozoic origin and suggests that the family radiated prior to the break up of Gondwana.

Family Tridactylidae BRULLÉ, 1835

Tridactyles BRULLÉ, 1835: Histoire naturelle des Insectes 9: 192.

Tridactylites BLANCHARD, 1845: Histoire des Insectes, 246, 255–257.

Tridactylites SAUSSURE, 1874: Bulletin de Société Vaudoise des Sciences Naturelles 13: 466–467.

Tridactylidae BRUNNER VON WATTENWYL, 1882: Prodrum der europäischen Orthopteren, 453.

Type genus: *Tridactylus* OLIVIER, 1789.

Nomenclatural note: Priority for family-group names based on the type genus *Tridactylus* OLIVIER, 1789 dates from Tridactyles BRULLÉ, 1835 and not Tridactylites SAUSSURE, 1874 as widely purported in the literature. Moreover, the name Tridactylites was first used by BLANCHARD (1845), almost 30 years before SAUSSURE (op. cit.).

Diagnosis: Tridactylidae are distinguished from the Cyldrachetidae by their saltatorial metathoracic legs with markedly enlarged femora and long, slender tibiae. As stated previously, Tridactylidae are most closely related to Rhipipterygidae, but can be distinguished from the latter by the male cerci two-segmented. The family is characterised by their very small size (a feature shared

with Ripterygidae) and significantly reduced tegminal venation comprising between two and four longitudinal veins. Members of the family are generally a glossy black and white with occasional brown/off-white patches and usually have fossorial prothoracic legs, often with a number of dactylar processes present on the protibia.

Subfamily Dentrictactylinae GÜNTHER, 1979

Dentrictactylinae GÜNTHER, 1979: Deutsche Entomologische Zeitschrift 26, 258, 263.

Type genus: *Dentrictactylus* GÜNTHER, 1974.

Diagnosis: The subfamily Dentrictactylinae comprises three extant genera, *Bruntrictactylus* GÜNTHER, 1979, *Dentrictactylus* GÜNTHER, 1974 and *Paratrictactylus* EBNER, 1943 and the fossil genus *Guntherictactylus* AZAR & NEL, 2008 from Eocene French amber, which are united based on the presence of a distinctive subapical denticular process on the metatarsus.

Genus *Burmadactylus* gen.nov.

Type species: *Burmadactylus grimaldii* sp.nov. by monotypy.

Etymology: The genus-group name is formed from a combination of "Burma" and "dactylus", a suffix commonly used in the genus-group names of tridactylids.

Diagnosis: *Burmadactylus* is distinguished from all other Dentrictactylinae by the unusually small paraproctal lobes which are much longer (as long as the cerci) in all other members of the subfamily. Moreover, *Burmadactylus* can be separated from *Bruntrictactylus* and *Guntherictactylus* by the absence of metatibial swimming plates, and from *Paratrictactylus* by the presence of tegmina. The new genus is similar to *Dentrictactylus*, particularly in the morphology of the metathoracic legs, but can be distinguished from the latter by the small paraproctal lobes and cerci with long setae.

Burmadactylus grimaldii sp.nov. (Figs 1-4)

Holotype: Adult ♂ in Upper Cretaceous amber from Burma (Union of Myanmar); Katchin, Tanai Village, on Ledo Rd. 105 km NW Myitkyna, leg. R. CRUICKSHANK, Leeward Capital Corp., 2000. AMNH number Bu1452. Syninclusions: in addition to the aforementioned tridactylid, this piece of amber also contains a small hemipteran nymph and several collembolans representing at least two species.

Etymology: The specific epithet is a noun in the genitive case and is named in honour of Dr David GRIMALDI (AMNH, New York) in recognition of his significant contribution to our knowledge of Burmese amber and its inclusions.

Diagnosis: As for the genus (vide supra).

Description: ♂: body 3.77 mm long measured from the head to the abdominal apex; the specimen has undergone some lateral compaction with its ventral and right lateral sides embedded in a large and turbid bubble (Figs 1A-B, 2). **Head:** hypognathous, capsulate; vertex somewhat inflated anteriorly; frons broadly rectangular; frontoclypeal sulcus prominent; clypeus quadrate, narrowing distally; labrum markedly smaller than clypeus, almost triangular; ocelli apparently absent; compound eyes large and suboval; antennae moniliform, with ten articles; scape and pedicel identical in size and shape to the flagellomeres; mandible largely obscured by turbidity of the amber; maxillary and labial palpi long, with clavate terminal palpomeres bearing numerous small setae. **Thorax:** pronotum large, shield-like, extending posteriorly to entirely cover the mesonotum; margins of pronotum with a prominent sulcus (Figs 1A-B, 2); prosternum largely obscured by the turbidity of the amber; tegmina strongly sclerotised though heavily distorted by compaction, with at least two longitudinal veins; hindwing absent. **Legs:** profemur robust, slightly curved distally, with a strongly concave ventral surface and very long external ventral setae (Fig. 3); protibia broad, strongly inflated distally with a dense covering of strong setae (Fig. 3); basitarsus short, with two pairs of pulvilli; apical tarsomere elongate, slightly curved distally; pretarsus with two prominent unguis; mesofemur markedly longer and narrower than the profemur (see Fig. 2); mesotibia similar in shape to the protibia but more pointed apically; mesotarsus almost identical to the protarsus; metathoracic leg saltatorial; metafemur very large, as long as the abdomen and greatly inflated along its entire length, with prominent dorsal carina; external genicular lobe prominent, smooth, with several irregularly spaced setae (Figs 1A, 2); metatibia almost as long as metafemur, very slender, subquadrate in section, with two parallel rows of 12 small and evenly spaced spines on the dorsal margins; two small subapical spurs and two much longer apical spurs (Figs 1C, 4); metatarsus a little over twice as long as the apical spurs, with prominent apical (dent¹) and subapical (dent²) denticular processes (Figs 1C, 4). **Abdomen:** terga and sterna equally well sclerotised, narrowing posteriorly toward abdominal apex and somewhat distorted by lateral compaction (Fig. 2); subgenital plate broad, without styli, bearing a marginal fringe of long setae; cerci long, two-segmented with numerous long setae; apical segment smaller than basal segment; paraproctal hooklets entirely obscured by a large bubble; paraproctal lobe cone-shaped, markedly smaller than the basal segment of the cercus, with numerous short apical setae.

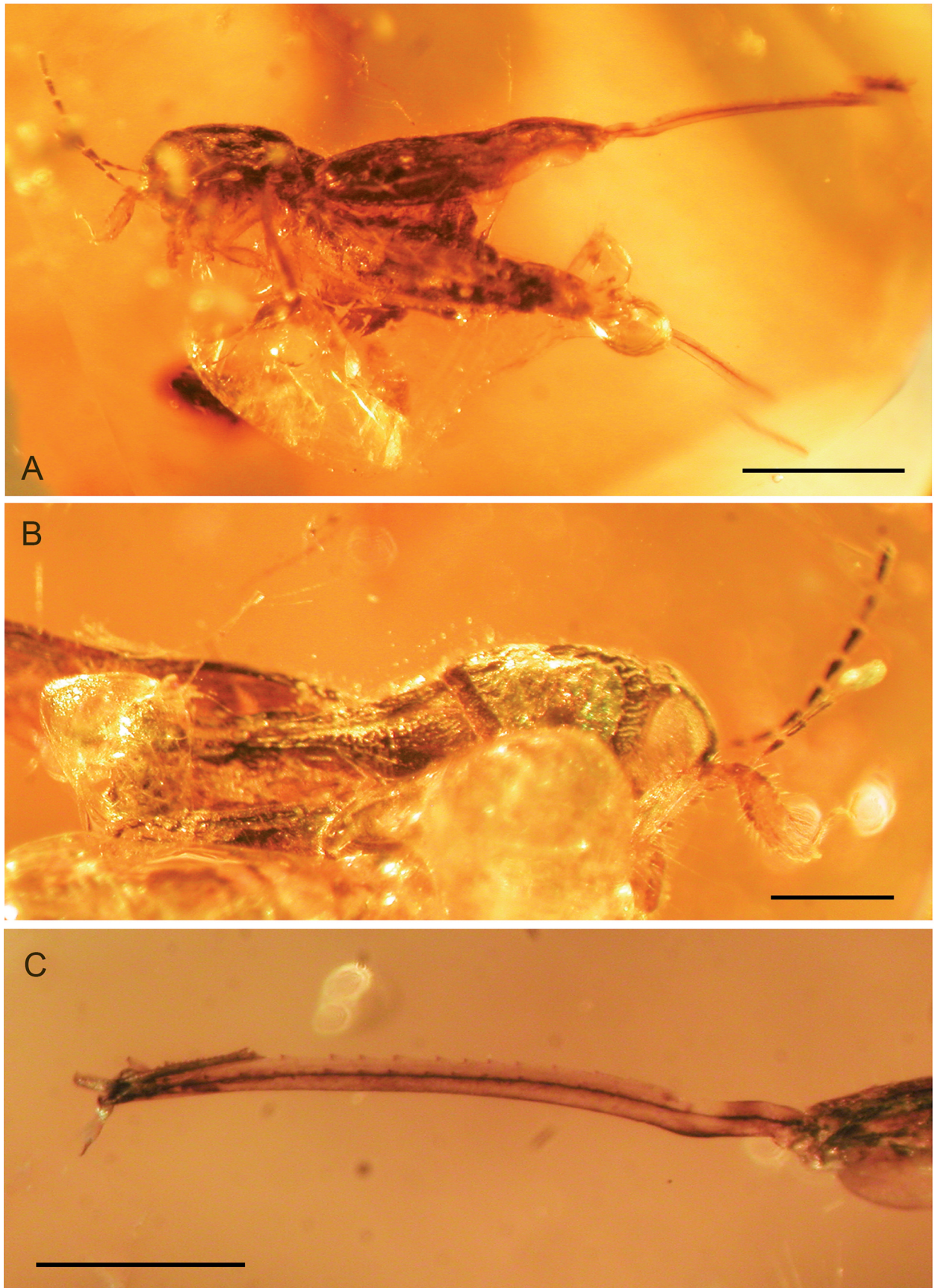


Fig. 1: Holotype of *Burmadactylus grimaldii* gen. et sp.nov. (AMNH Bu1452); **(A)** left lateral view of habitus; optical distortion of the metatibial apices is caused by curvature of the amber surface; scale bar 1.0 mm; **(B)** right dorsolateral view of the head, thorax and prothoracic leg; scale bar 0.5 mm; **(C)** left metatibia and apex of metafemur; scale bar 0.5 mm.

Figs 2-4:
Burmactylus
grimaldii gen. et
sp. nov. (AMNH
Bu1452).

(2) general habitus of the specimen; scale bar 0.5 mm;
(3) right prothoracic leg showing the arrangement of setae; scale bar 0.25 mm;
(4) apex of left metatibia (oblique dorsal view) showing details of the metatarsus, apical and subapical spurs; scale bar 0.25 mm.
Abbreviations: asp, apical spurs of metatibia; dent¹, apical denticular process of metatarsus; dent², subapical denticular process of metatarsus; sasp, subapical spurs of metatibia.

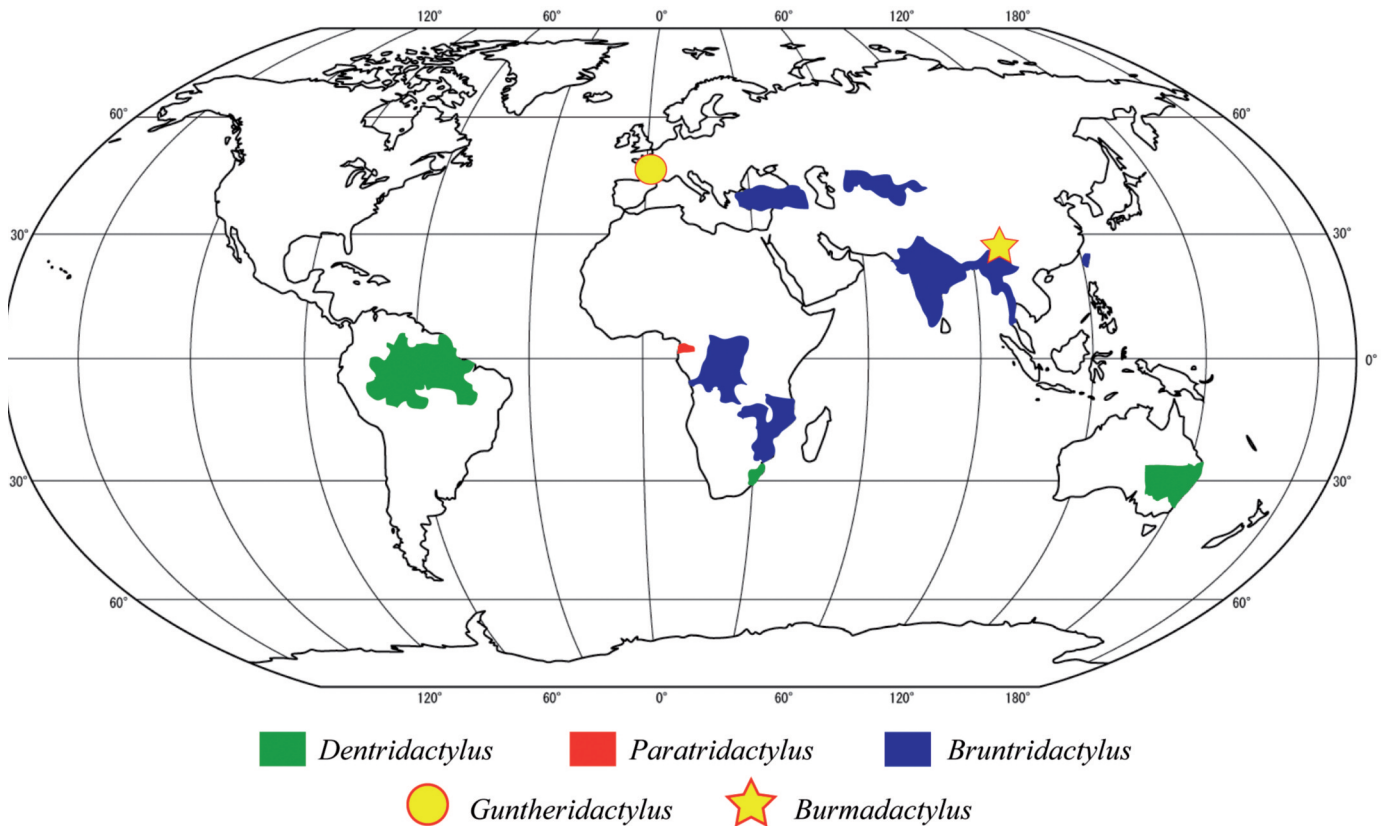
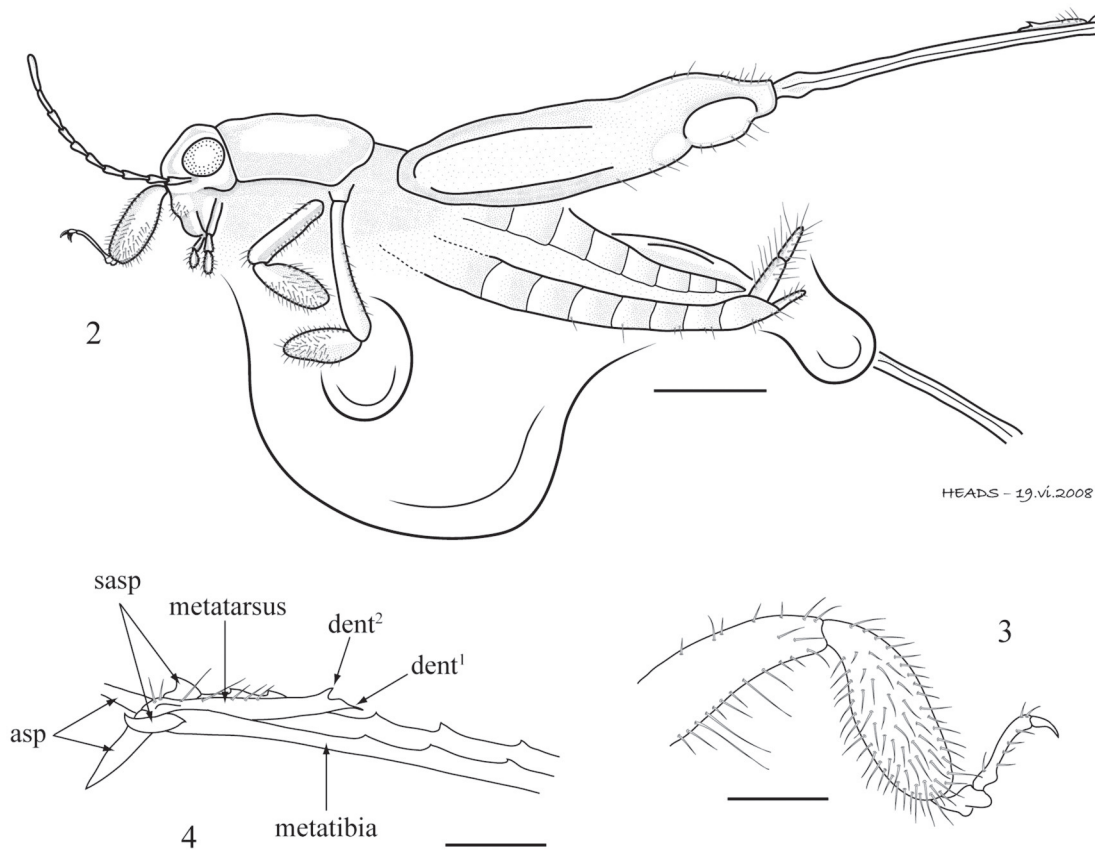


Fig. 5: Geographical distribution of Dentractylinae.

Key to the genera of Dentruidactylinae

- 1 Tegmina present 2
- Tegmina absent *Paratruidactylus* EBNER
- 2 Metatibia with swimming plates 3
- Metatibia without swimming plates 4
- 3 Antennae with only nine segments; tegmina with short longitudinal vein between costal margin and Sc and a straight longitudinal vein posterior of A1; metatibia with four pairs of swimming plates [Eocene French amber]
..... *Guntheridactylus* AZAR & NEL
- Paraproctal lobes of ♂ dorsoventrally compressed with numerous long setae, broad basally and narrowing to a blunt apex; ♀ subgenital plate not projecting posteriorly *Bruntruidactylus* GÜNTHER
- 4 Paraproctal lobes of ♂ near equal in length to the cerci, cigar-shaped; both cerci and paraproctal lobes without long setae; ♀ subgenital plate gently rounded posteriorly *Dentruidactylus* GÜNTHER
- Paraproctal lobes of ♂ much shorter than the cerci, cone-shaped, with short apical setae; cerci with numerous long setae; ♂ subgenital plate with a fringe of long setae around the posterior margin [Cretaceous Burmese amber]
..... *Burmuidactylus* HEADS

Discussion

Tridactylidae are undoubtedly an ancient group with a number of genera known from the Cretaceous (*Cratodactylus* MARTINS-NETO, 1990; *Cretoxya* GOROCHOV et al., 2006; *Mongoloxya* Gorochov, 1992; *Monodactylodes* SHAROV, 1968; and *Monodactylus* SHAROV, 1968). However, all of these genera are characterised by plesiomorphic tegminal venation, comprising numerous longitudinal veins and a rich crossvenation. Based on this feature, GOROCHOV (1992) and GOROCHOV et al. (2006) united the Cretaceous genera in the subfamily Mongoloxiinae, though its definition based on a plesiomorphy renders the monophyly of this group highly questionable. Indeed, Mongoloxiinae most probably represents a paraphyletic assemblage of stem-group taxa that gave rise to the two modern tridactylid subfamilies (and possibly the Ripterygidae) sometime in the late Mesozoic. The discovery of *B. grimaldii* confirms the antiquity of the Dentruidactylinae and supports the assertion that they, along with their likely sister-group the Tridactylinae, diversified before the mid-Cretaceous.

Burmuidactylus appears to be most closely related to *Dentruidactylus*, with both genera having a very similar arrangement of spines and spurs on the metatibiae. The geographical distribution of *Dentruidactylus* presents a classic example of austral disjunction (Fig. 5) and suggests that the genus was effected by the drifting of Gond-

wana continents during the Cretaceous; a situation not dissimilar to that of the closely related tridactylid family Cyliandrachetidae (GÜNTHER 1992; GRIMALDI & ENGEL 2005). The monotypic genus *Paratruidactylus* is known only from Equatorial Guinea and is characterised by the absence of tegmina and hindwings (GÜNTHER 1979, 1995). To date, the holotype male of *P. eidmanni* EBNER, 1943 remains the only specimen of this aberrant genus and little is known of its affinities other than its placement in Dentruidactylinae. The genus *Bruntruidactylus* is more geographically widespread than the other genera, occurring in central and southeastern Africa, Turkey, Uzbekistan, India, Bangladesh, Burma and Taiwan (Fig. 5). The fossil genus *Guntheridactylus* is known only from the Eocene French amber (AZAR & NEL 2008) and confirms the presence of Dentruidactylinae in Europe during the Cenozoic. Although the distribution of *Dentruidactylus* suggests a gondwanan origin for this genus, there is no evidence to suggest that the subfamily was restricted entirely to Gondwana. On the contrary, the discovery of *Burmuidactylus* confirms the presence of Dentruidactylinae in Laurasia during the mid-Cretaceous. Moreover, the patchy distribution of *Bruntruidactylus* across Africa and Eurasia suggests that large-scale Cenozoic extinctions might have contributed significantly to the present distributions of Old World Tridactylidae.

In summary, *Burmuidactylus* represents the first record of an essentially modern tridactylid from the Cretaceous and confirms the great antiquity of this group. Moreover, the presence of *Burmuidactylus* in Laurasia challenges the supposed Gondwanan origin for the Dentruidactylinae as suggested by the austral disjunction of *Dentruidactylus* and implies a formerly more widespread distribution for the subfamily. GRIMALDI (1992) and GRIMALDI & ENGEL (2006) showed that fossil representatives of crown group taxa can be used successfully to interpret the formerly more widespread distributions of Recent lineages. Nevertheless, a more detailed understanding of tridactylid relationships is required in order to interpret fully the interesting distribution of these fascinating and unusual orthopterans.

Zusammenfassung

Eine neue Gattung und Art der Familie Tridactylidae (Orthoptera: Caelifera: Tridactylodea, Grabschrecken) wird aus burmesischem Bernstein (mittlere Kreide) eingeführt und der Unterfamilie Dentruidactylinae zugeordnet. *Burmuidactylus grimaldii* gen. et sp. nov. ist der erste Tridactylide, der formal aus kreidezeitlichem Bernstein beschrieben wird. Die neue Gattung unterscheidet sich von allen anderen Dentruidactylinae durch ungewöhnlich kleine, paraproctale Loben bei Männchen. Ein Bestimmungsschlüssel zu den Gattungen der Dentruidactylinae wird präsentiert.

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