New Tridactyloidea in Miocene amber from the Dominican Republic (Orthoptera: Caelifera)

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Abstract. Two new Tridactyloidea of the families Ripipterygidae and Tridactylidae are described from the Early Miocene (Burdigalian) amber of the Dominican Republic, namely: *Archaeoellipes engeli* **n. gen.**, **n. sp.** (Tridactylidae: Tridactylinae) and *Mirhipipteryx antillarum* **n. sp.** (Ripipterygidae). These new taxa represent the first record of Tridactyloidea in Dominican amber and the first fossil record of Ripipterygidae, which are otherwise known only from the extant fauna.

Résumé. Nouveaux Tridactyloidea dans l'ambre miocène de la République Dominicaine (Orthoptera : Caelifera). Deux nouveaux Tridactyloidea des familles Ripipterygidae et Tridactylidae sont décrits de l'ambre miocène inférieur (Burdigalien) de la République Dominicaine. Il s'agit *Archaeoellipes engeli* n. gen., n. sp. (Tridactylidae : Tridactylinae) et *Mirhipipteryx antillarum* n. sp. (Ripipterygidae). Ces nouveaux taxa représentent le premier record de Tridactyloidea dans l'ambre dominicain et le premier record de fossile Ripipterygidae, qui sont autrement connus seulement des espèces existantes.

Keywords: Tridactylidae, Ripipterygidae, Early Miocene, Burdigalian, Hispaniola.

ridactyloidea are an ancient group with a by phylogenetic position near the base of the caeliferan radiation. The superfamily, comprising the families Cylindrachetidae, Ripipterygidae and Tridactylidae, is undoubtedly monophyletic and is defined by a suite of robust morphological characters including: the prosternum connected directly to the pronotum by means of a precoxal bridge; pro- and mesotarsi with only two tarsomeres; metatarsus reduced to a single tarsomere; absence of arolia; abdomen with nine fully sclerotised sterna in both sexes, the ninth forming a simple subgenital plate lacking styli; presence of abdominal repugnatorial glands; and the paraproct bearing distinctive cerciform lobes (secondarily lost in Cylindrachetidae) and in males prominent, highly sclerotised hooks (Rentz 1991; Heads 2009b). Tridactyloids are generally small, obscure orthopterans of cryptic habits and are characterised by their highly derived morphology, which is remarkably convergent on that of certain Grylloidea. Indeed, the tridactyloids have in the past been classified with the true mole crickets in the family Gryllotalpidae (e.g. Audinet-Serville 1838; Tillyard 1926; Tindale 1928), though their caeliferan identity has long been demonstrated

beyond any doubt (Ander 1934; Carpentier 1936; Rentz 1991). The Tridactyloidea are one of the best known groups of basal Caelifera in terms of their taxonomy, having been the focus of numerous careful revisionary studies by the late Kurt K. Günther (e.g. 1969, 1972, 1977, 1989, 1990, 1991, 1992, 1994*a*,*b*, 1995).

Morphologically, the tridactyloids share several characters in common with the Tetrigidae, including the pro- and mesotarsi with only two tarsomeres, absence of arolia, and the presence of a precoxal bridge connecting the pronotum to the prosternum. In both groups the wings are often markedly reduced or absent, but where present and well developed the hind wing has all veins unbranched except for a basal division of Cu, M closely associated or fused with R for much of its length, and a very large anal lobe with numerous anal veins. In addition, male tetrigids also have a simple subgenital plate, lacking styli and formed from the ninth abdominal sternite as in Tridactyloidea (Rentz 1991). These similarities suggest a close relationship between tetrigids and tridactyloids and several authors have united the two groups either at the superfamilial or infraordinal levels (e.g. Beier 1955; Dirsch 1961; Sharov 1968). However, recent molecular studies do not support a tridactyloid-tetrigid relationship, with most trees resolving the Tridactyloidea as sister-group to a clade comprising Tetrigoidea and Acridomorpha (e.g. Rowell & Flook 1998; Flook et al. 1999). Such

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conflict between morphological and molecular data is commonplace in the Orthoptera and is likely the result of problems in both datasets. The radiation of these groups appears to have occurred sometime in the mid to late Mesozoic, with the oldest definitive tridactyloids recorded from the Early Cretaceous, along with putative basal tetrigoids (Bouretidae, see Heads & Martins-Neto 2007). Indeed, the radiation of the basal Caelifera may well be too ancient for genes like 18S to probe effectively and problems such as longbranch attraction (Bergsten 2005) cannot be ruled out. If the original diversification of these lineages occurred rapidly in a short pulse of speciation, they would share very few DNA substitutions in common. If the initial radiation was then followed by a long period of independent evolution, then each lineage would accumulate many additional substitutions (including reversals) which may far outnumber the original synapomorphies and thereby obscure the true relationships (J. Daamgard pers. comm.). The morphological evidence for a tridactyloid-tetrigoid relationship is compelling, though certain characters such as the reduction of the pro- and mesotarsi and the loss of arolia may well be subject to some degree of homoplasy. The development of the precoxal bridge however is unlikely to be symplesiomorphic and is perhaps the strongest character uniting the two groups. Clearly more research is needed in order to elucidate their true relationships.

Fossil tridactyloids are frustratingly rare. The earliest definitive members of the superfamily are known as compression fossils from the Early Cretaceous of Brazil (Cratodactylus), Mongolia (Mongoloxya), Siberia (Monodactylus and Monodactyloides) and southern England (Cretoxya) though their affinities remain unclear. Gorochov (1992) and Gorochov et al. (2006) united all of these genera in the tridactylid subfamily Mongoloxyinae. However, this subfamily is defined solely on the basis of plesiomorphic tegminal venation and probably represents a paraphyletic grade. These Early Cretaceous genera are tridactylid-like in their gross morphology, but may represent the stemgroup to a Tridactylidae + Ripipterygidae clade (Heads 2009b). The first definitive Tridactylidae were only described very recently. The dentridactylines Burmadactylus grimaldii from mid-Cretaceous Burmese amber (Heads 2009b) and Guntheridactylus grimaulti from Early Eocene French amber (Azar & Nel 2008) constitute the only records of definitive Tridactylidae. Additional undescribed tridactyloids are known from the Early Cretaceous amber of Archingeay, southwest France (Perrichot 2004) and will form the basis of another paper (Heads & Nel in prep.). Here I describe

two new fossil tridactyloids from the Early Miocene (Burdigalian) amber of the Dominican Republic. The new taxa represent the first occurrence of Tridactyloidea in Dominican amber, with one of them constituting the first fossil record of Ripipterygidae, hitherto known only from extant species.

Material and methods

The material described here is deposited in the amber collection of the Division of Invertebrate Zoology (Entomology), American Museum of Natural History (AMNH), New York. The specimens were studied using a Zeiss stereomicroscope and drawings made with the aid of a *camera lucida*. Photomicrographs were produced using a digital SLR mounted on an Olympus stereomicroscope with the specimens immersed in oil. Terminology follows Heads (2009b). The age and origin of Dominican amber are reviewed by Itturalde Vinent & MacPhee (1996), Grimaldi & Engel (2005) and Penney (2008).

Systematic palaeontology

Family Tridactylidae Brullé 1835

The Tridactylidae are the most diverse of the three tridactyloid families comprising 16 genera and around 140 valid species. Commonly referred to as pygmy mole crickets due to their superficial resemblance to true grylloids, tridactylids and the closely related ripipterygids, are characterised by their small size (usually less than 15 mm long), disproportionately large metafemora and long, slender metatibiae. The Tridactylidae can be distinguished from the Ripipterygidae by their two-segmented male cerci (the cerci are primitively unsegmented in ripipterygids and cylindrachetids), inflated mesotibiae and by characters of the phallic complex (see for example Günther 1979). Both tridactylids and ripipterygids are generally smooth and shiny, usually black and often with white or brown patches. They frequent the margins of water bodies and construct subterranean galleries and tunnel complexes in sand or fine soils (Rentz 1991). The large, powerful hind legs are kept tightly folded when walking and digging, and serve to propel the insects out of danger when they are alarmed and when swimming on or beneath the surface of water in their riparian habitats. The close relationship between the Tridactylidae and Ripipterygidae is widely accepted and the two are often united, with Ripipterygidae as a subfamily of Tridactylidae (e.g. Gorochov 1992; Gorochov et al. 2006). However, as the relationships between these two distinct groups and the Early Cretaceous stem-group 'tridactylids' remain uncertain, it is perhaps wise to retain them as distinct families ad interim, at least until the Cretaceous forms have been revised. The Tridactylidae sensu stricto (i.e. excluding the Early Cretaceous 'Mongoloxyinae') are subdivided into two subfamilies: the Dentridactylinae and the Tridactylinae (Günther 1979).

Subfamily Tridactylinae Brullé 1835

This subfamily accounts for the vast majority of tridactylid diversity and has a cosmopolitan distribution. Distinguished from the Dentridactylinae by the absence of a subapical denticle on the metatarsus (Günther 1979; Heads 2009b) the Tridactylinae comprises 117 species in six genera: *Afrotridactylus* Günther 1994 (Africa and Madagascar); *Asiotridactylus* Günther 1995 (Central Africa and Asia); *Ellipes* Scudder, 1902 (New World); *Neotridactylus* Günther 1972 (New World); *Tridactylus* Olivier 1789 (South America, Africa, southeast Asia and Australia); and *Xya* Latreille 1809 (Africa, Europe, the Middle East, Asia and Australia).

Genus Archaeoellipes n. gen.

Type species. Archaeoellipes engeli n. sp.

Etymology. The genus-group name is formed from a combination of the Greek word *archaios* meaning 'ancient' and the extant tridactylid genus *Ellipes* Scudder 1902 to which *Archaeoellipes* is closely related (*vide infra*).

Diagnosis. Archaeoellipes can be distinguished from most other tridactylid genera by the complete absence of dorsal metatibial spines, a character shared with the New World genus *Ellipes* Scudder. However, Archaeoellipes can be separated from *Ellipes* by the absence of metatibial lamellae ('tibialblättchen' of Günther 1979; also referred to as 'swimming plates') and the well developed metatarsus. The new genus is also characterised by the shortened prothoracic leg (almost half the length of the mesothoracic leg), the acutely produced posterior margin of the terminal abdominal tergum and the unusually slender distal segment of the cercus.

Comments. Archaeoellipes constitutes the first fossil record of the subfamily Tridactylinae and is clearly



Figures 1-2

Dominican amber Tridactyloidea. 1, holotype of *Archaeoellipes engeli* n. gen., n. sp. (AMNH DR-14-1260) in oblique dorsolateral view; 2, holotype of *Mirhipipteryx antillarum* n. sp. (AMNH DR-15-193) in left lateral view.

very closely related to *Ellipes*. Both genera lack any dorsal metatibial spines, a character unique amongst the Tridactylidae but shared with the Ripipterygidae. Instead of spines, *Archaeoellipes*, *Ellipes* and the ripipterygids have longitudinal rows of short setae along the dorsolateral margins of the metatibia. The bladelike subapical and apical spurs of *Archaeoellipes* are also very similar to those of *Ellipes*, though in the latter



Figures 3-5

Archaeoellipes engeli **n. gen., n. sp. 3,** general habitus of holotype (AMNH DR-14-1260); the scale bar represents 1 mm; **4**, reconstruction of the head in anterior view and with antennal flagellae omitted; **5**, reconstruction of the terminalia in dorsal view; the fine setae on the cerci and cerciform lobes have been omitted for clarity.

genus the apical spurs are markedly longer. Despite these similarities, *Archaeoellipes* differs markedly from *Ellipes* in the absence of metatibial lamellae or 'swimming plates' and the presence of a long and well developed metatarsus. In *Ellipes* the metatarsus is vestigial, reduced to a minute nub nestled between the two subapical spurs (Günther 1977, 1979); a feature shared with the Old World genus *Xya* Latreille, though possibly of independent origin.

Archaeoellipes engeli n. sp. (Figs 1, 3–5)

Holotype. ♂: Dominican Republic: Early Miocene (Burdigalian) amber. Specimen deposited in the AMNH with accession no. DR-14-1260. Syninclusions: a mayfly (Ephemeroptera) of the family Leptophlebiidae and a small wasp (Hymenoptera). The piece of amber also contains abundant plant debris and frass.

Etymology. The specific epithet is patronymic and honours Dr Michael S. Engel (University of Kansas, USA) in thanks for his encouragement and in recognition of his numerous important contributions to the study of fossil insects.

Diagnosis. As for the genus (vide supra).

Description. Holotype ♂ (Figs 1, 3): body 3.9 mm long; pronotum 0.8 mm long at midline; tegmen 1.5 mm long (as preserved); metafemora 2.3 mm long; metatibiae 2.0 mm long. Body form typically compact. Head somewhat anteroposteriorly compressed; compound eyes large and well developed; ocelli present, minute; face broad with well defined circumocular sulci and prominent antior tentorial pits (Fig. 4); clypeus broad but narrow; antennae moniliform, 10-segmented, inserted beneath the compound eyes; maxillary and labial palpi long. Pronotum large, shield-like, with broadly rounded margins; somewhat tectate anteriorly.

Pterothorax largely disintegrated, with a large bubble developed within the cavity; left tegmen only partially preserved; Sc faint, partly obscured by the left metafemur; R prominent, taking a slightly curved path to the apex; base of A1 visible just posterior of R, though distal portion missing (posterior margin of tegmen obliterated (see Figs 1, 3). Hind wings are absent. Prothoracic leg markedly shorter than the mesothoracic leg (around half the length) and partly obscured by organic debris; protibia stout, only around half the length of the mesotibia, with anterior margin covered in short setae and bearing three short but strong dactyls. Mesothoracic leg almost twice as long as the prothoracic leg; mesofemur and mesotibia laterally compessed; mesotibia somewhat inflated with longitudinal rows of very short and evenly spaced setae on the anterior margins. Proand mesotarsi both with prominent and well sclerotised claws. Metafemur large, strongly inflated; prominent dorsal carina with distinctive white pigmentation; genicular lobes large and well developed. Metatibia long, slender, strongly quadrate in section with prominently raised dorsolateral margins bearing rows of short, black setae; spines and distal lamellae (so-called 'swimming plates') are entirely absent; one inner and one outer subapical spurs, both 0.48 mm long; apical spurs large, bladelike, 0.83 mm long, with rows of marginal setae; metatarsus well developed, slightly curved ventrally, 0.52 mm long. Abdominal terga are generally uniform and prominently convex medially, though lacking carinae; the ventral surface of the abdomen is largely obscured by the remains of a leptophlebiid mayfly and general turbidity of the amber, though the sterna appear simple. Terminal abdominal tergite with a distinct, diamond-shaped dorsal depression bordered by short setae; posterior margin acutely produced; epiproct small, lobate, with numerous marginal setae and a single, long apical seta (Fig. 5); paraproctal hooks strongly curved, blunt. Partly obscured by cerci and epiproct; cerci 0.65 mm long, proximal segment broad basally and covered with fine setae, distal segment very slender, narrowing to a pointed apex, with notably fewer setae; cerciform lobes of the paraproct approximatel 0.5 mm long, somewhat broader than the cerci and slightly curved, with a light covering of short setae; subgenital plate largely obscured, though clearly projects beyond the apex of the epiproct.

Family Ripipterygidae Ander 1939

The Ripipterygidae are almost cryptically similar in gross morphology to their close relatives the Tridactylidae and are considered by some (e.g. Gorochov 1992; Gorochov et al. 2006) as a subfamily of the latter. Although their relationship with the Tridactylidae is unquestioned, the ripipterygids nevertheless constitute a distinct group regardless of taxonomic rank, characterised by primitively unsegmented cerci, distinctive apical setae on the cerciform lobes and the prominent dorsolateral lobes of the epiproct bearing numerous, comblike transverse rows of teeth. Ripipterygidae can also be differentiated from the tridactylids by their uninflated mesotibiae and their unique phallic complex. The family was most recently revised by Günther (1969) who recognised some 68 species in two genera: Ripipteryx Newman 1834 and Mirhipipteryx Günther 1969.

Genus Mirhipipteryx Günther 1969

Mirhipipteryx Günther 1969: 365 **Type species.** *Ripipteryx pulicaria* Saussure 1896.

Diagnosis. *Mirhipipteryx* can be separated from *Ripipteryx* by its smaller body size (*Mirhipipteryx* 3.0–5.5 mm long; *Ripipteryx* 6.0–14.0 mm long); smaller interocular distance, equating to roughly half the diameter of the compound eyes; and the apical metatibial spurs at least twice as long as the metatarsus (the spurs are usually equal in length or only slightly longer than the metatarsus in *Ripipteryx*). *Mirhipipteryx* species are usually dark brown or black but lack the bright white markings typical of *Ripipteryx*, ocassionally possessing numerous dull yellow spots instead. Moreover, the elaborately modified cerciform lobes of the paraproct often seen in species of *Ripipteryx* are unknown in *Mirhipipteryx* (Günther 1969). The genus includes some 25 species distributed throughout Central America and northern and central parts of South America.

Mirhipipteryx antillarum n. sp. (Figs 2, 6)

Holotype. I Dominican Republic: Early Miocene (Burdigalian) amber. Specimen deposited in the AMNH with accession no. DR-15-193. The piece of amber is run through with several large fractures and is therefore quite fragile.

Etymology. The specific epithet means 'of the Antilles'.

Diagnosis. Mirhipipteryx antillarum is almost cryptically similar to the type species *M. pulicaria* (Saussure) but can be distinguished from the latter species by the prominent dorsal inflation of the terminal abdominal tergum, somewhat smaller paraproctal hooks and the unusual, apically hooked cerci. The holotype of *M. antillarum* also lacks the yellowish antennal segments of *M. pulicaria*, though this may be an artifact of preservation.

Description. Holotype \mathcal{J} (Figs 2, 6): body 4.4 mm long; pronotum 1.2 mm long at midline; tegmen 0.8 mm long; hind wing 2.4 mm long; metafemora 2.0 mm long; metatibiae 1.9 mm long. Body form typical of Mirhipipteryx, small and somewhat laterally compressed. The entire specimen is a dull dark brown and does not appear to have any distinctive markings. The head has been almost completely ground away, presumably during polishing of the amber; compound eye large, globose; antenna ten-segmented, scape robust, pedicel apically concave, flagellomeres, slender basally, broad apically; mouthparts mostly obliterated, labial palpi normal. Pronotum large and shield-like with a broadly rounded posterior margin; precoxal bridge of prosternum well developed and easily visible laterally. Tegmina strongly sclerotised with covering of stout setae; venation indistinct. Hind wings around three times as long as tegmina; remigium strongly sclerotised with a row of fine, evenly spaced short setae running along CuP; posterior part of hind wings typically hyaline and tightly folded. Profemur subcylindrical in section, approximately two thirds the length of the mesofemur; protibia laterally compressed with three prominent apical dactyles on the anterior margin; protarsus two-segmented, with slender claws. Mesofemur subcylindrical in section with well developed, spine-like genicular lobe bearing



Heads, 2009

Figure 6

Mirhipipteryx antillarum **n. sp.** Lateral view of holotype terminalia (AMNH DR-15-193); note the prominent paraproctal hook and distinctly setose cerciform lobes. The subgenital plate has moved somewhat ventrally, probably due to the development of a large bubble in the amber. The scale bar represents 0.1 mm.

five or six stout setae ventrally; mesotibia somewhat laterally compressed, without apical dactyls; mesotarsus markedly longer than protarsus, with long, robust claws. Metafemur typically large and somewhat laterally compressed with well developed genicular lobes bearing numerous short setae; metatibia very slender, quadrate in section, with dense rows of setae on the dorsal margins and a patch of ventral setae basally; subapical spurs blade-like, around three quarters the length of the metatarsus; apical spurs blade-like, a little over twice as long as the metatarsus with rows of dense marginal setae; metatarsus lamellate, with a fine apical spine. Terminal abdominal tergum dorsally inflated, with a narrow dorsal depression running anteriorly from the posterior margin; epiproct with distinctive dorsolateral lobes bearing at least six comb-like rows of teethlike setal processes; cerci 0.27 mm long, with few long and fine setae and small apical hooks (see Fig. 6); paraproctal hooks prominent and well sclerotised, 0.07 mm long; cerciform lobes 0.28 mm long, slightly curved basally, with one subapical and five apical ventral setae, long and slender. The subgenital plate appears to be somewhat curved distally, but is largely obscured by the development of a large bubble.

Comments. Mirhipipteryx antillarum constitutes the first fossil record of the Ripipterygidae which were hitherto known only from the extant fauna. Moreover, the assignment of the new species to an extant genus attests the antiquity of the family. As stated above, M. antillarum is very similar to M. pulicaria and the two species appear to be closely related. Nevertheless, M. antillarum is clearly a distinct species, characterised by the unusual hooks present on the apices of the cerci (see Fig. 6); a feature unique to this species. Today, the Ripipterygidae are widely distributed throughout Central and South America, though are absent from the West Indies with the exception of *M. pulicaria* interposita Günther 1969 which has been collected from Trinidad. The discover of *M. antillarum* in Dominican amber confirms the presence of ripipterygids on Hispaniola during the Early Miocene.

Discussion

Orthoptera are relatively abundant and diverse in Dominican amber and a number of taxa have been documented, including trigonidiine now phalangopsine gryllids, a mogoplistid, an and episactine eumastacid and two genera of cladonotine tetrigids (Vickery & Poinar 1994; Pérez-Gelabert et al. 1997; Heads 2009a, 2010). In addition, there are a number of specimens that still await formal description including several tettigoniid nymphs and a mole cricket (Gryllotalpidae). Interestingly, a number of the taxa known from Dominican amber are ground-dwelling (e.g. phalangopsine Gryllidae, Gryllotalpidae, Tetrigidae) and this is also true of the new Tridactyloidea described here. This suggests that resin was occassionally secreted directly onto the forest floor, trapping a wide variety of litter-dwelling organisms; a scenario not dissimilar to that suggested

by Perrichot (2004) for the Early Cretaceous amber of Archingeay, France. Nevertheless, ground-dwelling Orthoptera are still very rare and the Dominican amber orthopteran assemblage is clearly dominated by the abundant arboreal Trigonidiinae (Gryllidae).

Tridactyloidea are not particularly diverse in the West Indies with only *Ellipes minuta* (Scudder) known from Hispaniola today (Pérez-Gelabert 2008), so the discovery of two fossils representing two families in Dominican amber is quite remarkable. As discussed above, Archaeoellipes is clearly closely related to Ellipes and its presence on Hispaniola during the Miocene suggests a long association of tridactylines with the island. In contrast, Ripipterygidae are almost entirely unknown from the West Indies. Mirhipipteryx pulicaria interposita has been reported on Trinidad, though its distribution suggests that it arrived there fairly recently, probably from Venezuela (Günther 1969). Nonetheless, the discovery of *Mirhipipteryx* in Dominican amber suggests that the genus was more widespread during the Miocene and has subsequently become extinct in the West Indies.

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