

An archaic new genus of Evaniidae (Insecta: Hymenoptera) and implications for the biology of ancestral evanioids

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SYNOPSIS. A new genus and species of Evaniidae (Hymenoptera: Insecta) is described from Burmese amber (probably Late Cretaceous) and its phylogenetic affinities are discussed. Possession of a swollen and highly modified hind tibia suggests the presence of a large subgenual organ, which is used among recent Hymenoptera to detect vibrations from concealed, xylophagous hosts. Possession of a large mesosoma, short metasoma and a well-developed petiole are derived characters shared with extant Evaniidae. The multi-segmented antenna (with more than 14 antennomeres) and complete wing venation are plesiomorphic characters of the genus and are indicative of a basal position within the family.

INTRODUCTION

The systematic position of the family Evaniidae, or ensign wasps, has long been subject to disagreement. Although evaniids have traditionally been classified within the Apocrita, they were sometimes treated as a family closely related to Proctotrupoidea (Townes, 1949 – as Serphoidea) or placed with a mixture of taxa including some proctotrupoids, ichneumonoids, stephanoids, trigonaloids and megalyroids (Bradley, 1908). However, a separate superfamily, the Evanioidea, comprising the Evaniidae together with two other extant families, the Aulacidae and Gasteruptiidae, has been widely accepted (e.g. Crosskey, 1951; Gauld & Bolton, 1988; Hanson & Gauld, 1995).

Two extinct families, the Praeaulacidae (Rasnitsyn, 1972) and the Cretevaniidae (Rasnitsyn, 1975), known from the Upper Jurassic and Lower Cretaceous, and from the Lower and mid-Cretaceous respectively, have also been placed in the superfamily. One synapomorphy that has been proposed to unite both extinct and extant families is the possession of a small propodeal foramen situated far above the coxal foramina (e.g. Königsmann, 1978; Rasnitsyn, 1988). This character, the high attachment of the metasoma on the mesosoma, may be homoplastic as it also occurs in several disparate ichneumonoid, cynipoid and chalcidoid lineages. Another putative synapomorphy proposed for the monophyly of the superfamily, the loss of all functional metasomal spiracles except for the eighth (Gauld & Bolton, 1988), is also more widely distributed (Gibson, 1986), and has been hypothesised as a synapomorphy for a larger clade embracing the infraorders Evaniomorpha and Proctotrupomorpha, that is, all Apocrita except Ichneumonoidea and Aculeata (Rasnitsyn, 1988).

The Praeaulacidae has been proposed as representing the ances-

tral group of the whole Evanioidea because of the absence of any apparent synapomorphy (Rasnitsyn, 1988), while the other families (Gasteruptiidae, Aulacidae, Evaniidae and Cretevaniidae) form a monophyletic clade united by a number of synapomorphies, including 14-segmented antennae, medially short pronotum, loss of median mesoscutal sulcus, and very reduced hindwing venation. However, the fossil described here invalidates the first of these (14-segmented antennae).

The Gasteruptiidae and Aulacidae, considered by Rasnitsyn as one family, may form a sister group to the Evaniidae + Cretevaniidae, with the following inferred synapomorphies. Gasteruptiidae *sensu* Rasnitsyn have gained a semicircular pterostigma (apparently reversed in some extant forms) and, less certain, sexually dimorphic flagellomere number (14 in female, 13 in male, though the latter is not quite certain for the Mesozoic fossils). The Evaniidae and Cretevaniidae are united by their characteristic synapomorphic habitus with a large head not situated at the end of a long 'neck' (and therefore probably only weakly movable), high and short mesosoma, and short metasoma with long, tubular petiole. Several other putative synapomorphies are rendered invalid by the fossil described below. The synapomorphies postulated for the monophyly of Evaniidae (Rasnitsyn, 1988) or Evaniidae + Trigonalidae (Basibuyuk & Quicke, 1995), have all either been invalidated by subsequent fossil findings (Basibuyuk *et al.*, in press, and below), or not yet confirmed in any Cretaceous fossils e.g. jugal lobes in both wing pairs and modified antennal cleaner. This draws the monophyly of Evaniidae into question with respect to Cretevaniidae, but until wing and antenna cleaner structures become known in the Mesozoic Evaniidae, we are employing a conservative approach and retain the family rank for Cretevaniidae.

The Evaniidae contains about 17 genera and 500 described species with a more or less cosmopolitan distribution, but the majority of

species occur in the tropics. As the classification of the group is still largely based on Kieffer (1912), the validity of many genera is questionable (Huben, 1995). Until recently, the known extinct species of the family were attributed to the extant genera *Evania* (Burmeister, 1831; Brues, 1933) and *Brachygaster* (Brischke, 1886), but two new genera from Late Cretaceous, New Jersey amber have recently been described (Basibuyuk *et al.*, in press). Another Mesozoic fossil, *Praevania* Rasnitsyn, possibly also belongs to the Evaniidae, and is known from the middle Lower Cretaceous of Mongolia (Rasnitsyn, 1991).

Here, we describe a distinctive new species of evaniid belonging to a new genus from Burmese amber. The fossil described has a considerable part of the head distorted while the legs, meso- and metasoma are covered with organic debris. Nevertheless those observable characters, notably the modified hind tibia, forewing venation and antennal morphology, are sufficient to distinguish this insect from all other known evaniid genera. It has several forewing and antennal features that are plesiomorphic for the whole of the Evanioidea, as well as several characters that are synapomorphic for the Evaniidae. This fossil, together with the two new genera described from New Jersey amber, permits us to suggest possible transitions leading to modern evaniids.

The material studied is in the Department of Palaeontology, The Natural History Museum, London, U.K. Morphological terminology largely follows Gauld & Bolton (1988).

Family EVANIIDAE Latreille, 1802

Genus *MESEVANIA* Basibuyuk & Rasnitsyn, gen. nov.

TYPE SPECIES. *Mesevania swinhoei* Basibuyuk & Rasnitsyn, sp. nov., here designated.

NAME. Combining meso, meaning middle, with *Evania*, in reference to this being a primitive Mesozoic evaniid. The name is feminine.

DIAGNOSIS. Female. Size small (body length about 3 mm). Mesosoma and metasoma not heavily sclerotized (Figs 1, 2). Antenna with more than 15 segments, clavate, not elbowed; antennal

insertion slightly above the mid point of eye, inserting on slight shelf; scape and pedicel short, first flagellar segment not much longer than any of the following six segments (Fig. 3a). Pronotum short medially. Petiole joining propodeum at a point much closer to metanotum than to hind coxa (Fig. 2). Forewing venation complete, with 10 enclosed cells (Fig. 3c); veins 2m-cu and 3rs-m present, veins 2rs-m and 3rs-m bordering an hexagonal 3rd submarginal cell; vein M & Rs (basal vein) straight, not angled at junction of veins M and Rs, meeting vein R well before pterostigma, meeting vein M+Cu much closer to pterostigma than to wing base; vein 1m-cu meeting 2nd submarginal cell well beyond its base; vein M angled at junction with vein 1m-cu forming a pentagonal 2nd submarginal cell; vein Rs angled at junction with 3rd submarginal cell, otherwise straight, reaching the anterior margin of wing (Fig. 3c). Hindwing venation presumably reduced, only indications of veins R and M+Cu can be seen, with few (4 or 5) distal hamuli. Fore tibia enlarged apically with outer face compressed (but this may be due to deformation of the leg) (Fig. 3a). Hind tibia highly modified; expanded and compressed apically, its inner face with a finely striate, mirror-like structure. Tarsi of all legs 5-segmented (Fig. 3b). Metasoma short, longer than petiole, ovate. Ovipositor exerted (Fig. 2).

REMARKS. The peculiar modification of the hind tibia is the single most prominent character of the new genus (Fig. 3b). Whether the swollen tibia is a synapomorphy of *Mesevania*, or a symplesiomorphy, is difficult to say (see Discussion below). In addition to the tibial swelling, several other characters of *Mesevania* are also unusual for the Evaniidae, notably the very complete forewing venation and the multi-segmented antenna with a short scape. *Mesevania* differs from the rest of the Evaniidae (including the two new genera from New Jersey amber; Basibuyuk *et al.*, in press) in having the forewing with 10 enclosed cells, veins 2m-cu and 3rs-m being present (see Figs 4a, c–e) and in having the antenna without an elbow, multi-segmented, and with a short scape. A relatively complete forewing venation, particularly the presence of veins 2m-cu and 3rs-m, is the ground plan character state for Evanioidea, as represented by the Praeaulacidae and Aulacidae (Figs 4f–h). *Praevania sculpturata*



Fig. 1 *Mesevania swinhoei* new species, holotype, In.20192, Burmese amber. Forewing length 2.4mm.

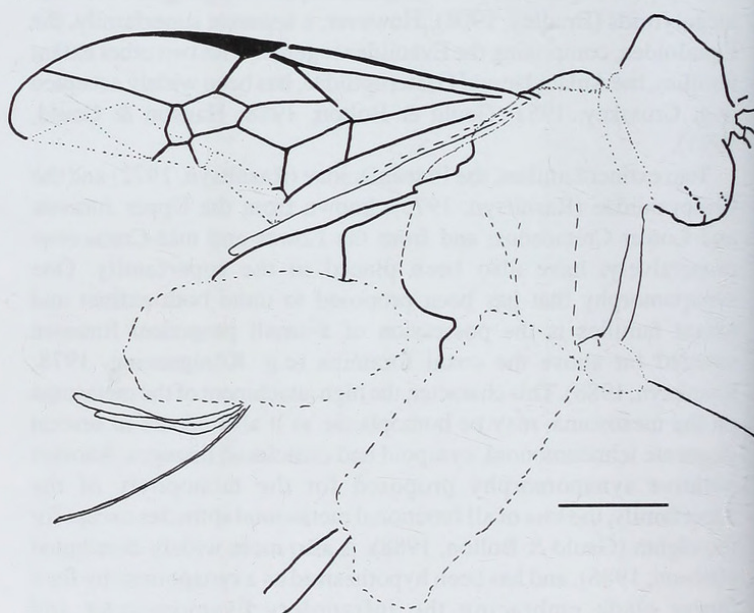


Fig. 2 *Mesevania swinhoei* new species, holotype (Scale: 0.5 mm) In.20192, Burmese amber. Lateral aspect.

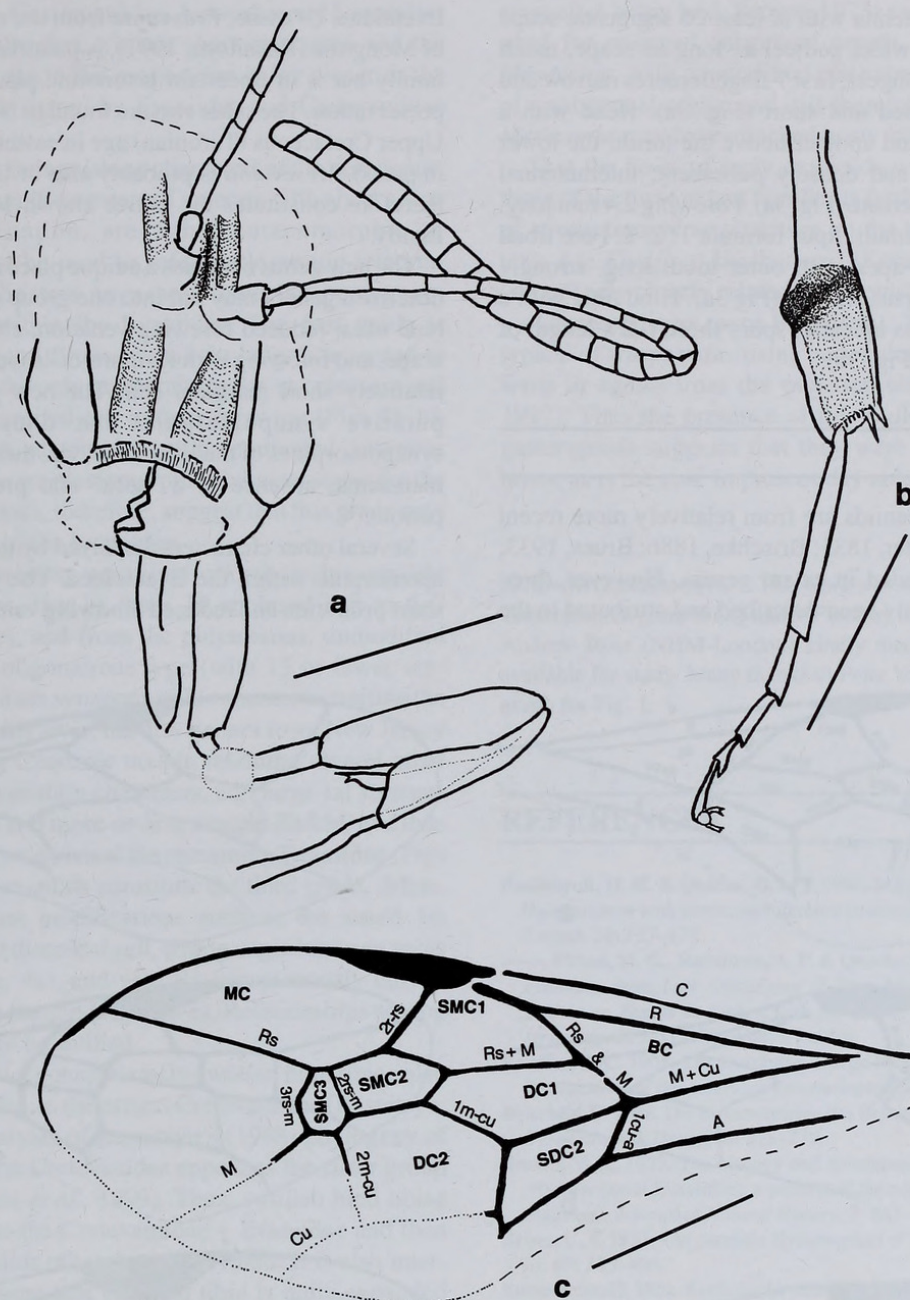


Fig. 3 *Mesevania swinhoei* new species, holotype (Scales: 0.5 mm) In.20192, Burmese amber. **a**, Head, antenna and foreleg; **b**, Hind tibia, inner face; **c**, Forewing veins and cells. Cell names. BC: basal cell, DC: discoidal cell, MC: marginal cell, SDC: subdiscoidal cell, SMC: submarginal cell.

Rasnitsyn, from the Lower Cretaceous of Mongolia (Rasnitsyn, 1991), is possibly similar to *Mesevania* in this respect. Although the only known fossil of *Praevania* is incomplete, it can be distinguished easily from *Mesevania* in having a long 3rd submarginal cell, forewing vein 2r-rs being closer to vein 2rs-m (Fig. 4b), and in having a much longer ovipositor. Polymerous antenna can also be seen in the *Praevania*. The shape of the scape of *Mesevania* is rather similar to that of aulacids, though much shorter. *Mesevania* can be differentiated from the *Praevania* by the short pronotum and by the insertion of the petiole closer to the metanotum. *Cretevaniidae* differ from *Evaniidae* (including *Mesevania*) by the petiole being expanded subapically, and by the very different forewing venation with a narrow marginal cell and straight vein Rs which is more or less in line with 1rs-m. Unfortunately, a prominent synapomorphy known for the *Evaniidae*, the presence of the jugal lobe at the base of both fore- and hindwing, cannot be seen in the specimen described here

because of the orientation of the inclusion. However, the massive mesosoma, lack of a conspicuous 'neck', presence of a long and slender petiole, high attachment of metasoma to propodeum, small metasoma and relatively short ovipositor, together with its general habitus, best relate this new genus to the *Evaniidae*.

***Mesevania swinhoei* Basibuyuk & Rasnitsyn, sp. nov**

Figs 1–3

NAME. After R.C.J. Swinhoe, who presented the holotype to The Natural History Museum in 1920.

TYPE MATERIAL. Holotype In.20192, Department of Palaeontology, NHM, London.

LOCALITY AND HORIZON. Burmese amber, probably Upper Cretaceous, Hukawng Valley, Myanmar (Burma) (for details, see Zherikhin & Ross, this volume).

DESCRIPTION. Female. Antenna with at least 26 segments; scape stout and short, as long as wide; pedicel as long as scape, much narrower; 1st flagellomere longest; first 7 flagellomeres narrow and long, the remainder thickened and short (Fig. 3a). Head with a longitudinal furrow below and another above the toruli, the lower furrow strongly developed and densely pubescent; interantennal carina present; mandible tridentate (Fig. 3a). Forewing 2.4 mm long. Hindwing with 4–5 distal hamuli. Spur formula 1: 2: 2. Fore tibial spur modified; bifurcate at apex with outer tooth long, strongly enlarged at base; fore basitarsus slender (Fig. 3a). Hind tibia with a transverse row of short spines apically; spurs short, 0.2 x length of basitarsus. Claws bifurcate (Fig. 3b).

DISCUSSION

Most of the known fossil evaniids are from relatively more recent geological periods (Burmeister, 1831; Brischke, 1886; Brues, 1933; Poinar, 1992), and are included in extant genera. However, three Mesozoic genera have recently been described and attributed to the

Evaniidae. Of these, *Praevania* from the middle Lower Cretaceous of Mongolia (Rasnitsyn, 1991), is putatively the oldest genus in the family but is of uncertain taxonomic placement owing to its poor preservation. The other two are found in New Jersey amber of lower Upper Cretaceous (Turonian) age in eastern USA (Basibuyuk *et al.*, in press). *Mesevania* is probably also of Upper Cretaceous age and therefore constitutes the fourth known Mesozoic member of this family.

The new genus occupies a unique place in the Evaniidae. All other described genera may fall into one group on the basis of the simple hind tibia, reduced forewing venation, elbowed antenna with long scape, and forewing with Rs more-or-less anteriorly curved and with relatively short marginal cell. The new genus has none of these putative synapomorphies but does possess some other synapomorphies of the Evaniidae, viz. the massive mesosoma, short metasoma, absence of a 'neck' and presence of a conspicuous petiole.

Several other characters displayed by the new genus appear to be apomorphic within the Evanioidea. The possession of a medially short pronotum and reduced hindwing venation are synapomorphies

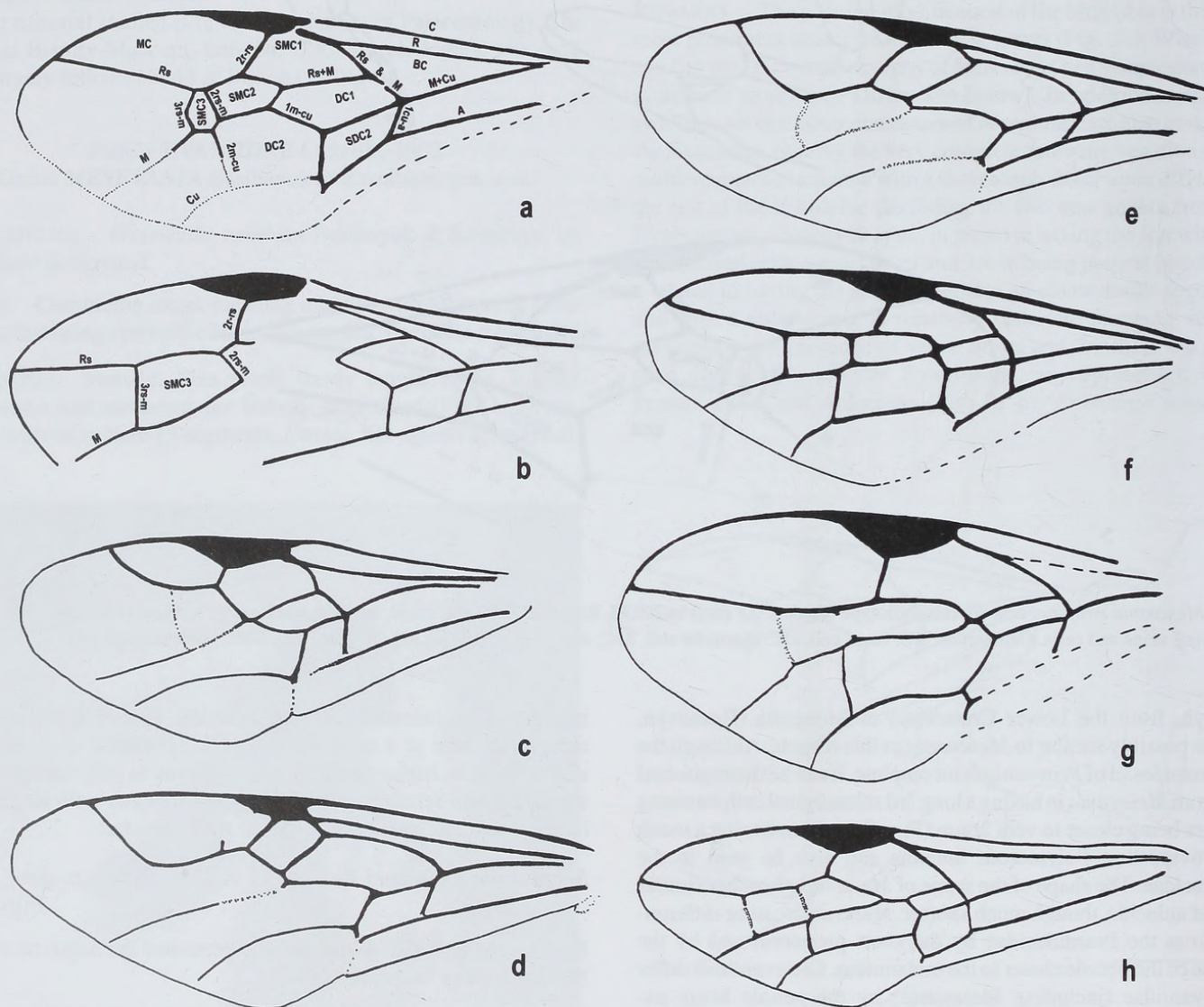


Fig. 4 Forewing venation in selected taxa of Evanioidea. **a**, *Mesevania swinhoei* new species (Evaniidae); **b**, *Praevania sculpturata* Rasnitsyn, illustration constructed from both left and right wings (Evanioidea incertae sedis); **c**, New species from New Jersey amber (Evaniidae); **d**, *Evania appendigaster* (L.) (Evaniidae); **e**, *Prosevania* sp. (Evaniidae); **f**, *Praeaulacinae* gen. sp. (Paleontological Institute, Moscow no. 4270–1544: Lower Cretaceous) (Praeaulacidae); **g**, *Baissa magna* Rasnitsyn (Gasteruptionidae); **h**, *Aulacus longiventris* Kieffer (Aulacidae).

uniting the Cretevaniidae, Gasteruptiidae, Aulacidae and Evaniidae, but excluding the Praeaulacidae, while a short metasoma and the attachment of the metasoma to the propodeum being closer to the metanotum are characters shared by Evaniidae and Cretevaniidae (see above).

The most conspicuous distinguishing characters of the new genus, viz. modified hind tibia, multi-segmented antenna with short scape and complete wing venation, are either autapomorphic or plesiomorphic and cannot be used to infer phylogenetic relationships (see Figs 3a–c). At the same time, these characters permit us to recognise three grades within the Evaniidae. The first grade is composed by *Mesevania* and *Praevania* (if the latter is assigned to the Evaniidae), which are the only taxa retaining 3rs-m crossvein and thus the closed 3rd submarginal cell in their forewing (Figs 4a–b). Likewise, the possession of simple, multi-segmented antennae together with a short scape are plesiomorphic character states for the Evanioidea. These conditions, therefore, suggest that this grade may represent the stem group of the Evaniidae.

The transition of the forewing venation from relatively complete to less complete venation, that is, from 10 enclosed cell to 6–7 enclosed cells (Figs 4c–e), and from the polymerous, unmodified antenna to the elbowed, oligomeric type (with 13 or fewer segments), indicates that there are synapomorphic characters uniting the remaining Evaniidae. At this level, the new genera from New Jersey differ from the remaining Cenozoic taxa in retaining several other plesiomorphic forewing venation characters, e.g. large 1st submarginal cell, wide basal cell, and more-or-less straight Rs&M, and thus form a grade between *Mesevania* and the remaining Evaniidae (Figs 4c cf. 4d). The Cenozoic evaniids constitute the third grade, delimited by further venational modifications such as the small 1st submarginal cell, large 1st discoidal cell, strong angle between veins Rs and M (Rs & M: Fig. 4a), and vein Rs conspicuously curved towards the anterior wing margin (Figs 4d–e). Relationships among Cenozoic genera are yet to be studied.

In addition to *Mesevania*, conspicuously swollen hind tibiae also occur among the Evanioidea, in the extinct Cretevaniidae (Rasnitsyn, 1975). In the recent reanalysis of Rasnitsyn's (1988) phylogeny of hymenopteran families, the Cretevaniidae appear as the sister group to the Evaniidae (Ronquist *et al.*, 1999). Thus, swollen hind tibiae may be plesiomorphic for the Cretevaniidae + Evaniidae and then subsequently lost in evaniids other than *Mesevania*. It is also interesting in this context to note that the hind tibia is quite expanded distally in male and female gasteruptiids, putatively the sister group of Cretevaniidae + Evaniidae. The function and internal structure of the swollen tibial apex in gasteruptiids, which differs somewhat from that of *Mesevania* in lacking a plate structure, is currently unknown and warrants detailed investigation.

The hind tibial modification of *Mesevania* is also of particular interest because of its implications for host use by early Evaniidae (and Cretevaniidae). The only hosts of extant evaniids are cockroach oothecae (Brown, 1973), though other extant evanioids have very different biologies: aulacids being koinobiont endoparasitoids of wood-boring sawflies and beetles while gasteruptiids are cleptoparasitoids of solitary bees and masarine wasps (Haack & Wilkinson, 1987; Naumann & Cardale, 1987; Gauld & Bolton, 1988). The swollen hind tibiae of *Mesevania* are rather similar, at least superficially, to those of the fore leg in female Orussidae, and to a lesser extent, those of the hind legs of Stephanidae. Tibiae swollen in this way, at least in extant taxa, usually indicate the presence of large subgenual organs, which are important in detecting substrate-borne vibrations, and are typically most well developed in females of taxa attacking vibration-producing, xylophagous hosts. Modern evaniid hosts do not produce vibrations (as the oothecae are attacked

soon after being laid: Brown, 1973) and so extant evaniids have no need for enlarged subgenual organs. The swollen hind tibia of *Mesevania*, with its modified plate structure, suggests the presence of a subgenual organ, and it is therefore tempting to speculate that *Mesevania* may have attacked hosts other than cockroach oothecae.

That the hosts of early evanioids were generally different from those of the three extant families is further suggested by the presence of strong transverse sculpture on the mesoscutum in some extinct taxa, e.g. *Kotujisca kholbotensis* (Kotujellitinae) (Rasnitsyn, 1991) (supposedly closely related to the putative ancestor of gasteruptiids — Gasteruptiinae *sensu* Rasnitsyn). This mesoscutal sculpture is typical of wasps parasitising endoxylous hosts and perhaps aids the wasp in egress from the pupation site (Eggleton, 1989; Quicke, 1997). Thus the presence of this sculpture in putatively ancestral gasteruptiids suggests that they were parasitoids of wood-boring hosts, as is the case in present day aulacids.

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