A revision of the family Rhachiberothidae Tjeder, 1959, stat.n. (Neuroptera)

U. ASPÖCK and M. W. MANSELL* Naturhistorisches Museum Wien, Vienna, Austria, and *Plant Protection Research Institute, Pretoria, South Africa

Abstract. The subfamily Rhachiberothinae Tjeder, 1959, originally included in the Berothidae and recently transferred to the Mantispidae, is revised and elevated to family rank. A historical review and redescriptions of the family Rhachiberothidae stat.n. and of the genera Rhachiberotha Tjeder, 1959, and Macroberotha Tjeder, 1959, are presented. Five new species, R. ingwe, R. sheilae, M. aethiopica, M. angolana and M. minteri, are described and differentiated from the five hitherto-known species. The hypothesis of a sister-group relationship of the Rhachiberothidae to the Berothidae is re-established. The phylogenetic position of the Dilaridae as an adelphotaxon of the monophyletic group ([Rhachiberothidae + Berothidae] + Mantispidae) is discussed.

Introduction

The Rhachiberothidae are an intriguing and enigmatic group of insects whose phylogenetic relationships and systematic status have evoked lively debate since they were first described by Tjeder in 1959. Although originally tentatively placed as a subfamily of the Berothidae, their striking similarity to symphrasine Mantispidae raised questions about their possible affinities with mantispids. The identity and monophyly of both these families had never been questioned before Tjeder’s (1959) paper, despite the lack of defined autapomorphic characters which the discovery of Rhachiberothinae demanded.

The present study was initiated to address these issues, and to document the new taxa and data which have accumulated since Tjeder’s (1959, 1968) studies. During the course of our investigations all available specimens of Rhachiberothinae, including the types, and data were studied.

However, before this work could be published, Willmann (1990) transferred the Rhachiberothinae to the Mantispidae after studying only the holotype of Macroberotha fasciata Tjeder. His arguments have been carefully assessed, relative to the comprehensive material now available to us, and are discussed below. We still argue in favour of a sister-group relationship with the Berothidae, based upon synapomorphies of larvae and adults which are more convincing than the raptorial forelegs in terms of parsimony. We further propose that the Rhachiberothinae be elevated to full family rank.

This paper includes a historical review of the subject, a revision of the Rhachiberothidae with descriptions of five new species and a discussion of the phylogenetic relationships of the Rhachiberothidae, Berothidae, Mantispidae and Dilaridae, and their relevant autapomorphies and synapomorphies.

The study is based on 170 specimens, including eight holotypes, in the following collections: The Natural History Museum, London, England (BMNH); California Academy of Sciences, San Francisco, California (CASC); H. & U. Aspöck Collection, Vienna, Austria (HUAC); L. R. Minter Collection, Pietersburg, South Africa (LRMC); Naturhistorisches Museum Wien, Vienna, Austria (NHMV); National Museum of Zimbabwe, Bulawayo, Zimbabwe (NMBZ); Natural Museum, Pietermaritzburg, South Africa (NMSA); P. Ohm Collection, Kiel, Germany (POCG); R. B. Miller Collection, Project City, California, U.S.A. (RBMC); National Collection of Insects, Pretoria, South Africa (SANC, accession code AcNE); Staatliches Museum für Naturkunde, Stuttgart, Germany (SMSG); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Zoological Institute, Lund University, Lund, Sweden (ZILS); Institut und Zoologisches Museum, Hamburg, Germany (ZMUH).

Terminology and abbreviations are as follows: A1–A3, anal veins; bc, bursa copulatrix; C, costa; c, ninth gonocoxite; cat., catalogue; charact., characterization; chor., chorology; com, comment; CuA, anterior cubitus; CuP, posterior cubitus; cuA-cup, crossovein; descr, description; e, ectoproct; f, penisfilum; fe, femur; fig, figure; foss, fossil; g, gonarcus; gl, gonapophysis lateralis; h, hypandrium internum; M, median; MA, anterior median; MP, posterior

Correspondence: Dr U. Aspöck, Zweite Zoologisch Abteilung, Naturhistorisches Museum Wien, Burgring 7, A-1014 Wien, Postfach 417, Austria.
Tjeder (1968) did not think that these similarities indicated time. Tjeder noted that a considerable degree of sexual homology of the similar penisfilum in the two genera. He could clearly be referred to the Berothidae. Similarities in the foreleg, are insignificant as they also occur in many other, distantly related, groups of Neuroptera. Despite their criticism of Tjeder's arguments, they agreed with him in main ideas of relationships. They interpreted the synapomorphies. MacLeod & Adams (1967) indicated that some of the characters in Tjeder's list of similarities, such as the pectinate branching pattern of Rs in the forewing, the presence of trichosors, the occurrence of similarly shaped mouthparts and the similarity of the distal tarsomere of the foreleg, are insignificant as they also occur in many other, distantly related, groups of Neuroptera. Despite their criticism of Tjeder's arguments, they agreed with his main ideas of relationships. They interpreted the similarities of many structures in the male genitalia of Berothidae and Mantispidae as parallelism in more highly developed representatives of both families.

Upon the discovery of males of Mucroberotha and the description of the new species M. vesicaria and M. nigrescens, Tjeder (1968) revived the discussion on the systematic position of the Rhachiberothinae. He was, however, unaware of MacLeod & Adam's (1967) paper at the time. Tjeder noted that a considerable degree of sexual dimorphism in the wing (vesicae) and in the foretarsus of Mucroberotha not only accentuated the peculiarity of the subfamily, but also aggravated the uncertainty surrounding their systematic status. Whereas the genital segments and the foretarsus of male Mucroberotha are strikingly similar to those of Trichoscelia Westwood (Platymantisinae), Tjeder (1968) did not think that these similarities indicated closer relationship between them, nor did he believe in the homology of the similar penisfilum in the two genera. He did concede that, had he had access originally to males rather than females, he would certainly have placed the genera in the Platymantisinae, although he did not venture a definitive phylogenetic arrangement.

Schlüter (1978) described the fossil Retinoberotha stuerneri from the Middle Cretaceous of northwestern France, but did not elaborate on its systematic position. Whalley (1980) described another fossil, Paraberthina acra Whalley, from the Lower Cretaceous amber of Lebanon, placing it within the Rhachiberithinae because it displayed most of the typical berothid characters, as well as raptorial forelegs. He specifically drew attention to the short pronotum, which is, however, a primitive character.

Three years later, Whalley (1983) described Fera venatrix from British (Baltic) Eocene/Oligocene amber, placing it in the Platymantisinae (Mantispidae). He argued that although the new species resembled Berothidae: Rhachiberothinae, F. venatrix had only four tarsal segments in the foreleg, whereas all Rhachiberithinae had five. He was apparently unaware of Tjeder's (1968) study in which a male of the Rhachiberithinae was described with only four tarsomeres.

Schlüter (1983) tried to reconstruct a palaeobioscne in which R. stuerneri could have existed. Schlüter & Stürmer (1984) then discussed the phylogenetic interrelationships of the Berothidae, Rhachiberithinae and Mantispidae, with reference to the two fossil representatives, R. stuerneri and P. acra. Although these two authors referred to Hennig (1969), they failed to question the classification of the two taxa as Rhachiberithinae, reducing the whole problem to the rhetorical forelegs. They offered two hypotheses: (1) that the Rhachiberithinae and Mantispidae are sister-groups by virtue of the synapomorphic raptorial forelegs, or (2) that the Berothidae and Rhachiberithinae are sister-groups, albeit with only synplesiomorphic conformities in wing venation – in this case the raptorial forelegs of Rhachiberithinae and Mantispidae are considered to be a homoplasy.

Lambkin (1986) excluded the Rhachiberithinae from his revision of the Australian Mantispidae, but suggested that they represented a sister-group of either all the Mantispidae or just the Symphrasinae, as indicated by the possibly synapomorphic raptorial forelegs. In the only biological studies on the Rhachiberithinae, Minter (1990) compared the eggs and first-instar larva of M. vesicaria with those of a species of Podallea Navás and Mantispa capeneri Handschin. He commented that the first instar larva of Rhachiberithinae and Berothidae resemble each other and therefore suggest a closer relationship of the two rather than with the Mantispidae. He also left many unresolved questions, e.g. whether the sessile eggs of M. vesicaria are primitive or derived. Although he did not contribute to the discussion on phylogeny of the Rhachiberithinae, his work provided some valuable morphological data on the immature stages.

Despite the above studies, the relationships of the Rhachiberithinae remained obscure, a situation which the present paper attempts to resolve through a critical phylogenetic analysis.

**Historical review**

In 1959 Tjeder described the Rhachiberithinae as a subfamily of the Berothidae, with Rhachiberotha Tjeder as type genus. He included two species, R. signifera Tjeder and R. smithersi Tjeder, and also erected the monotypic genus Mucroherotha Tjeder with M. fasciata Tjeder as type species. At that stage only females were known.

In his phylogenetic discussions, Tjeder argued that despite great similarities with the Platymantisinae (raptorial nature and modification of the tarsi of the foreleg and trichosors along the wing margins), the Rhachiberithinae could clearly be referred to the Berothidae. Similarities in wing venation (course of Cu = Cu) in the hindwing and forked costals in the forewing), the presence of tubercules on the vertex and the shape of the female genitalia supported this conclusion. The lack of male specimens of Rhachiberithinae caused a dilemma in comparisons with the polyphyletic Platymantisinae, as none of the pertinent characters were based upon synapomorphies.

MacLeod & Adams (1967) indicated that some of the characters in Tjeder's list of similarities, such as the pectinate branching pattern of Rs in the forewing, the sinuate course of the base of MA ('r-m vein') in the hindwing, the presence of trichosors, the occurrence of similarly shaped mouthparts and the similarity of the distal tarsomere of the foreleg, are insignificant as they also occur in many other, distantly related, groups of Neuroptera. Despite their criticism of Tjeder's arguments, they agreed with his main ideas of relationships. They interpreted the similarities of many structures in the male genitalia of Berothidae and Mantispidae as parallelism in more highly developed representatives of both families.
Rhachiberothidae Tjeder, 1959, stat.n.

Rhachiberothinae Tjeder, 1959: 262 (odescr), type genus: Rhachiberotha Tjeder, 1959, by original designation: MacLeod & Adams, 1967 (descr, syst); Tjeder, 1968 (com); Whalley, 1980 (com), 1983 (com); Schlüter & Stürmer, 1984 (foss, phyI); Mansell, 1985 (ment); Aspöck, 1986 (syst, chor); Lambkin, 1986 (phyI); New, 1986 (ment, com); Aspöck & Aspöck, 1988a (ment), 1988b (ment); Aspöck, 1989 (ment); New, 1989 (ment, key); Aspöck, 1990 (chor); Minter, 1990 (syst); Willmann, 1990 (phyI, transfer to Mantispidae); Oswald & Penny, 1991 (cat).

Description. Head: vertex with two lateral tubercles and one median tubercle or tubercles fused; postocular zone prominent or inconspicuous; mouthparts short. Pronotum elongated anterior to coxae, curving slightly downwards behind the coxae. Forelegs raptorial, coxae elongate, femora rounded, with two complete or incomplete rows of teeth against which the slightly bent tibia may be reflected: tarsus of female with five segments, only four in the male, the first tarsomere being enlarged, terminating in a spur. Wings subequal, with rounded apices. Forewing: veins of ecological situations.

Key to the genera of Rhachiberothidae

1 Vertex of head with three tubercles: forewing with stem of M free to wing base (Fig. 17) .............. Rhachiberotha
   - Vertex of head forming one dome: forewing with stems of M and R fused at wing base (Fig. 29) .............. Mucroberotha

Key to the species of Rhachiberotha

1 Forewing with two vesicae at hind margin ........ R.sheilae
   - Forewing without vesicae at hind margin .............. 2
2 Forewing with blackish spot over apex of Rs1, Rs2: antenhal flagellum blackish-brown basally .............. 3
   - Forewing without dark spot at apex of Rs1, Rs2: antenhal flagellum completely yellow .............. R.smithersi
3 Pterostigma more darkish-brown proximally than distally, veins of pterostigma with a brownish tinge: only one basal segment of antenhal flagellum black ..................... R.signifera
   - Pterostigma uniformly pale, veins of pterostigma with yellowish tinge: three basal segments of antenhal flagellum blackish-brown .............. R.ingwe

Key to the species of Mucroberotha

1 Forewing hyaline, maculated with contrasting dark-brown spots; antenhal flagellum totally black ........ M.minteri
   - Forewing hyaline with light-brown shading only or with a maximum of four additional brown spots; antenhal flagellum partly or totally yellow .............. 2
2 Antennal pedicel yellow ...................... M.angolana
   - Antennal pedicel black .............. 3
3 Antennal flagellum yellow ...................... 4
   - Basal segments of antenhal flagellum blackish-brown ..................... 5
4 Dorsum of abdomen yellow ...................... M.fasciata
   - Dorsum of abdomen black with yellow areas .......... M.vesicaria
5 Crossveins of forewings uniformly shaded ........ M.aethiopica
   - At least two proximal m-cu crossveins with dark-brown spots .............. M.nigrescens

Rhachiberotha Tjeder, 1959

Rhachiberotha Tjeder, 1959: 262 (odescr), type species: Rhachiberotha signifera Tjeder, 1959, by original
Rhachiberotha signifera Tjeder, 1959

Rhachiberotha signifera Tjeder, 1959: 264 (odescr): MacLeod & Adams, 1967 (ment); Whalley, 1980 (ment); Aspöck, 1990 (choir); Willmann, 1990 (ment).

Systematic position. Closely related to R. ingwe sp.n.

Distribution (Fig. 47). South Africa, Transvaal; Zimbabwe.

Description. Based on female holotype and one female paratype.

Size: length of forewing 7 mm.

Head pale yellow with light-brown and pale yellow hairs, vertex with two brown stripes and flatish median tubercle, lateral tubercles distinct, postocular zone inflated, sandy-coloured; clypeus with brown transverse band. Maxillary and labial palpi brown. Antennae: scape (Fig. 5) about as long as following three segments; scape, pedicel and three basal flagellomeres dark brown, remainder of flagellum pale yellow.

 Pronotum: pale yellow with broad brown stripes laterally; meso- and metanotum yellow to sandy-coloured with brown median line.

Legs yellow: forelegs with brown lines on inner and outer surfaces of coxa; forefemur thickened, with a double row of strong teeth of differing lengths on ventral surface; brown lines present along tooth rows, teeth yellow basally, dark brown apically. Tibia curved, with small dark central spot on outer surface.

Wings (Fig. 49): forewing hyaline with light-grey shaded areas and three narrow parallel brown stripes at wing apex; longitudinal veins yellow or brown; costal veins brown; crossveins brown, mostly shaded. Membrane and veins of pterostigma yellow. Three sc-r and three r-rs crossveins present; stem of M free to wing base; A2 and A3 forming a cell (R. signifera-group) or approximating this condition (R. sheilae-group). Hindwings with stem of M free towards base, basal part of MA sinuate, CuP short, crossvein-like proximally, joining A1 distally; cua-cup long, parallel to wing margin. Male with vesicae in both wings, female with vesicae in forewings only or without vesicae.


Female genitalia: sternite 7 reduced to tiny lateral sclerites. Tergite 8 narrow with apodeme along anterior margin. Subgenitale reduced to a narrow midventral selerite. Tergite 9 + ectoprocts with apodeme along anterior margin. Pseudohypocaudae clearly or almost separated from tergite 9, with rounded, claw-like or process-like apices. Gonapophyses laterales without distinct hypocaudae, joined to paired sclerotized claspers. Bursa copulatrix funnel-shaped; receptaculum seminis coiled, with inflated element.

Systematics. The genus comprises four species, which constitute two groups: (1) the ‘R. signifera-group’ with the closely related R. signifera, R. ingwe sp.n., R. smithersi, and (2) R. sheilae sp.n.

Distribution. South Africa. Transvaal; Zimbabwe.

Rhachiberotha signifera Tjeder, 1959

Rhachiberotha signifera Tjeder, 1959: 264 (odescr): MacLeod & Adams, 1967 (ment); Whalley, 1980 (ment); Aspöck, 1990 (choir); Willmann, 1990 (ment).

Systematic position. Closely related to R. ingwe sp.n.

Distribution (Fig. 47). Zimbabwe.


Tjeder’s (1959) original description is adequate, and as no further material is available it is not supplemented here.

Rhachiberotha ingwe sp.n. (Figs 1–5, 47, 49)

Similar to R. signifera, pale yellow with contrasting markings on body and wings.

Description. Based on female holotype and one female paratype.

Size: length of forewing 7 mm.

Head pale yellow with light-brown and pale yellow hairs, vertex with two brown stripes and flatish median tubercle, lateral tubercles distinct, postocular zone inflated, sandy-coloured; clypeus with brown transverse band. Maxillary and labial palpi brown. Antennae: scape (Fig. 5) about as long as following three segments; scape, pedicel and three basal flagellomeres dark brown, remainder of flagellum pale yellow.

 Pronotum: pale yellow with broad brown stripes laterally; meso- and metanotum yellow to sandy-coloured with brown median line.

Legs yellow: forelegs with brown lines on inner and outer surfaces of coxa; forefemur thickened, with a double row of strong teeth of differing lengths on ventral surface; brown lines present along tooth rows, teeth yellow basally, dark brown apically. Tibia curved, with small dark central spot on outer surface.

Wings (Fig. 49): forewing hyaline with light-grey shaded areas and three narrow parallel brown stripes at wing apex; longitudinal veins yellow or brown; costal veins brown; crossveins brown, mostly shaded. Membrane and veins of pterostigma yellow. Three sc-r and three r-rs crossveins present; stem of M free to wing base; A2 and A3 forming a cell. Hindwing hyaline with pale shading along crossveins only; longitudinal veins pale, almost colourless, crossveins and marginal branches brown; membrane and veins of pterostigma yellow; five gradate crossveins apparent; CuP distally weak. Hairs on wings predominantly yellow mixed with brown hairs, marginal fringes rather short.

Abdomen: sternite 1 extremely weak, reduced to pleural apodeme; sternites 2–4 with transverse apodeme. Female genitalia (Figs 1–4) with subgenitale small, ribbon-like with a few bristles laterally. Pseudohypocaudae almost separated from tergite 9, tapering ventrally. Receptaculum seminis with a large pear-shaped element.

Male unknown.

Systematic position. Closely related and superficially similar to R. signifera. The latter may be differentiated by a dark spot in the pterostigma, only one dark flagellar segment and an inconspicuous pear-shaped element in the receptaculum seminis. Rhachiberotha smithersi lacks any markings on the wings, has a uniformly yellowish-white flagellum and pseudohypocaudae without acute apex. The distinction between R. ingwe and R. sheilae sp.n. is discussed under the latter species.

Etymology. From the type locality which takes its name.
Revision of Rhachiberothidae 185

Figs 1–5. *Rhachiberotha ingwe sp.n.*, holotype, female. 1, genital segments, lateral; 2, same, ventral; 3, bursa copulatrix and receptaculum seminis, lateral; 4, same, dorsal; 5, scape, pedicel and first flagellomere, caudolateral.

from the Zulu word for leopard (*Panthera pardus*), which frequent these mountains.

**Distribution** (Fig. 47). South Africa, Transvaal.

**Material examined.** SOUTH AFRICA, Transvaal. Holotype ♀, AcNE 202, Soutpansberg, Ingwe Motel Valley, 22.58S 29.57E, 31.1.1984 (Mansell) (SANC); 1 ♀ paratype same data but (NHMV).

**Rhachiberotha smithersi** Tjeder, 1959


**Systematic position.** Probably the adelphotaxon to *R. signifera* and *R. ingwe*.

**Distribution** (Fig. 47). Zimbabwe. **Locus typicus:** Southern Rhodesia (Zimbabwe), Vumba Mountains near Umtali (Mutare).

**Material examined.** Type unavailable, no further material known.

**Rhachiberotha sheilae** sp.n. (Figs 6–18, 47, 50)

General appearance characterized by conspicuous vesicae especially in the males. Length of forewing in male 7.8 mm, in female 7.8–8.2 mm.

**Description of male holotype.** Head yellow, frons with a brown mark between tentorial pits; vertex with three dark spots in front of tubercles; occiput with brown spot;
Fig. 6. Rhachiberosha shielae sp.n., holotype, male.
Postocular zone inflated, golden-brown; clypeus brown, labrum yellow. Antenna: scape (Fig. 10) as long as following three segments, yellow with lateral brown stripe; pedicel and flagellum yellow, apical segments light brown. Vertex with two distinct lateral tubercles, median tubercle rather flat. Hairs on head predominantly pale yellow mixed with some brown hairs.

Pronotum yellow dorsomesally, dark brown laterally; meso- and metanotum brown with yellow median fascia.

Legs: foreleg with brown patches on yellow coxa; trochanter yellow; femur (Fig. 11) thickened with one row of short teeth and three larger teeth within this row, two large teeth occur on an imaginary inner line; tibia slightly curved with basal angle; tarsus (Fig. 12) with first tarsomere very long, third tarsomere shortened. Coxae of middle and hind legs predominantly brown; femora yellow with transverse brown stripe; tibiae yellow with brown spot proximally; tarsi yellow.

Wings (Figs 6, 50): forewing hyaline with two vesicae at hind margin and one at pterostigma; dark shading present along crossveins; wing membrane somewhat fuscous between marginal branches; longitudinal veins pale, almost colourless with brown granulations; crossveins predominantly brown; four sc-r, three r-rs and six gradate crossveins present; stem of M free to wing base; A2 and A3 almost forming a cell. Hindwing: hyaline with a few shadows at wing apex and along crossveins; spectacular oval vesicae covering and extending pterostigma, forcing R to curve downwards; veins pale, almost colourless with brown granulation; stem of M free; basal part of MA sinuate; one r-rs and five gradate crossveins present; CuP crossvein-like proximally, distal part sharply flexed and

Figs 7–12. Rhachiberotha sheilae sp.n., holotype, male. 7, genital segments, lateral; 8, same, caudal; 9, ninth gonocoxites and gonarcus, lateral; 10, scape, pedicel, first flagellomere, posterior view; 11, right forefemur, ventral; 12, right foretarsus, dorsal.
weak, joining A1. Hairs on wings predominantly brown mixed with yellow; marginal fringes rather short.

Abdomen: tergites 1 and 2 with transverse apodeme; sternite 1 extremely weak, reduced to pleural apodeme; sternites 2–4 with strong transverse apodeme, 5–6 with weaker apodeme. Male genitalia (Figs 7–9) with tergite 9 narrow, slightly bent ventrocaudally; sternite 9 shovel-like. Ectoprocts separated from tergite 9, with blunt apex. Ninth gonocoxites and gonarcus united into a broad bow. Paramere—mediuncus complex comprising three sclerotized claspers which unite into an arrow-like sclerite apically. Hypandrium internum tiny.

Female similar in general appearance, but differing in several characters.

Wings (Figs 17, 18): the pterostigmal region of both wings is reddish-brown pigmented but lacks vesicae. Foreleg with tooth-row on femur with only two large additional teeth, inner row lacking large teeth but with a few small teeth distally. Foretarsus with tarsomere 1 as long as 2 and 3 together, tarsomere 4 the shortest.

Abdomen with brown tergites, pale yellow spots uniting into longitudinal fascia with a brown median line. Sternites light greyish-brown, yellow caudally. Sternites 2 and 3 with apodeme along pleural margin, sternites 2–4 with transverse apodeme. Female genitalia (Figs 13–16) with sternite 7 reduced to small laterally placed sclerites. Tergite 8 with strong apodeme along anterior margin. Subgenitalae reduced to a narrow midventral selerite. Tergite 9 and ectoprocts with a very strong apodeme along anterior margin. Pseudohypocaudae clearly separated from tergite 9, forming long proximally directed processes. Gonapophyses laterales relatively long, without hypocaudae, connected to two well-sclerotized claspers (see arrow in Fig. 14). Bursa copulatrix funnel-shaped; receptaculum seminis coiled, with voluminous horn-shaped element.

Systematic position. An isolated species, probably the adelphotaxon of the R.signifera-group. It is characterized and easily identified by vesicae at the hind margin of the forewings.

Etymology. Dedicated to Sheila Mansell in gratitude for her enthusiasm and support of our work on the Neuroptera.

Distribution (Fig. 47). South Africa, Transvaal.

Material examined. SOUTH AFRICA, Transvaal. Holotype δ, AcNE 25, Rustenburg Nature Reserve, 25.40S 27.12E, 22.ii.1982 (Mansell), At light (SANC); 2 ♀ ♀ paratypes same data; 1 ♀ paratype, AcNE 26, same data but 23–26.ii.1981 (Millar) (SANC, NHMV); 1 ♀ paratype, Rustenburg Kloof, 25.40S 27.10E, iii.1976 (Picker) (SANC).

Mucroberotha Tjeder, 1959

Mucroberotha Tjeder, 1959: 276 (odescr) (Type species: Mucroberotha fasciata Tjeder, 1959, by original designation); MacLeod & Adams, 1967 (ment); Rouset, 1968 (ment); Tjeder, 1968 (descr male, syst); Whalley, 1980 (ment); Schlüter & Stürmer, 1984 (ment); Aspöck & Aspöck, 1985 (ment); Mansell, 1985 (ment); Aspöck, 1986 (syst, chor), 1990 (chor); Lambkin, 1986 (ment); New, 1986 (ment), 1989 (ment); Willmann, 1990 (syst); Oswald & Penny, 1991 (cat).

Description. Head short, tubercles fused into a single dome: postocular zone rather inconspicuous. Antennae twice as long as broad. Forefemora thickened, with one row of four (three and one) large and several small teeth along the row and a second incomplete row of teeth. Foretibiae slightly curved with basal angle. Apical tarsomere with delicate paired claws. Forewings with costal veins only partly forked, stems of M and R originating together at wing base, with A2 and A3 sometimes forming a cell. Hindwing with stem of M free to wing base, basal part of MA sinuate; CuP short, joining A1 distally; cu-a cup more or less parallel to wing margin; males with vesicae in forewings.

Male genitalia with sternite 8 narrow, fused with shovel-like sternite 9 and spiracle 8 situated slightly dorsally. Tergite 9 narrow, partly fused with shell-like ectoprocts. Ninth gonocoxites and gonarcus connected to a rather large flat rectangular sclerite. Paramere-mediuncus complex with compact basal part and a long penislum. Hypandrium internum tiny.


Systematics. The genus comprises six species constituting two groups: (1) the ‘M.vesicaria-group’ with the closely related M.fasciata and M.vesicaria, M.nigrescens, M.aethiopica sp.n. and M.angolana sp.n., and (2) M.minteri sp.n.


Mucroberotha fasciata Tjeder, 1959

Mucroberotha fasciata Tjeder, 1959: 277 (odescr); Tjeder, 1968 (descr male); U. Aspöck, 1990 (chor); Willmann, 1990 (fig).

Systematic position. Closely related to, and perhaps identical with M.vesicaria; see discussion under that species.

Distribution (Fig. 47). Zimbabwe.

Comparison of all available material with specimens collected at the type locality (Soutpan, Pretoria District) clearly shows a geographically correlated (west to east) variation which is, however, partially obscured by strong individual variation. The species has a totally dark scape and an orange tinge in the eastern populations, whereas specimens of other provenance are more sandy-coloured and paler, the scape being sandy-coloured anteriorly. Variability of the wings and also the genital structures warrant further investigation. Subspecific classification with nomenclatural consequences is premature at present, requiring further detailed studies, also with regard to the relationship between *M. vesicaria* and *M. fasciata*. The holotype of *M. fasciata* is pale and the genitalia are slide-
mounted. It is not certain whether the pale appearance is natural or due to chemical-induced fading, and details of the genitalia are difficult to discern. Consequently, it is presently impossible to determine whether the two species are conspecific, whether M. fuscifutu is a subspecies of M. fasciata or whether they are distinct. These questions will only be resolved when further material of M. fasciata is obtained from the type locality.

**Distribution (Fig. 47).** Namibia, South Africa, Zimbabwe.

**Material examined.** SOUTH AFRICA. Transvaal. 2 δ, δ, Mosdene, Naboomspruit Dist., 24.36S 28.47E, 1972 (Minter) (LRMC); 5 δ, δ, Soutpan, Pretoria Dist. 25.24S 28.05E, 1175 m, 21.i.1976 (Minter) (LRMC); 1 δ, AcNE 214, same data but 11.i.1984 (Mansell) (SANC); 1 δ, AcNE 463, same data but 22.ii.1985 (H., U. & Ch. Aspöck, Hölzel, Mansell) (SANC); 3 δ, δ, 3 ♀, ♀, same data but (8512) (HUAC); 12 δ, δ, AcNE 1258, same data but 9.xii.1987 (Mansell, Minter) (SANC); 3 δ, δ, 2 ♀, ♀ (in alcohol), Pietersburg, 23.54S 29.28E, 7.xii.1977 (Minter) (USNM); 3 δ, δ, 2 ♀, ♀, AcNE 23, Langjan Nature Reserve, 22.52S 29.14E, 830 m, 23–24.i.1982 (Mansell) (SANC); 3 δ, δ, AcNE 193, Rustenburg Nature Reserve, 25.40S 27.12E, 1300 m, 7.xii.1983 (Mansell) (SANC); 1 δ, ♀, same data but (H. & U. Aspöck) (85/9) (HUAC); 1 δ, AcNE 1263, Loskop Dam Nature Reserve, 25.25S 29.20E, 1240 m, 12–13.xi.1985 (Moolman) (SANC); 1 ♀, Sand River, Pietersburg, 23.53S 29.37E, 1250 m, 13.i.1986, (Minter) (LRMC); 3 δ, δ (in alcohol), same data but 22.i.1986 (LRMC); 1 δ, ♀, AcNE 1261, D‘Nyala Nature Reserve, Ellisras Dist., 23.45S 27.49E, 850 m, 23–26.i.1987 (Mansell) (SANC); 3 ♀, ♀, AcNE 1259, Mogoto Nature Reserve, Zebediela, 24.15S 29.12E, 1400 m, 10.i.1988 (Minter) (SANC); 32 δ, δ (in alcohol), 11 ♀, ♀ (pinned), same data but 13.i.1988 (LRMC); 1 δ, 3 ♀, ♀, AcNE 1262, Wyllie’s Poort, 22.55S 29.55E, 900 m, 21–24.i.1988 (Kroon) (SANC); 1 ♀, The Folly, 10 km N. Wyllie’s Poort, 22.52S 29.52E, 900 m (Minter) (LRMC); 1 δ, 3 ♀, ♀, AcNE 1260, Dunstable Farm, Hoedspruit Dist., 24.26S 30.45E, 900 m, 18–20.i.1990 (Oberprieler) (SANC); 1 δ, Soutpansberg, Ingwe Motel, 22.58S 29.57E, 1200 m, 24.xi.1992 (Hölzel, Mansell, Ohm) (SANC). CAPE PROVINCE: 1 δ, AcNE 1264, Witsand, Postmasburg Dist., 28.33S 22.29E, 1282 m 17.iii.1982 (Londt) (SANC); 1 δ, Olifantshoek, 27.56S 22.44E, 1250 m, 27.i.1988 (Mansell, Minter) (LRMC); 1 δ, ♀, same data but (H. & U. Aspöck) (HUAC, NHMV); 43 δ, δ, 8 ♀, ♀, same locality but 20.i.1991 (Mansell) (SANC).

**Namibia.** 1 δ, Farm Abachaus, Otjiwarongo (19.44S 16.47E), 22.i.1944 (Hobohm), ’Gust. Meyer’ (ex collection). No. 26, 1952 (ZMUH); 2 δ, δ, Tiervallei, 10 km N Kombat on Groofoetine Road 19.40S 17.50E, 1650 m, 3.i.1972 (Minter) (LRMC); 2 δ, δ, 3 ♀, ♀, AcNE 1265, Elefantenberg, Farm Achalm, 9 km S Otavi, 19.44S 17.21E, 1500 m, 12.iii.1987 (Oberprieler) (SANC); 1 δ, same data but (Wittmer) (HUAC); 2 δ, δ, 10 km N Windhoek, 22.27S 17.05E, 1500 m, 24.ii.1988 (Minter) (LRMC); 1 δ, 2 ♀, ♀, same data but (H. & U. Aspöck) (HUAC, NHMV).

**Zimbabwe.** 1 ♀, Bulawayo, 20.10S 28.43E, 25.xii.1975 (Lucas) (POCG); 1 δ, 2 ♀, ♀, St. Luke’s Hospital, c. 30 km SE Lupane, 19.00S 27.46E, 26.xii.1975 (Lucas) (POCG); 7 δ, δ, Iris Vale, Balla Balla, 20.30S 29.05E, 27.xii.1975 (Toms) (LRMC).

**Microberotha nigrescens** Tjeder, 1968


**Systematic position.** Belonging to the M. vesicaria-group of the genus but adelphotaxon not yet clear.

**Distribution (Fig. 47).** Zimbabwe.


**Microberotha aethiopica** n.sp. (Figs 19–28, 51)

Of delicate appearance, superficially similar to M. nigrescens.

**Description of male holotype**

Size: length of forewing 7.2 mm.

Head ochre-coloured, face with a tinge of orange. Postocular region inopinuous. Maxillary and labial palpi brown. Scape (Fig. 19) yellow anteriorly, brown posteriorly, about as long as following three segments. Pedicel dark brown, first flagellomere yellow, basal flagellomeres dark brown, middle segments yellow, apical flagellomeres brown. Tubercles of head fused into a single dome. Pubescence predominantly golden and yellow. Pronotum yellow; mesonotum yellow with brown stripes medially and laterally; metanotum brown. Legs yellow, only meso- and metathoracic coxae brown. Forefemora (Fig. 21) with one row of small teeth and a few additional ones indicating the inner row. Proximal part with three large teeth along the outer row, and one on the inner side, all teeth yellow basally and dark brown apically. Foretibiae with a small dark spot. First tarsomere longest, third tarsomere shortest.

Wings (Figs 20, 51): forewing hyaline with brown shading along crossveins and branches of veins; veins yellow or brown, membrane and veins of pterostigma with a tinge of orange centrally. Small vesicle present distal to pterostigma; three sc-r and four r-rs crossveins present; stem of M fused with R; A2 and A3 forming a cell. Hindwing hyaline with shading mainly along gradate veins and distal branches; veins pale or colourless with brown granulation in shaded areas; membrane and veins of pterostigma ochre-coloured with a tinge of orange; six gradate crossveins present. Hairs on wings mainly yellow, mixed with brown, marginal fringes rather short.

Abdomen: tergites brown with yellow spots, sternites yellow; pubescence golden-yellow. Tergite 2 and sternites...
Figs 19–21. *Mucroberotha aethiopica* sp.n., holotype, male. 19, scape, pedicel, base of flagellum, frontal view; 20, right forewing, pterostigmal region; 21, left foreleg, outer surface.

2–4 with transverse apodemes, sternites 2 and 3 with apodemes along lateral margins, sternite 1 almost obliterated.


Female unknown.

**Systematic position.** Not yet clear. The only other species of which the males are known, *M.vesicariu* and *M.minteri*, differ in the shape of the ventrally tapering ectoprocts. *Mucroberotha aethiopica* differs from *M.fasciata, M.angolana* and *M.minteri* in having a dark flagellum base, but is similar in this respect to *M.nigrescens*. *Mucroberotha aethiopica*, however, has the crossveins uniformly shaded, whereas in *M.nigrescens* the two proximal m-cu crossveins are surrounded by intense pigmentation.

**Distribution.** Ethiopia.

**Material examined.** ETHIOPIA. Holotype ♂, Bahar Dar (11.33N 37.25E), June/July 1969 (*Schäufele*) (SMSG).

*Mucroberotha angolana* n.sp. (Figs 29–36, 52)

A delicate pale species.

**Description of female holotype**

**Size:** Length of forewing 7.8 mm.

Head yellow, only frons with brown spot and inner side of mandibles brown. Vertex slightly raised; postocular zone inconspicuous. Antennae yellow, apex of flagellum somewhat darker; scape as long as following three segments; vestiture brown and yellow. Pronotum ochre-coloured; vestiture yellow and brown; meso- and metanotum sandy-coloured with dark brown median line. Legs yellow; forefemora with one row of small teeth and a few additional small teeth indicating a second line; three large teeth occur outside the row and one on the inner side. First tarsomere as long as second and third tarsomeres together.

Wings (Figs 29, 30, 52): forewing hyaline with sandy-coloured shading along crossveins and along distal branches. Pterostigma sandy-coloured. Veins sandy-coloured but proximal m-cu brown; three sc-r and four r-rs crossveins present; stem of M fused with R; six gradate crossveins; A2 and A3 forming a cell. Hind wing hyaline with sandy-coloured shading along gradates and distal branches; pterostigma sandy-coloured; veins colourless to sandy; one sc-r and three r-rs crossveins present; four and five gradate crossveins; CuP resembling a crossvein proximally, rudimentary distally. Vestiture yellow and brown, marginal fringes rather short.

Abdomen: sternite 1 reduced to an apodeme, sternite 2 with pleural apodeme, sternites 2–4 with transverse apodeme.

Female genitalia (Figs 33–36) with sternite 7 paired. Tergite 8 with apodeme along anterior margin. A mem-

Systematic position. Belongs to the *M. vescaria*-group, but adelphotaxon not yet clear. *Mucrobertha angolana*
Figs 29–32. *Mucroberotha angolana* sp.n., holotype, female. 29, base of left forewing; 30, portion of left hindwing; 31, head, frontal; 32, outer side of left foreleg.

can be easily identified by the completely yellow scape, pedicel and basal flagellomeres.

**Distribution.** Angola.

**Material examined.** ANGOLA. Holotype ♀, 20 km NE Sa da Bandiera (14.52S 13.32E), 5600, 4.iii.1970 (Ross) (CASC).

*Mucroberotha minteri* sp.n. (Figs 37–46, 47, 53)

General appearance dominated by hyaline forewings heavily maculated with dark-brown spots. Length of forewing in males 6.0–6.8 mm, females 6.2–7.0 mm.

**Description of the male** (Figs 37–42)

Head (Fig. 37) intensely yellow, inner surface of mandibular apex, maxillary and labial palpi brown; postocular zone inconspicuous, vertex slightly raised. Antennal scape blackish-brown with a yellow spot anteriorly and posteriorly, pedicel and flagellum blackish-brown, vestiture predominantly golden-yellow.

Pronotum reddish-yellow, vestiture reddish-yellow; meso- and metanotum yellow with a large dark-brown spot laterally, metanotum with a dark-brown median line. Legs: forelegs (Fig. 38) yellow, femora with a double row of teeth on the ventral surface, three large teeth along outer row with another large tooth at inner row; all teeth yellow basally, brown apically; tibiae with brown line along outer surface; first tarsomere as long as 2–4 combined, tarsomere 3 the shortest; middle and hind legs predominantly yellow, only coxae brown.

Wings: forewing hyaline with intensely contrasting dark
brown spots on crossveins and distal branches, with a small vesicle distal to pterostigma. Longitudinal veins yellow, brown within the spots, crossveins brown. Membrane of pterostigma yellow with a brown spot, veins similarly coloured; three sc-r and three r-rs crossveins present; stem of M unites with R at wingbase; A2 and A3 forming a cell. Hindwing hyaline with a few brown spots; membrane of pterostigma yellow with brown spots; veins similarly coloured; one sc-r, three r-rs crossveins and four gradate crossveins (in two rows) present. Vestiture of wings predominantly yellow, marginal fringes short.

Abdomen: tergites with a longitudinal median blackish-brown ornamentation; pleurites and sternites yellow.

Male genitalia (Figs 39–42): tergite 8 narrow with a small
Figs 37–42. *Mucrobrotha minteri* sp.n., paratype. male, Namibia. 37, head, frontal; 38, left foreleg, outer side; 39, genital segments, lateral; 40, same, caudal; 41, gonarcus, ninth gonocoxites, paramere–mediuncus complex, and hypandrium internum, lateral; 42, hypandrium internum, ventral.
dorsally situated spiracle. Sternite 8 fused with sternite 9 along a distinct apodeme; sternite 9 large, shovel-like, with a small processus laterally. Tergite 9 extremely narrow, with a ventrally forked apodeme. Ectoprocts distinctly separate from tergite 9, tapering ventrally into stronger sclerotized apices. Ninth gonocoxites and gonarcus joined to a rather large flat sclerite. Paramere—mediuncus complex with compact basal part and a long penisfilum. Hypandrium internum tiny.

**Description of the female** (Figs 43–46, 53).

With only minor sexual dimorphisms.

Pronotum yellow but without reddish tinge. The vesicle in the forewing is replaced by a small brownish spot (Figs 43, 53).

Abdomen with the dark median ornamentation on the tergites broader than in the male.

Female genitalia (Figs 44–46): sternite 7 paired. Tergite 8 with weak apodeme anteriorly. No distinct subgenitale, but midventral bristles present. Tergite 9 + ectoprocts fused, with distinct apodeme; pseudohypocaudae clearly separate from tergite 9, with finger-shaped processus slightly curved caudally; gonapophyses laterales with short broad hypocaudae. Genital opening associated with a sclerotized loop. Bursa copulatrix funnel-shaped, receptaculum seminis coiled, tube-shaped ductus with rippled texture.

The females from Namibia are not as intensely coloured as the one from the type locality, and the pseudohypocaudae are less curved caudally. As the specimen from Zimbabwe (taken *in copula*) carried a spermatophore which is deeply embedded in the genitalia the curvature of the pseudohypocaudae may be influenced by this. The spermatophore is similar in general appearance and in its extraordinary

**Fig. 43.** *Microberotha minteri* sp.n., paratype, female, Namibia. Right fore- and hindwing.
Figs 44-46. *Microberotha minteri* sp.n., paratype, female, Namibia. 44, genital segments, lateral; 45, same, caudal; 46, bursa copulatrix and receptaculum seminis, larger scale.
length to those found in the Berothidae (e.g. Tjeder, 1959, fig. 311, ‘ovipilum’), but slightly club-shaped at the end.

**Systematic position.** An isolated species representing the adelphotaxon of the other Mucroberotha species. Easily distinguished from other species by the characteristic wing markings.

**Note.** Initially only the material from Namibia was available for the description: the drawings of the genitalia had already been completed when the male and female from Zimbabwe were collected. As the male from Namibia is in poor condition and the male from Zimbabwe is excellently preserved, the latter was chosen as the holotype.

**Etymology.** This species is named for our friend and colleague, Les R. Minter (University of the North, Sovenga, South Africa) who first discovered this species, and made material in his possession available for this study.

**Distribution** (Fig. 47). Namibia, Zimbabwe.

**Material examined.** ZIMBABWE. Holotype δ, Matapos Siding, 20.27S 28.30E, 1000 m, 4.xii.1990 (Miller); 1♀ paratype, same data (flying in copula with δ holotype) (SANC). NAMIBIA, 1♂, 1♀ in alcohol, Tiervallei, 10 km N Kombat on Grootfonteinroad, 19.40S 17.40E, 3.i.1972; 5♀♀ pinned, same data; 2♀♀ pinned, Otavi, 19.39S 17.20E, 4.i.1972; 1♀ pinned, Grootfontein, 19.34S 18.07E, 3.i.1972 (Minter) (LRMC, SANC, NHMV).

**Discussion**

The numbers of the synapomorphies and autapomorphies listed in the phylogenetic diagram (Fig. 48) correspond with the numbers in the following text.

(i) **Synapomorphies of the Dilaridae, Berothidae, Rhachiberothidae and Mantispidae**

We consider the Dilaridae to be the sister-group of the monophyletic group (Berothidae + Rhachiberothidae) + Mantispidae (cf. Aspöck, 1992). The architecture of the larval head provides several relevant characters: (1) The elongate stipes and cardo, running stripe-like parallel to
the postlabium (cf. Minter, 1990, 1992) are a synapomorphy. Whether the flatness of the head is secondary and a synapomorphy of this group or a symplesiomorphy with the Neuroptera is uncertain. (2) The styles of the larvae are interpreted as synapomorphic, evolved independently from those of Osmylidae and others. (3) Tubercles on the vertex of the imaginal head have generally been interpreted as a primitive character, but may, however, be synapomorphic but secondarily lost in some of the Rhachiberothidae and the Mantispidae. Cephalic tubercles are not known in other families of Neuroptera, although setose patches occur in a few Psychopsidae. (4) The ovipositor of female Dilaridae and Symphrassinae (Mantispidae) has elicited much discussion relative to the ovipositor of the Raphidioptera (e.g. Tjeder, 1937), which at a glance looks similar but is clearly not of identical construction (literature summarized in Aspöck et al., 1991). The ovipositors of Dilaridae and Symphrassinae (see Aspöck et al., 1980, figs
431, 432, and Ferris, 1940) may be interpreted either as parallel evolution in Dilaridae and Symphrasinae or as a synapomorphy of Dilaridae and (Berothidae + Rhachiberotidae) + Mantispidae constituting the sister-group, and we assume the latter. This means, however, that only the Dilaridae and Symphrasinae retained the ovipositor which has been reduced and modified significantly in the others.

As a basis for the arguments concerning the above monophyletic grouping, the following should be stated. The monophyly of the Dilaridae is undoubted. Their most conspicuous autapomorphy is the pectinate antennae of the male (28). Further taxonomic involvement with the Dilaridae is beyond the scope of this paper.

Autapomorphies of the Berothidae include: the bundle of long bristles arising from the paramere—mediuncus complex in the male (29) and the p Ludicum (30), a sclerite associated with the eighth sternite in the female. The Ludicum may be an archaic structure (perhaps eighth gonocoxites) but it is nevertheless an apomorphic condition in Berothidae. The termitophily of the larvae and the physogasy of the second instar larva may be further apomorphies (31), although we have no information on the Rhachiberothidae in this regard.

The Mantispidae, recently the subject of an excellent phylogenetic analysis by Lambkin (1986), comprise four subfamilies, Symphrasinae, Drepanicinae, Calomantispinae and Mantispinae. The Symphrasinae, which manifest many plesiomorphic characters, are the sister-group of the other three. Autapomorphies of the Mantispidae in this sense are: elongation of the pronotum behind the forelegs (32); pairs of trichosors between branches along the wing margin (33).

Willmann (1990) transferred the Rhachiberothidae from the Berothidae to Mantispidae, interpreting the Rhachiberothidae as an additional subfamily and sister-group of all hitherto known mantispids. The autapomorphies of the Mantispidae, in this revised sense, and of its subgroups as listed by Willmann (1990: 254) are quoted and critically discussed below:

‘Left mandible equipped with an additional tooth’. This character does not qualify as an autapomorphy for several reasons. The strong cu-cup crossovein is also found in Neurorthidae in a clearly primitive constellation. There seems to be a necessity for a strong cu-cup crossovein across the claval furrow which runs along the actual CuP or the imaginary one where it has been reduced or lost (Wooton, 1979). Moreover, the CuP constellation in the hindwing is comparatively primitive in the Symphrasinae, e.g. Trichoscelia (Willmann, 1990, fig. 4), CuP being intact proximally and distally. In the Rhachiberothidae CuP is reduced distally, with a tendency to proximal reduction (see Fig. 30, M. angolana). The extreme apomorphic character state is found in the Berothidae with an almost complete reduction of the proximal part of CuP and either the distal part of CuP highly reduced or a prolonged part of CuP branching along the wing margin. This character cannot thus be considered a synapomorphy in Rhachiberothidae and Symphrasinae. In the Dilaridae, which are considered the sister-group of Berothidae + Mantispidae (Aspöck, 1992, and below), there is a primitive and simple CuP. In large specimens such as Dilar turcicus Hagen, however, the proximal part of CuP forms a broad loop together with the cu-cup crossovein. The distal part of CuP then appears separately as a twig of CuA. In tiny species of Dilar CuP may be reduced and the basal part and/or cu-cup crossovein appear as cu-aal.

‘Possession of raptorial forelegs’. This is a strong argument for the possible mantispid nature of the Rhachiberothidae, although parallel evolution is, however, more convincing. Symphrasinae and Rhachiberothidae have similar modifications in the tarsus of the raptorial legs which Willmann (1990: 257) interprets as convergences rather than a synapomorphy of Rhachiberothidae and Mantispidae. We agree in this respect, and think that the fact that Rhachiberothidae have this modification in the male only, and Symphrasinae in males and females, is a strong indication of parallel evolution of the raptorial legs. Raptorial legs of similar appearance in other orders of insects also support this interpretation (cf. Beier, 1968, fig. 25: Aspöck et al., 1980).

‘Number of thick ventral bristles on the middle and hind tarsi increased to two on each side’. It is uncertain whether two bristles in Trichoscelia are a reversal of four on each side in Plega (Willmann, 1990: 260).

The Berothidae have one bristle on each side which is considered plesiomorphic by Willmann but, in our opinion, this may be a reduction as well. The Dilaridae we examined do not show any corresponding modifications. Groups of corresponding bristles are to be found in the hemerobid genera Drepanepteryx Leach and Wesmaelius Krüger. The character thus appears too irrelevant as a synapomorphy at subfamily level.

(ii) Synapomorphies of the monophyletic group (Berothidae + Rhachiberothidae) + Mantispidae

(5) Elongation of the antennal pedicel and, (6) overlapping scales on antennae, mandibles and maxillae (cf. Minter, 1990) are convincing larval synapomorphies. (7) A ‘creeping’ CuP, with small branches along the hindmargin of the hindwing, visible in the Berothidae and Symphrasinae, reduced but traceable in Rhachiberothidae, and lost in the Mantispidae, provides an imaginal synapomorphy.

(iii) Synapomorphies of the Rhachiberothidae and Berothidae

(8) The extreme elongation of the larval postlabium (cf. Minter, 1990) is a convincing synapomorphy. (9) The cylindrical larval antennae are most probably synapomorphic, the basally constricted antennal segments of the Mantispidae plesiomorphic because in Dilaridae the segments also seem to be constricted rather than cylindrical. As the larval antennae are extremely delicate and vulnerable structures, this interpretation requires re-investigation and further comparison. The imagines provide several characters which are possibly synapomorphic: (10) the elongation of the pronotum anterior to the coxae, (11) the pronounced postocular zone (which seems to be secondarily reduced in Mucroberotha), (12) the long tube-shaped spermatophores, and (13) the pseudohypocaudae. The females of the boethid genera Austroberothella U. Aspöck & H. Aspöck and Protobiella Tillyard have a remarkable digitiform processes on their tergite 9 + ectoprocts, the pseudohypocaudae (Aspöck & Aspöck, 1985). In a further approach, Aspöck & Aspöck (1988b) identified these sclerites as being homologous with the digitiform processes in Rhachiberothinae and with less
spectacular appendices of tergite 9 in other berothid genera, e.g. in the Cyrenoherothinae, and also with appendices of tergite 9 + ectoprocts in Podallea and particularly in Spernaphorellina Tillyard. We now interpret these particular pseudohypocaudae as a synapomorphy of the Rhachiberothidae and Berothidae, irrespective of what they really are: the true gonocoxites or gonapophyses (cf. Weidner, 1982) or any other derivatives of tergite 9.

(iv) Autapomorphies of the Rhachiberothidae

(14) We assume that the raptorial forelegs have evolved independently of those of the Mantispidae. Parallel evolution in related taxa is certainly more frequent than generally assumed, and quite natural due to a similar gene pool. (15) The modification of the tarsus in the male, only four tarsomeres, the first elongated with a spine, the second arising from its medial face, is undoubtedly caused by parallel evolution. (16) The vesicae in the wings are a unique evolutionary novelty of unknown function.

(17) Finally, we interpret the sessile eggs of Mucroberotha (Minter, 1990) as an autapomorphy at the family level.

The following two arguments of Willmann (1990) are based on reductions only: the third argument is irrelevant.

‘In the hindwing, the cu-a-cup crossvein runs almost parallel to the hindmargin’. We agree, but as it is the result of reductions in a highly variable part of the wing it is a rather weak criterion.

‘The number of branches to CuP has decreased.’ The plesiomorphic condition is supposed to be at least three branches, retained in the Symphrasinae (Willmann, 1990, fig. 4). We think that the reduction could also be derived from a branched CuP as occurs within the Berothidae. But it should be stressed again that reductions in this area of the wing are weak criteria.

‘Prothorax elongate’ is no argument as an autapomorphy, because an elongated pronotum, anterior to the coxae, is a synapomorphy of Berothidae and Rhachiberothidae.

(v) Autapomorphies of Rhachiberotha

(18) Elongation of the scape and pedicel. (19) In the male, fusion of the gonarcus and ninth gonocoxites into a broad bow and, (20) in the female, paired sclerotized claspers which link the gonapophyses laterales with the genital opening.

We cannot accept the following arguments of Willmann (1990) as autapomorphies of Rhachiberotha:

‘Femur of the foreleg with an outer row of long spines along its entire length’. This character is not manifest in all species. Moreover, two rows of short teeth, as well as one row and an incomplete second one occur in both Rhachiberotha and Mucroberotha. The teeth on the femora do not provide reliable criteria.

‘In the female the ectoprocts are completely fused’. Rhachiberotha and Mucroberotha have a similar state of fusion of tergite 9 + ectoprocts and an indistinct apodeme in this region. Fusion of T9 + ectoprocts occurs independently and frequently in allied taxa, and is therefore not an appropriate criterion in this regard.

(vi) Autapomorphies of Mucroberotha

(21) The trochanters of the vertex are fused into one large dome. (22) In the forewing, the proximal part of M is fused with the stem of R. (23) Fusion of sternites 8 and 9 in the male. (24) Gonarcus and ninth gonocoxites fused into a rectangular canopy. (25) Paramere—medianuncus complex terminating in a long membranously connected more or less coiled penisfilum. (26) An extremely long receptaculum seminis in the female. (27) Genital opening of the female associated with sclerotized loop.

The following arguments of Willmann (1990) do not qualify as autapomorphies of Mucroberotha:

‘In the forewing, A2 and A3 are fused distally’. This fusion does not occur in a consistent manner within the genus, a tendency to this state may also be seen in Rhachiberotha and in several Dilaridae.

‘Males with vesicae on the wings’. The male of Rhachiberotha also has vesicae.

‘In the female there is no subgenitale’. We agree that there is no sclerite-like subgenitale, but there may be some unsclerotized differentiation in this region.

‘The ectoprocts of the female are fused with tergite 9’. See our comments under autapomorphies of Rhachiberotha.

List of autapomorphies and synapomorphies used in the text and cladogram

Synapomorphies of Dilaridae, Berothidae, Rhachiberothidae and Mantispidae

1. Larval stipes and cardo elongate, stripe-like, parallel to postlabium.
2. Straight mandibles and maxillae of larvae.
3. Tuberces on vertex of imaginal head.
4. Long ovipositor in females of Dilaridae and Symphrasinae (Mantispidae); reduced in others.

Synapomorphies of Berothidae, Rhachiberothidae and Mantispidae

5. Larval antennae with elongated pedicel.
6. Overlapping scales on larval antennae, mandibles and maxillae.
7. ‘Creeping’ CuP with small branches along margin of hindwing.

Synapomorphies of Rhachiberothidae and Berothidae

8. Elongation of larval postlabium.
9. Cylindrical larval antennae.
10. Elongation of pronotum anterior to forelegs.
11. Pronounced postocular zone.
12. Long tube-shaped spermatophores.
13. Pseudohypocaudae in females.

Autapomorphies of Rhachiberothidae

15. Modification of foretarsus in the male, homoplastic with Symphrasinae.
16. Vesicae on the wings.
17. Sessile eggs.
Autapomorphies of Rhachiberothida
18. Elongation of imaginal scape and pedicel.
19. Fusion of gonarcus and ninth gonocoxites into a broad arch in the male.
20. Paired sclerotized claspers linking gonapophyses laterales and genital opening in the female.

Autapomorphies of Microberothida
21. Tubercles on vertex fused into one dome.
22. Proximal part of M fused with R in the forewing.
23. Fusion of sternites 8 + 9 in the male.
24. Gonarcus and ninth gonocoxites fused into a rectangular canopy in the male.
27. Genital opening of female associated with sclerotized loop.

Autapomorphies of Dilaridae
28. Pectinate antennae of males.

Autapomorphies of Berothidae
29. Bundle of long bristles arising from the paramere–mediocus complex in males.
30. Pudiculum (sclerite associated with sternite 8) in females.
31. Termitophily of larvae and physogastric second-instar larva.

Autapomorphies of Mantispidae (independently from Rhachiberothidae)
32. Elongation of pronotum posterior to the forelegs.
33. Paired trichosors between branches along wing margin.

Conclusion
An analysis of the autapomorphies and synapomorphies of larvae and adults, as summarized in the above list, has led to the following hypotheses:
1. The Rhachiberothidae stat.n. are the sister-group of the Berothidae and not of the Mantispidae as postulated by Willmann (1990). The Mantispidae, with Symphrasinae, Drepanicinae, Calomantispinae and Mantispinae, but without the Rhachiberothinae, are monophyletic. The Berothidae, with Berothinae, Nosybininae, Cyrenoberothinae and Nyrminae are monophyletic.
2. Rhachiberothidae and Berothidae are the sister-group of the Mantispidae in the sense of Lambkin (1986) but not of Willmann (1990). The three families are the sister-group of the monophyletic Dilaridae.

Acknowledgments
We are grateful to the following persons, mainly the curators of collections and Institutions mentioned in the text, for the loan or donation of material: Dr W. Wittmer (Basel), Dipl. Biol. C. Saure (Berlin), Mrs R. Sithole (Bulawayo), Prof Dr H. Strümpfel (Hamburg), Dr P. Ohm (Kiel), Mr R. Danielsson and Dr B. Tjeder (Lund), Mr S. J. Brooks (London), Dr J. G. H. Londo (Piemaritzburg), Drs P. H. Arnaud and N. D. Penny (San Francisco), Dr T. Osten (Stuttgart), Dr O. S. Flint (Washington). Messrs L. R. Minter (University of the North, Sovenga, South Africa) and R. B. Miller (Project City, California, U.S.A.) are especially thanked in this regard.

Mrs A. Schumacher and Ing. R. Krbeci (Naturhistorisches Museum Wien) are acknowledged for their assistance with photography.

Finally, and especially, we wish to thank H. Aspöck (University of Vienna, Austria) for much valuable discussion since the inception of this study, and for participation in field trips.

References


Accepted 18 May 1994
Bibliography of the Neuropterida

Bibliography of the Neuropterida Reference number (r#):
7532

Reference Citation:

Copyrights:
Any/all applicable copyrights reside with, and are reserved by, the publisher(s), the author(s) and/or other entities as allowed by law. No copyrights belong to the Bibliography of the Neuropterida. Work made available through the Bibliography of the Neuropterida with permission(s) obtained, or with copyrights believed to be expired.

Notes:

File: