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The Phylogeny of Southeast Asian and Indo-Pacific Calicnemiinae (Odonata, Platycnemididae)[1]

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Abstract. Phylogenetic relationships of Southeast Asian and Indo-Pacific damselflies of the subfamily Calicnemiinae (Odonata: Platycnemididae) are examined by cladistic analyses using morphological characters. The strict consensus cladogram of the resulting equally most parsimonious trees supports the monophyly of the Papuan genus *Idiocnemis* Selys, the Philippine genus *Risiocnemis* Cowley and its subgenera, but leaves the basal relationships of the African genera and the Palawan genus *Asthenocnemis* Lieftinck partly unresolved. A preferred phylogenetic hypothesis is presented showing a well supported 'Indo-Pacific clade' consisting of Philippine, New Guinean and Solomon island taxa, and as sister group *Asthenocnemis*. *Risiocnemis* turns out to be a sister group of *Lieftinckia/Salomocnemis* (Solomon Islands), the sister taxon of those being the central New Guinean *Arrhenocnemis* Lieftinck. Together, these form a monophyletic group with the remaining Papuan taxa. *Idiocnemis leonorae* Lieftinck is transferred to *Rhyacocnemis* Lieftinck **comb. nov.** The possible effects of taxon sampling are discussed.

Key words. Taxonomy, biogeography, morphology, Southeast Asia, phylogeny, cladistic analysis, *Rhyacocnemis leonorae* **comb. nov.**

1. INTRODUCTION

The odonate subfamily Calicnemiinae Fraser, 1957 represents small to medium-sized damselflies (Zygoptera) inhabiting small running waters throughout the old world. The group is almost exclusively tropical. Due to the confinement to stable habitats and lacking dispersal capacities in the rainforest environment, the majority of species shows a high degree of endemism, both at species and genus level. Therefore, the group is well suited for historical biogeographical analyses (GASSMANN in prep.).

SELYS (1863) distinguished seven subgenera in his 'legion Platycnemis'. Together, those subgenera, which were later given generic rank by the same author (SELYS 1886) represented a large part of the Afrotropical, Southeast Asian and Indo-Pacific Calicnemiinae known today. TILLYARD (1917) raised SELYS' legions to subfamily level resulting among others in a subfamily Platycnemidinae (he used the incorrect name 'Platycneminae'). However, the family-group name had already been introduced earlier (YAKOBSON & BIANKI 1905). TILLYARD & FRASER (1938/40) finally erected the family Platycnemididae. In the most recent account on the group, MARTENS (1996) provided five diagnostic characters (at least with regard to Coenagrionidae) for the family: the comparatively long and obtuse discoidal cell (quadrilateral), the length of the pterostigma (matching no more than one wing cell), the variable position of arculus (at or distal to Ax2), the course of the longitudinal veins MA and IR3 (mainly straight, only apically zigzagged), and size (small to medium-sized). Another character of Platycnemididae, long ciliae on the legs, was already mentioned by Selys (1886) for his legion Platycnemis; however, this trait is shared by other zygopteran families (SCHMIDT 1951b).

The Platycnemididae now consist of two subfamilies, Platycnemidinae Yakobson & Bianki, 1905, and Calicnemiinae Fraser, 1957.

The subfamily Platycnemidinae

FRASER (1957) was the first to define the subfamily in its present form, containing the two genera *Platycnemis* Burmeister, 1839, and *Copera* Kirby, 1890. The dilation of the male tibiae, which is the most distinct feature Fraser used to characterize the subfamily, has turned out to be not diagnostic for the group. Several species currently assigned to Platycnemidinae, for example, some Madagascan ones (SCHMIDT 1951a) have undilated tibiae. Contrarily, one species of Calicnemiinae, *Risiocnemis atropurpurea* (Brauer), does have dilated tibiae.

Within the genus *Platycnemis*, 31 species are currently recognized (derived from MARTENS 1996 and HÄMÄLÄINEN 2003). The group exhibits a disjunct pattern of distribution, involving the western Palaearctic region, eastern Asia, northwestern/ western Africa as well as the Madagascan region (SCHMIDT 1951a; MARTENS 1996). No representatives were known from Southeast Asia until recently. However, the recent discovery of a new species from Laos (P. *phasmovolans* Hämäläinen) extends the distribution of the group far into the Indo-Chinese region (HÄMÄLÄINEN 2003).

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

Within the genus *Copera* (*Copera* spec., Plate 1b) currently nine species are recognized (MARTENS 1996). The group is largely replacing *Platycnemis* in Southeast Asia, but there is an area of overlap in eastern Asia (MARTENS 1996). The generic borders between *Copera* and *Platycnemis* are weakly defined, and their identity recently has been put in question by HÄMÄLÄINEN (2003).

The subfamily Calicnemiinae

The damselfly subfamily Calicnemiinae was erected by FRASER (1957) to accomodate species of platycnemidid damselflies which did not fit into the subfamily Platycnemidinae. Fraser himself stated: "This subfamily is formed mainly for convenience to separate the true Platycnemiines, and one has only to compare the genera composing it, to note how artificial it appears to be...". Unfortunately, Fraser did not provide diagnostic characters for the subfamily, except for the absence of dilated tibiae, which on the other hand is a striking feature in the second subfamily Platycnemidinae. BECHLY (1996) found no autapomorphies for the group. Later authors (MARTENS 1996) have provided additional distinguishing characters for Calicnemiinae, i.e. the comparatively acute discoidal cell (quadrilateral) and the length of the anal vein.

The Calicnemiinae reach their highest diversity in Southeast Asia and the Indo-Pacific region. Remarkably, the group is absent from Wallacea (Sulawesi, Smaller Sunda Islands, Moluccas), which has been confirmed, at least for Sulawesi, by several odonatological surveys during the last decades (VAN TOL 2000).

The African genera of Calicnemiinae

The African genera of the subfamily are a rather heterogenous assemblage comprising only about a dozen species in total (SCHORR et al. 2004). The family status of some of them, in particular that of *Mesocnemis* Karsch, 1891 (Western Africa, 4 species) and *Metacnemis* Selys, 1863 (Southern Africa, Madagascar; 3 species), has been doubted (MARTENS 1996; WATERSTON 1984). Except for *Allocnemis* Selys, 1863 (Southern Africa, 2 species), all remaining African genera are monotypic: *Leptocnemis* Selys, 1886 and *Paracnemis* Martin, 1903 (Madagascar), *Oreocnemis* Pinhey, 1971 (eastern Africa) and *Arabicnemis* Waterston, 1984 (Arabian Peninsula). *Allocnemis* and *Arabicnemis* also extend into subtropical areas.

The Oriental genera of Calicnemiinae

From the Oriental region, four calicnemiine genera have been recognized. *Calicnemia* Strand, 1928 is a medium-sized genus with 17 described species (SCHORR et al. 2004) which reaches its highest diversity in the Himalayan region (LIEFTINCK 1984); however, its distributional range further extends southeast into the Indo-Chinese mainland as well as to Taiwan and Hainan. Interestingly, no representatives of *Calicnemia* are known from the Greater Sunda Islands. *Indocnemis* Laidlaw, 1917, is a monotypic genus; *I. orang* (Förster in Laidlaw, 1907) occurs in India and mainland Southeast Asia. *Coeliccia* Kirby, 1890 is by far the largest genus of Calicnemiinae, currently comprising 59 species according to SCHORR et al. (2004). Its distribution area ranges from the Himalayan region via the Southeast Asian mainland into the Greater Sunda Islands and even into the western and southwestern Philippines; south to the Philippines, along the Greater Sunda Islands, the eastern border of *Coeliccia* matches the Wallace line, except for the island of Bali from where no representative of the genus is known. A taxonomic and phylogenetic revision of a presumably monophyletic subgroup of the genus, consisting of Sundaland and Philippine taxa, is in work (DIJKSTRA & GASSMANN, in prep.). The fourth Oriental genus, *Sinocnemis*, comprises two species and was established quite recently (WILSON & WEN-BAO 2000); however, it could not be studied in detail for the present analysis.

The Indo-Pacific Calicnemiinae

Recently, a large part of the New Guinean and Philippine taxa have been revised taxonomically (GASSMANN 1999, 2000; GASSMANN & HÄMÄLÄINEN 2002; HÄMÄLÄINEN 1991a/b, 2000). Based on recently collected specimens from different sources, several new species were recognized. The New Guinean genus *Idiocnemis* Selys now amounts to 19 species and thus represents the largest genus in the Papuan region, followed by *Lieftinckia* Kimmins (Solomon Islands; 6 species), *Rhyacocnemis* Lieftinck (New Guinea; 3 species, see below), *Paramecocnemis* Lieftinck (New Guinea, 2 species). The remaining Papuan genera *Cyanocnemis* Lieftinck, *Lochmaeocnemis* Lieftinck, *Thaumatagrion* Lieftinck, *Torrenticnemis* Lieftinck (New Guinea) and *Salomocnemis* Lieftinck (Solomon Islands) are all monotypic (for *Arrhenocnemis* see below). The Philippine genus *Risiocnemis* Cowley now comprises 36 described species, with subgenus *Igneocnemis* Hämäläinen (20 species) being somewhat larger than the nominal subgenus *Risiocnemis* Cowley (GASSMANN & HÄMÄLÄINEN 2002). Within the Philippine Calicnemiinae, the Palawan genus *Asthenocnemis* Lieftinck is an outstanding representative. Originally, Lieftinck thought that the peculiar female specimen from the Martin collection of which he based the description of the new species, *A. stephanodera*, would originate from New Guinea (LIEFTINCK 1949). Later, with the arrival of additional (male) specimens from Palawan Island, he stated his error (LIEFTINCK 1971, 1974).

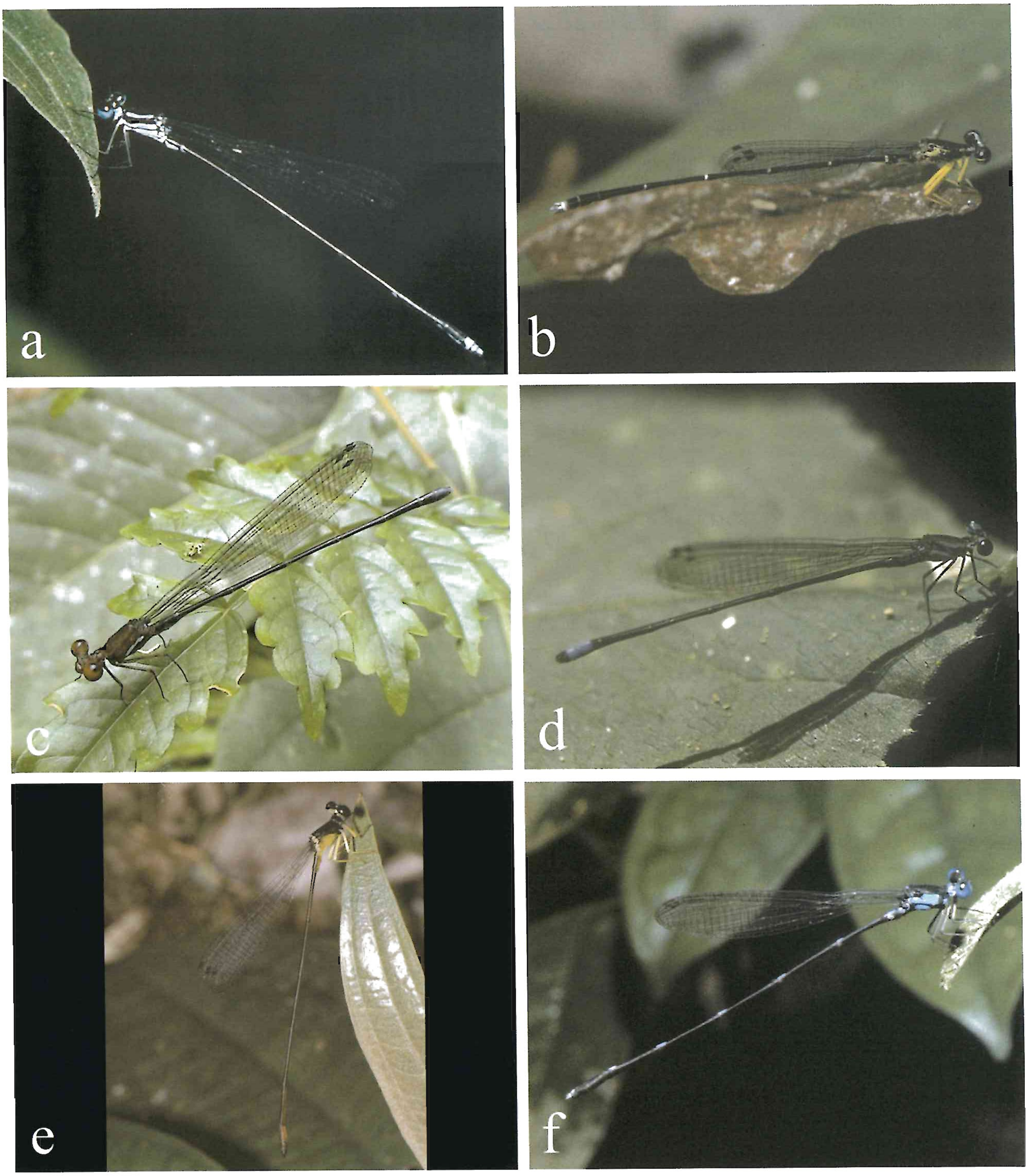


Plate 1: a) *Coeliccia membranipes*, ♂, Java; Photo: J. van Tol. b) *Copera* spec., ♂, Sarawak, Borneo; Photo: D. Paulson. c) *Idiocnemis australis*, ♂, Lake Kutubu, Papua New Guinea; Photo: J. Michalski. d) *Idiocnemis inaequidens*, ♂, Morobe Province, Papua New Guinea; Photo: D. Gassmann. e) *Risiocnemis kaiseri*, ♂, Samar, Philippines; Photo: R. A. Müller. f) *Risiocnemis serrata*, ♂, Luzon, Philippines; Photo: D. Paulson.

Preexisting hypotheses on phylogenetic relationships within Calicnemiinae

Several authors have occasionally discussed the presumed relationships between different genera of Calicnemiinae (FRASER 1932; LIEFTINCK 1958, 1963). Since these considerations were not yet influenced by the methodological tools provided by W. HENNIG'S phylogenetic systematics (1950, 1966), they were determined to remain rather vague assumptions which were not necessarily founded on synapomorphic traits (see discussion). Also FRASER's 'reclassification of Odonata' (1957) is not based on cladistic concepts, and up to now no phylogenetic study on platycnemidid damselflies has been available. However, BECHLY (1996) and recently REHN (2003) performed morphological-phylogenetic higher-level analyses of Odonata, including some selected representatives of the superfamily Coenagrionoidea, respectively.

2. MATERIALS AND METHODS

2.1. Specimens examined

The present study is based on preceding revisional work on the taxonomy of Papuan and Philippine Calicnemiinae by GASSMANN (1999, 2000) and GASSMANN & HÄMÄLÄINEN (2002). The reader is referred to those references for detailed material lists. However, in the meantime, many additional taxa, among them the entire subgenus *Risiocnemis*, have been studied for a more inclusive analysis of phylogenetic relationships between the Indo-Pacific representatives of the subfamily; those specimens are listed in Appendix 4. Despite the fact that they are not yet formally described, the male of *Risiocnemis moroensis* as well as the females of *R. gracilis* and *Idiocnemis leonorae* have been included in the analysis.

2.2. Taxon sampling

Relationships between the Indo-Pacific taxa were examined down to species level; all the known species were included (Appendix 1). However, for the Oriental genera, in particular the huge genus *Coeliccia* Kirby, 1890, this was not possible due to practical constraints. Thus, for both the Oriental and the African genera, only single representatives were included in the analysis. *Thaumatagrion funereum* from New Guinea was examined, but finally not included in the analysis, because its current status within Platycnemididae should be seriously doubted (see results and discussion). On the other hand, the author did not see any reason not to include the two known *Arrhenocnemis* species; their habitus and wing venational characters - especially the distinctly crenulate wing margin - strongly resembles the Calicnemiinae (although Lieftinck considered them to belong to the Megapodagrionidae (LIEFTINCK 1965, 1971; see discussion)). Due to the lack (or limited availability) of material, the African genera *Metacnemis* Selys, 1863 and *Oreocnemis* Pinhey, 1971 as well as the comparatively recently described Oriental genus *Sinocnemis* Wilson and Wen-bao, 2000 had to be excluded from the analysis. It should be noted that currently also phylogenetic revisions of *Calicnemia* Strand, 1928 (GASSMANN, in prep.) and the Philippine and Bornean representatives of *Asthenocnemis* and *Coeliccia* (DIJKSTRA & GASSMANN, in prep.) are in work, eventually providing a better understanding of the West Malesian calicnemiine fauna.

2.3. Outgroup choice

The second subfamily of Platycnemididae and presumed sister group of Calicnemiinae, the Platycnemidinae, were chosen as outgroup for the analysis. Unfortunately, it was not possible to include more taxa than one representative for each of the two genera *Platycnemis* and *Copera*; however, a literature survey revealed that the majority of species within Platycnemidinae are at least structurally very similar (e.g. SCHMIDT 1951a).

2.4. Scanning electron microscopy (SEM)

The male ligulae of almost all species and the male appendages and female prothoracices of selected species were examined by scanning electron microscopy (SEM). The scanning electron micrographs were taken by the author, mainly using a JEOL SEM 6400 microscope. The objects were cleaned in 70% ethanol, air-dried and subsequently sputtered with gold for 1.5 - 2.0 min at 20 mA before examination. Figures 5-6, 9-10, 17-18, 19-20, 23-24 and 35-36 were made using a JEOL SEM 840A microscope.

2.5. Terminology

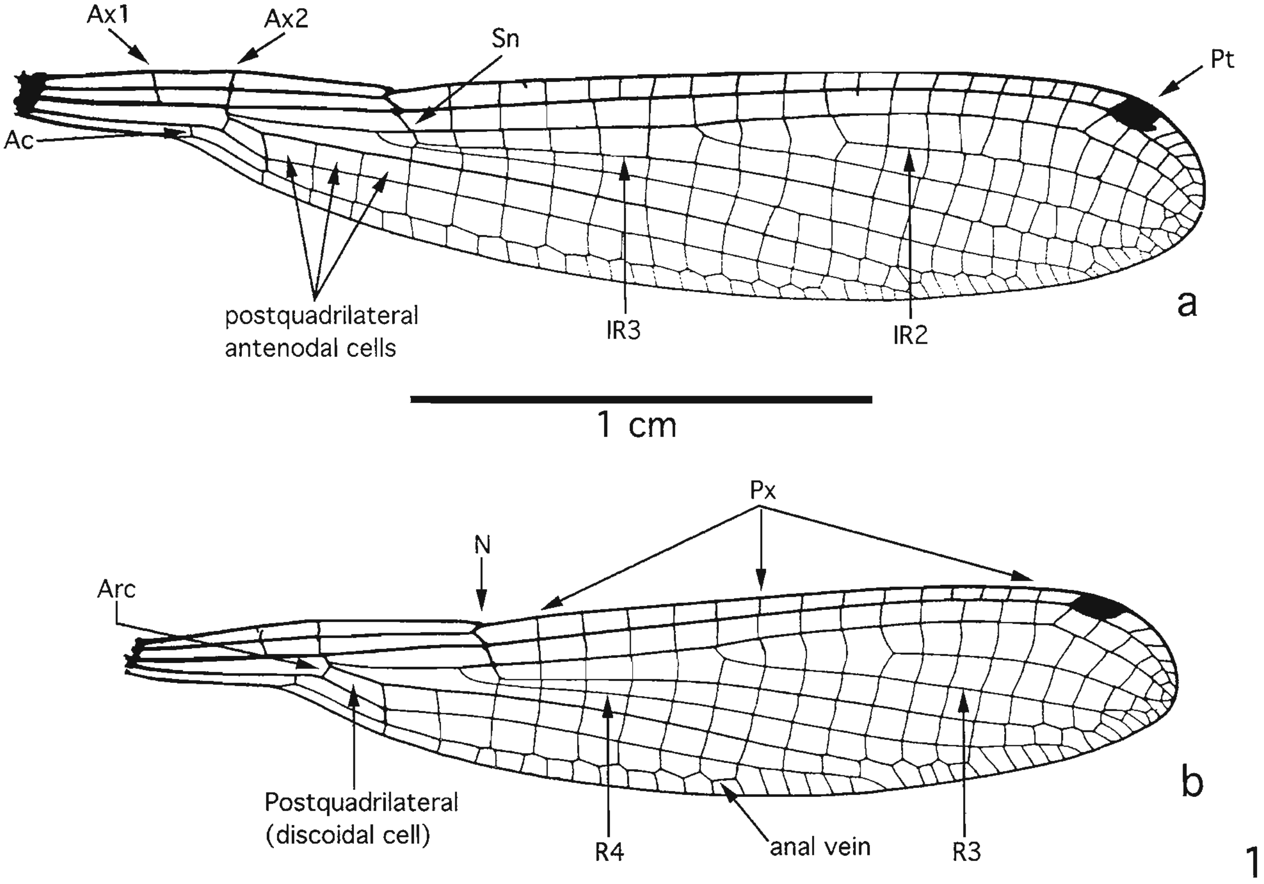
Although the modified Tillyard-Fraser system of odonate wing venation (cf. WATSON & O'FARRELL 1991) is controversial (loc. cit.), it is further applied here, because it has already been used in preceding revisional work on Calicnemiinae (GASSMANN 1999, 2000; GASSMANN & HÄMÄLÄINEN 2002).

2.6. Measurements

The measurements of wings and abdomens were taken within a precision of 0.5 mm. Measurements of the additional specimens examined for the present paper are not given here but can be obtained from the author. In a few cases, measurements had to be taken from the literature.

2.7. Character coding

In several cases, coding of character states for the cladistic analysis was problematic, because an unambigious (i.e. objective) delimitation of discrete states was not possible. However, the attempt was made to divide, for instance, a gradually changing character into a



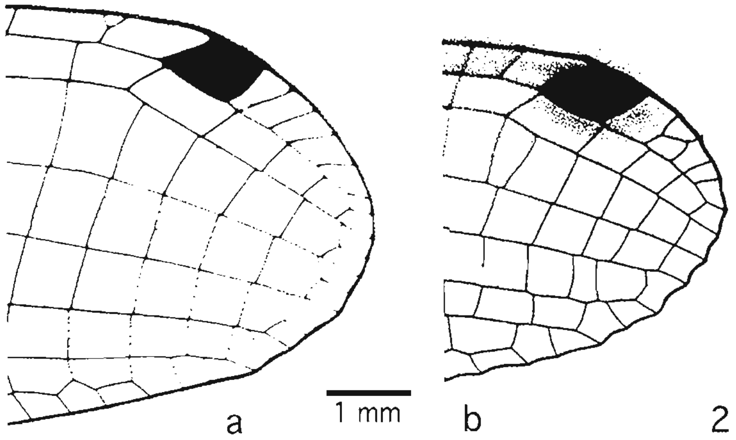


Fig. 1: Left forewing of *Calicnemia eximia*, ♂ (a) and *Platycnemis pennipes*, ♂ (b). Abbreviations: Ac = antenodal crossvein; Arc = arculus; Ax = antenodal vein; N = nodus; Px = postnodal vein; Pt = pterostigma; (I)R = (intercalary) radius; Sn = subnodal vein.

Fig. 2: Wing apex of *Risiocnemis (Igneocnemis) tendipes*, ♂, (a), *Risiocnemis (Risiocnemis) laguna*, ♂, (b).

series of discrete intervals which were chosen as small and precise as possible (cf. character 56). For the treatment of continuous morphometrical traits: cf. characters 17 and 55.

Polymorphisms were entered as separate character states (scaled coding; different methods reviewed in WIENS 1999 and KORNET & TURNER 1999), but left unordered. However, in a few cases in which character states were not unambigiously codable (e.g. colour traits of deteriorated specimens), the states concerned were entered as polymorphies while applying the 'uncertainty' option in PAUP (SWOFFORD & BEGLE 1993) to minimize the potential effect of erroneously delimitated character states on the analysis.

2.8. Cladistic analysis

Morphological characters of imagines were compiled in a data matrix which consisted of 88 binary and multistate characters (listed below); due to our scarce knowledge of larval forms and the probably doubtful assignment of larval to adult specimens in the literature, larval characters were not considered for the present analysis. Since the female sex is unknown in several species, only three female characters were used to keep the amount of missing values in the data matrix low. In cases of characters exhibiting more than nine states, the consecutive states were labelled with Roman capital letters in the data matrix (Appendix 2); however, in the character list below, all states are numbered numerically for better readability. Four uninformative characters were excluded from the analysis. A parsimony analysis using PAUP* 4.0b4a (SWOFFORD 2002) was applied to examine relationships of 84 taxa in total. The resulting topology was rooted a posteriori by designating 2 taxa (see above) as outgroup. The heuristic search settings were chosen as follows: all characters unordered and equally weighted, starting tree(s) obtained via stepwise addition, random addition sequence with 100 replicates; branch-swapping algorithm: tree-bisection-reconnection (TBR). Character optimization was performed by accelerated transformation (ACCTRAN); character evolution was traced and examined by applying MacClade 3.04 (MADDISON & MADDISON, 1993): see Appendix 3. Analyses testing clade stability were performed using Autodecay 4.0 (ERIKSSON 1998) and PAUP* 4.0b4a (SWOFFORD 2002), the latter run under the same settings as above, but with only 10 replicates.The trees were rooted by applying the paraphyletic rooting option to avoid assignment of many ambiguous character states to the ingroup node while using only two outgroup taxa.

2.9. List of characters

Male characters:

Wings

1. Apical wing margin: shape.

(0) not crenulate (Fig. 1a/b); (1) smoothly sinuous (Fig. 2a); (2) distinctly crenulate (Fig. 2b).

All Papuan representatives of Calicnemiinae (but see below for *Thaumatagrion funereum*) as well as the species of subgenus *Risiocnemis* have a distinctly crenulate apical wing margin: from the level of the pterostigma up to about the distal third of posterior margin. The wing apex is furnished with concave inlets between the vein endings (Fig. 2b). Contrarily, the wing apex of *Igneocnemis* species is smoothly sinuous ('smoothly crenulate' in GASSMANN 1999, 2000 and GASSMANN & HÄMÄLÄINEN 2002): the posterior half of the apical wing margin is divided into shallowly deepened or, occasionally, straight areas, divided by more or less distinct emarginations at the levels of veins R_2, R_3, R_4 and - more proximal and less distinct - at CuP (Fig. 2a). This feature is largely shared by *Leptocnemis cyanops* from the Seychelles; however, it is slightly less distinct in that species and lacking the emargination at R_2.

2. Wing petiolation.

(0) between Ax1 and Ax2 (Fig. 1a/b); (1) proximal to Ax1.

In most species examined, the basal petiolation of the wings reaches up to a level just distal to the first antenodal crossvein (Ax1). Only in *Arabicnemis caerulea* and *Mesocnemis singularis*, the level of petiolation ends proximally to the level of Ax1.

3. Position of anal crossvein (Ac).

(0) distinctly distal to Ab (Fig. 1a/b); (1) at or slightly distal/proximal to Ab (about halfway between Ax1 and Ax2); (2) somewhat proximal to Ab (closer to Ax1 than to Ax2); (3) far proximal to Ab.

The position of the anal crossvein (Ac) relative to the insertion of the anal bridge (Ab) can be readily classified in distinct character states; however, there is some variation in those taxa showing condition (0): in *Mesocnemis singularis* and *Paracnemis alluaudi*, Ac is situated about 2.5 to 3.5 times its own length distal to Ab, whilst in other taxa as in *Cyanocnemis aureofrons*, the distance amounts to just about the length of Ac. *Lieftinckia* species have Ac situated far proximal to Ab, i. e. about halfway between wing base and Ax2.

4. Anal vein: length.

(0) short, reaching no further than up to about the level of Px6 (Fig. 1b); (1) long, reaching further than the level of Px6 (Fig. 1a).

The condition (0) usually means that R3 inserts at the level where the anal vein ends: a character originally used to dicriminate between the two subfamilies of Platycnemididae (MARTENS 1996; see also Fig. 1). However, the relation between these two veins cannot be applied to taxa where R3 and IR2 appear to be moved much more distally, as in *Risiocnemis* and some species of *Lieftinckia*. Therefore, in the present study the length of the anal vein is put in relation to the corresponding number of Px.

5. Arculus: position.

(0) proximal to Ax2; (1) at or slightly proximal to Ax2; (2) at Ax2 (Fig.1a); (3) at or distal to Ax2; (4) distal to Ax2.

The position of the arculus relative to the second antenodal vein (Ax2) has often been used as a taxonomic character in platycnemidid classification; however, the degree of variation differs between different genera.

6. Medio-anal link.

(0) straight or nearly straight (Fig.1b); (1) straight or slightly hooked; (2) slightly hooked (Fig. 1a); (3) distinctly hooked.

The shape of the medio-anal link corresponds with the shape of the quadrilateral: the posterior distal angle of the latter can be either nearly right, or very acute; consequently, the medio-anal link appears either straight or broken.

7. Third postquadrangular cell (forewing).

(0) absent (Fig. 1b); (1) absent or present; (2) present (Fig. 1a).

Both in forewing and hindwing, the majority of the examined species has two cells between quadrilateral and the vein descending from the subnodal vein. However, in some taxa the number of postquadrilateral cells can amount to three or four cells.

8. Fourth postquadrangular cell (forewing).

(0) absent; (1) absent or present; (2) present.

9. Third postquadrangular cell (hindwing).

(0) absent; (1) absent or present; (2) present.

10. Fourth postquadrangular cell (hindwing).

(0) absent; (1) present.

11. Position of R4 (forewing).

(0) distinctly proximal to Sn (Fig. 1a/b); (1) slightly proximal to Sn; (2) at Sn; (3) at or distal to Sn; (4) distal to Sn.

12. Position of IR3 (forewing).

(0) at Sn (Fig. 1a/b); (1) slightly distal to Sn; (2) between Px1 and Px2; (3) at about the level of Px2; (4) between Px3 and Px7.

13. R4 and IR3: fused/separate.

(0) separate; (1) fused at base.

In *Paramecocnemis*, the R4 and IR3 veins are fused from shortly distal to wing base up to about the level of Px1 to Px2. In all remaining taxa, the two veins are distinctly separate.

14. Pterostigma (forewing): length.

(0) matching one cell or less (Fig. 1b); (1) reaching well beyond one cell (Fig. 1a).

The length of the pterostigma was examined in relation to the posteriorly neighbouring cell.

15. Pterostigma (forewing): colour.

(0) brown; (1) white.

16. Wing colour.

(0) entirely clear; (1) with a slight brownish breath; (2) brownish at base; (3) entirely brownish.

17. Hind wing length.

(0) short (mean value = 17.0); (1) medium-sized (mean values = 19.6-29.4); (2) long (mean value = 30.7); (3) very long (mean value = 32.2).

To transform the measurement values into discrete states, gap-coding as described by ARCHIE (1985) was applied. The pooled within-group standard deviation (s_p) was calculated, and the group means (of species) were arranged by size; subsequently, every sub-row of means which leaves a gap greater than s_p (= 1.0) to neigbouring mean values, is assigned an integer score, respectively. *Arrhenocnemis sinuatipennis* was not considered, because only one measurement value (from the literature) was available.

Head

18. Labrum: ground colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) yellow-orange; (4) yellow or yellowish-white; (5) bright red; (6) blue; (7) bluish-grey; (8) greenish-blue.

19. Anteclypeus: ground colour.

(0) black; (1) dark brown to black; (2) dark brown; (3) medium to dark brown; (4) medium brown; (5) light to medium brown; (6) light brown; (7) reddish-brown; (8) reddish-brown to black; (9) orange-brown; (10) yellow-orange; (11) yellowish or yellowish-white; (12) blue; (13) bluish-grey; (14) green.

20. Postclypeus: ground colour.

(0) black; (1) black, basal area orange; (2) dark brown to black; (3) dark brown.

(4) medium to dark brown; (5) medium brown; (6) reddish-brown; (7) orange-brown; (8) orange; (9) blue; (10) bluish-grey; (11) green.

21. Genae: colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) light to medium brown; (4) yellow-orange; (5) greenish-yellow; (6) greenish-blue; (7) bluish-grey; (8) blue.

22. Postclypeus: shape (in lateral view).

(0) bulgy, edge rounded; (1) slightly curved, edge bulgy; (2) slightly curved, edge semi-sharp; (3) angulate, edge sharp.

23. Frontal stripe.

(0) present; (1) absent.

The anterior part of the head may show several kinds of distinct or diffuse markings. A comparatively distinct feature is the frontal stripe which, if present, runs from eye to eye (for an exception see below), covering the frons and the parts lateral to it.

24. Frontal stripe: extension.

(0) reaching to a level just anterior to antennae, not including antennal sockets; (1) up to and including antennal sockets; (2) up to and including antennal scapus.

In *Asthenocnemis stephanodera*, as an exception, the frontal stripe is not reaching the eye margin, respectively, but instead is only slightly exceeding the width of postclypeus.

25. Frontal stripe: shape.

(0) more or less complete, not interrupted; (1) interrupted in the center of frons.

26. Frontal stripe: colour.

(0) reddish-brown; (1) blue; (2) greenish-blue; (3) greenish-yellow; (4) bluish-grey to violet; (5) orange; (6) pale orange; (7) chrome.

27. Brown stripes lateral to postclypeus.

(0) present, reaching from postclypeus to eye margin; (1) short, rudimentary, reaching only halfway the distance from postclypeus to eye margin; (2) absent.

The character state is coded as unknown for those taxa in which the lower anterior part of the head is black throughout, so that no discrete stripes are recognizable.

28. Vertical stripe at the level of ocellar area.

(0) present; (1) reduced to a pair of transverse elongate spots; (2) reduced to a pair of longitudinal elongate spots; (3) reduced to diffuse stripe; (4) absent.

29. Vertex: ground colour.

(0) black; (1) black to reddish-brown; (2) reddish-brown to bright red; (3) bluish-grey.

30. Antennal scapus: ground colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) light brown; (4) orange; (5) bright red; (6) yellow-white; (7) bluish-grey; (8) blue.

31. Antennal pedicellus: ground colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) light brown; (4) orange; (5) bright red; (6) yellow-white; (7) bluish-grey; (8) blue.

32. Length ratio antennal pedicellus/scapus.

(0) subequal in length; (1) about 1.25 times the length; (2) about 1.5 times the length; (3) about twice the length; (4) about 2.5 times the length; (5) about 3 times the length.

33. Subquadrangular marking around ocelli.

(0) absent; (1) present.

Except for *I. nigriventris*, the vertex of species of the *Idiocnemis bidentata* species-group is marked by a subquadrangular black marking (cf. GASSMANN 2000, fig. 31).

34. Postocellar spots on vertex.

(0) absent; (1) small, circular, framed; (2) large, subtriangular; (3) very large, subtriangular.

35. Distinct elongate spots on occiput.

(0) present; (1) absent.

36. Brown spots lateral to ocelli.

(0) absent; (1) present.

Thorax

37. (Male) pronotal tubercles: size.

(0) flat or only slightly raised; (1) distinct; (2) very distinct.

Males of most taxa studied have the right and left half of the median lobe either not raised or only slightly rounded in lateral view. However, they can be raised to distinct protrusions, reaching their extreme in *Asthenocnemis stephanodera.*

38. Prothorax: ground colour.

(0) black or brown-black; (1) brown-black; (2) light, reddish- or medium brown.

39. Legs: coloration.

(0) Black throughout or mainly black; (1) mainly black or dark brown; (2) light to medium brown, darkened to a varying extent; (3) yellow-light brown with black markings; (4) yellow-brown or -black; (5) red-black; (6) bright orange; (7) orange-red; (8) black-bluish(-white).

40. Legs: shape of tibiae.

(0) distinctly dilated; (1) not distinctly dilated.

41. Synthorax: robust mesonotal processes.

(0) absent; (1) present.

Arrhenocnemis amphidactylis shows a conspicuous, finger-like outgrowth at either side of dorsal carina of anterior part of synthorax.

42. Synthorax: black line/marking on dorsal carina.

(0) narrow; (1) broad; (2) dorsal surface of synthorax black or brown-black throughout (except for antehumeral stripes, if present).

The extension of black coloration on synthorax is either restricted to the dorsal carina, or it fills the entire upper surface of synthorax (occasionally reaching beyond the humeral suture). In *Idiocnemis dagnyae*, as an exception, the black carinal stripe varies in width from exactly matching the median carina up to reaching the width of the carinal forks.

43. Antehumeral stripe.

(0) complete stripe; (1) distinct, interrupted; (2) half stripe; (3) short anterior stripe, joining humeral suture (4) distinct, reduced to anterior spot, joining carinal fork; (5) rudimentary, interrupted; (6) diffuse stripe; (7) absent.

44. Metepisternal stripe.

(0) absent; (1) rudimentary; (2) present.

45. Metepisternal stripe: colour.

(0) blue; (1) turquoise; (2) diffuse light brown; (3) greyish-purple; (4) orange; (5) bluish-grey; (6) green, intermingled with orange; (7) yellowish.

46. Distinct metepimeral marking.

(0) not clearly defined; (1) short, subquadrangular.

This feature is included here to characterize some species of subgenus *Risiocnemis* of which the metepimera are furnished with distinct subquadrangular colour markings (see HÄMÄLÄINEN 1991a). In the remaining taxa, the metepimeron is either entirely or largely uniform in coloration.

47. Meso- and metathoracic markings.

(0) absent; (1) present.

In some species of the *inornata* species-group of *Idiocnemis*, the mes- and metepisternal fossae at posterior ends of first and second lateral sutures are covered by an elongate black spot, respectively. This character was examined and scored only for *Idiocnemis* species.

48. Pruinescence

(0) absent; (1) parts of head, pro- and synthorax and legs pruinescent; (2) pruinescent throughout.

49. Underside of synthorax: bristles.

(0) absent or only minute; (1) a well-delimited patch of robust spines present.

Abdomen

50. Abdomen: basic colour pattern.

(0) rather uniform (often with more or less distinct annules), but lacking a clear separation in two different colours; (1) abdomen distinctly separated in anterior (brown-)black and posterior reddish part.

51. Posterior dorsal abdominal marking: colour.

(0) blue to violet/purple; (1) yellow-orange or yellow-white; (2) blue-whitish-pruinescent.

A variably shaped, mostly subquadrangular colour marking covers the dorsal surface of last abdominal segments in several taxa studied.

52. Dorsal marking on segment 9.

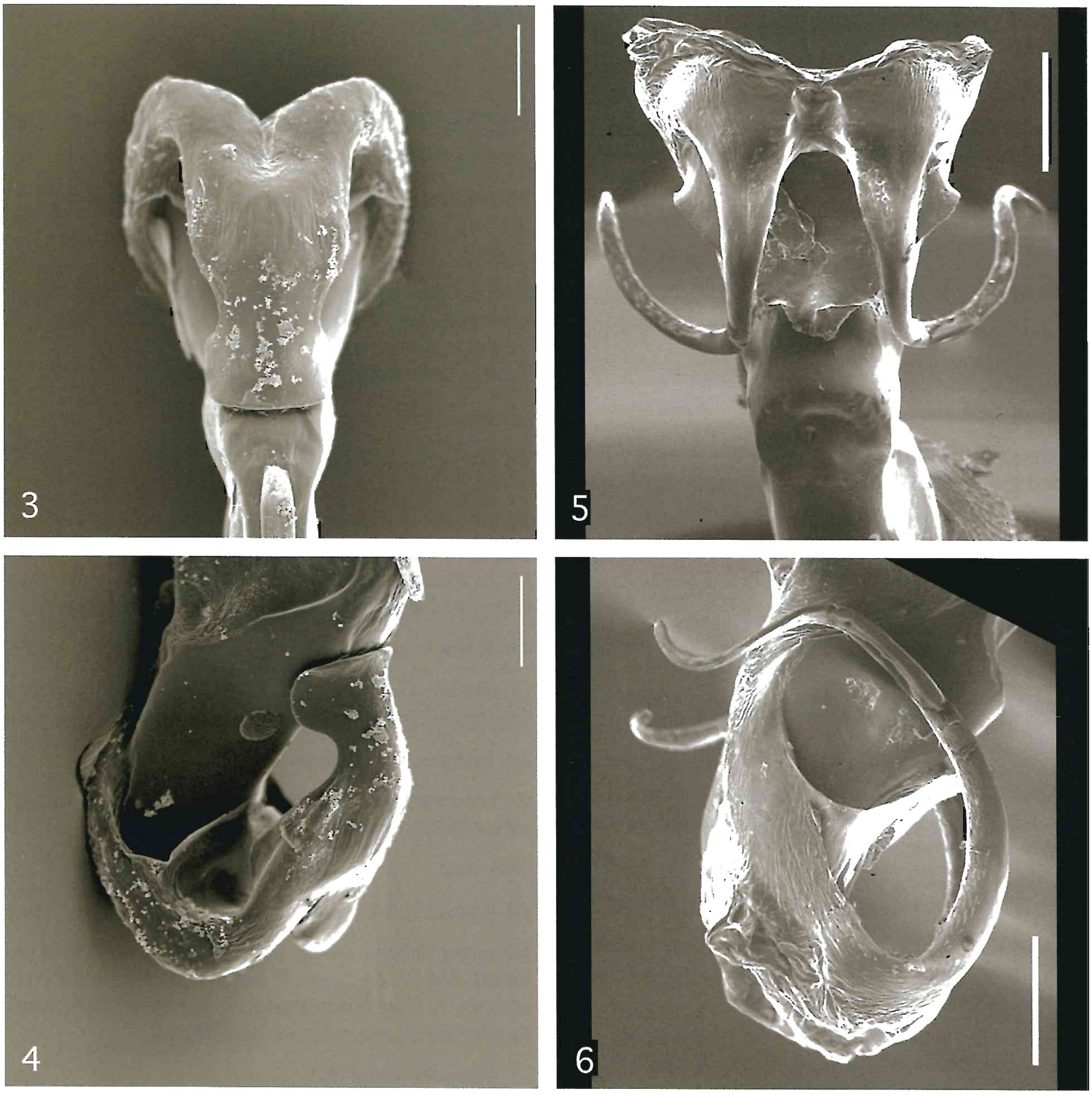
(0) absent; (1) present.

53. Dorsal marking on segment 10.

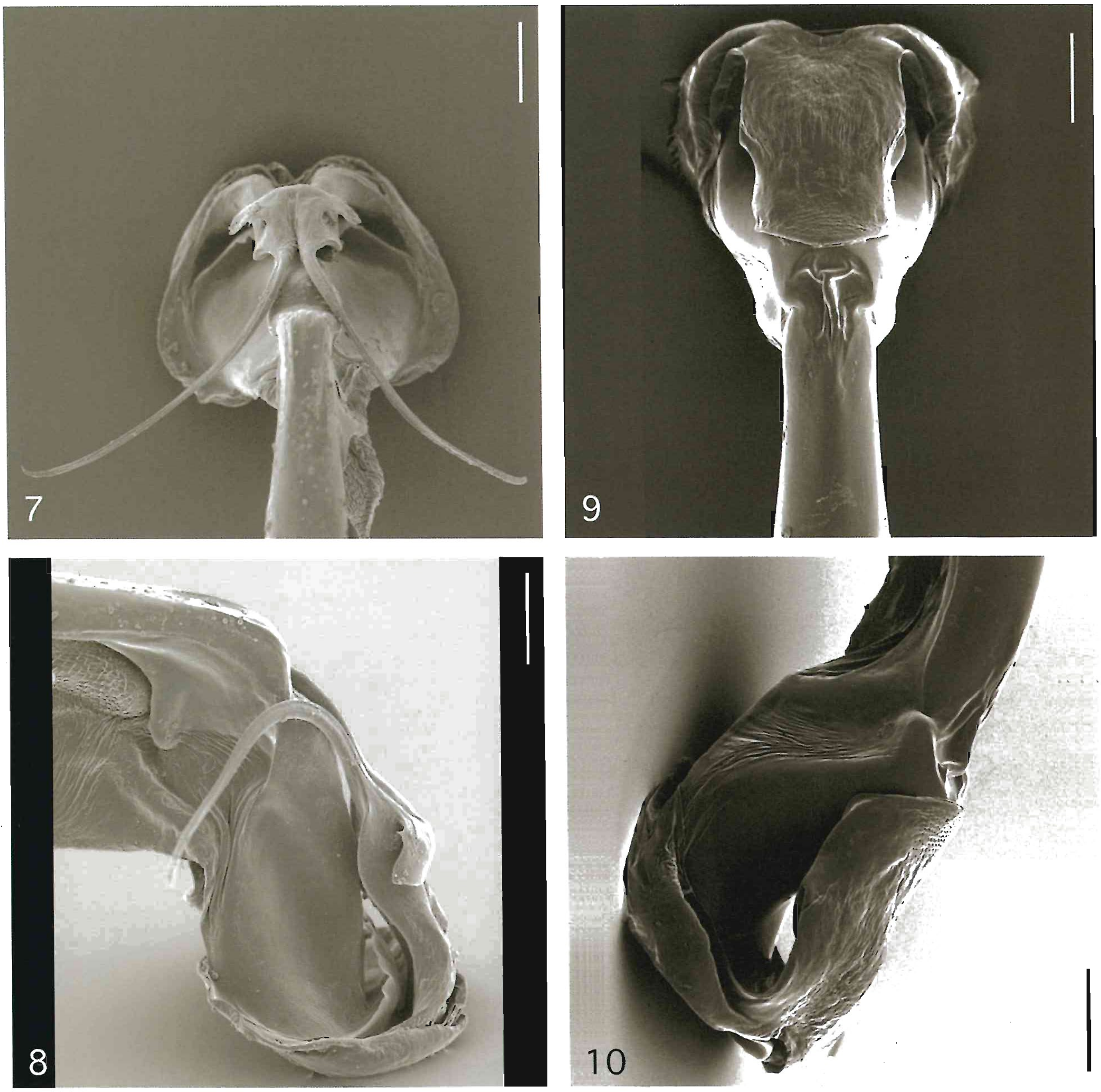
(0) absent; (1) present.

54. Terminal abdominal segments: shape.

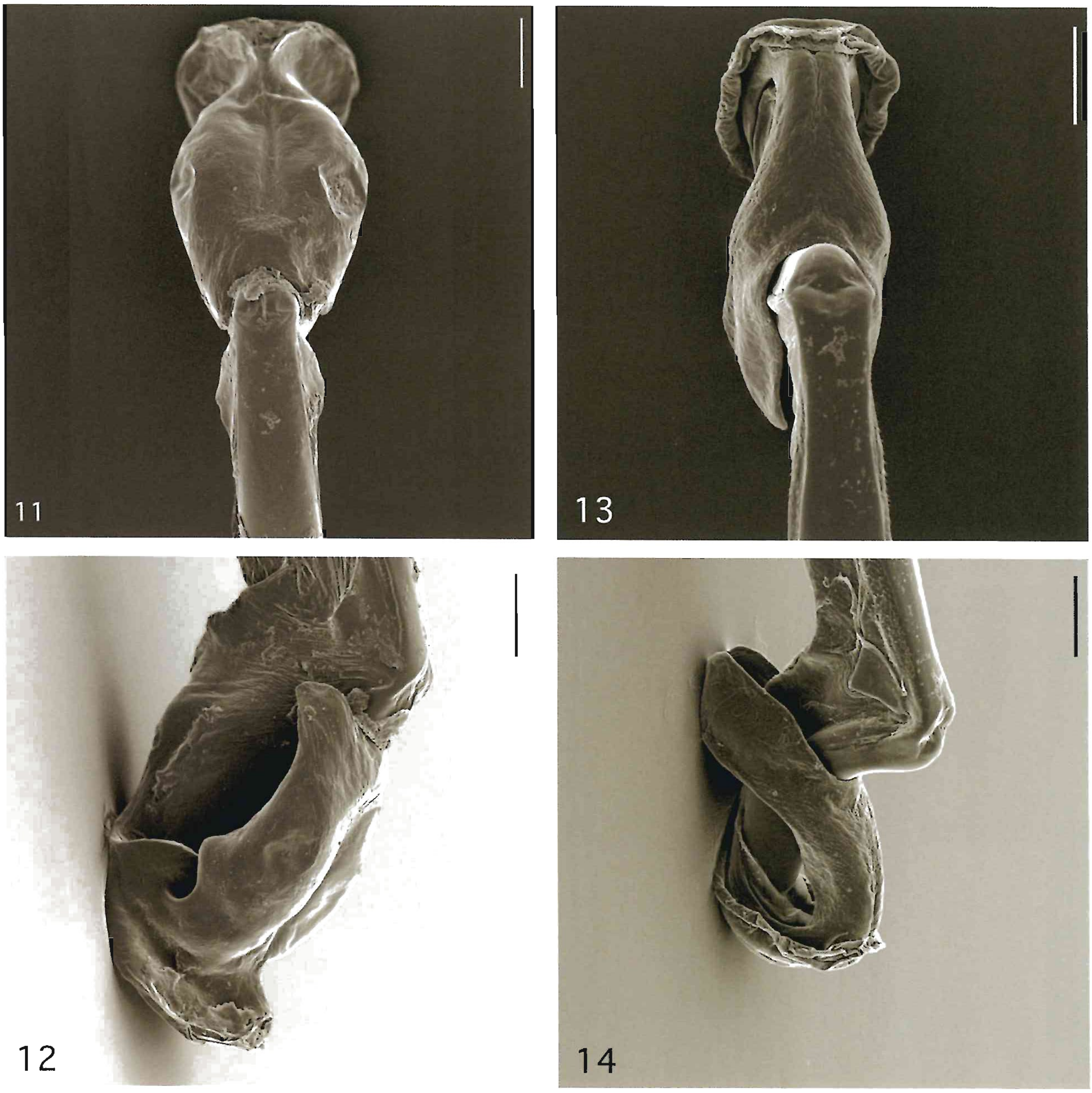
(0) not or only slightly inflated; (1) distinctly inflated.



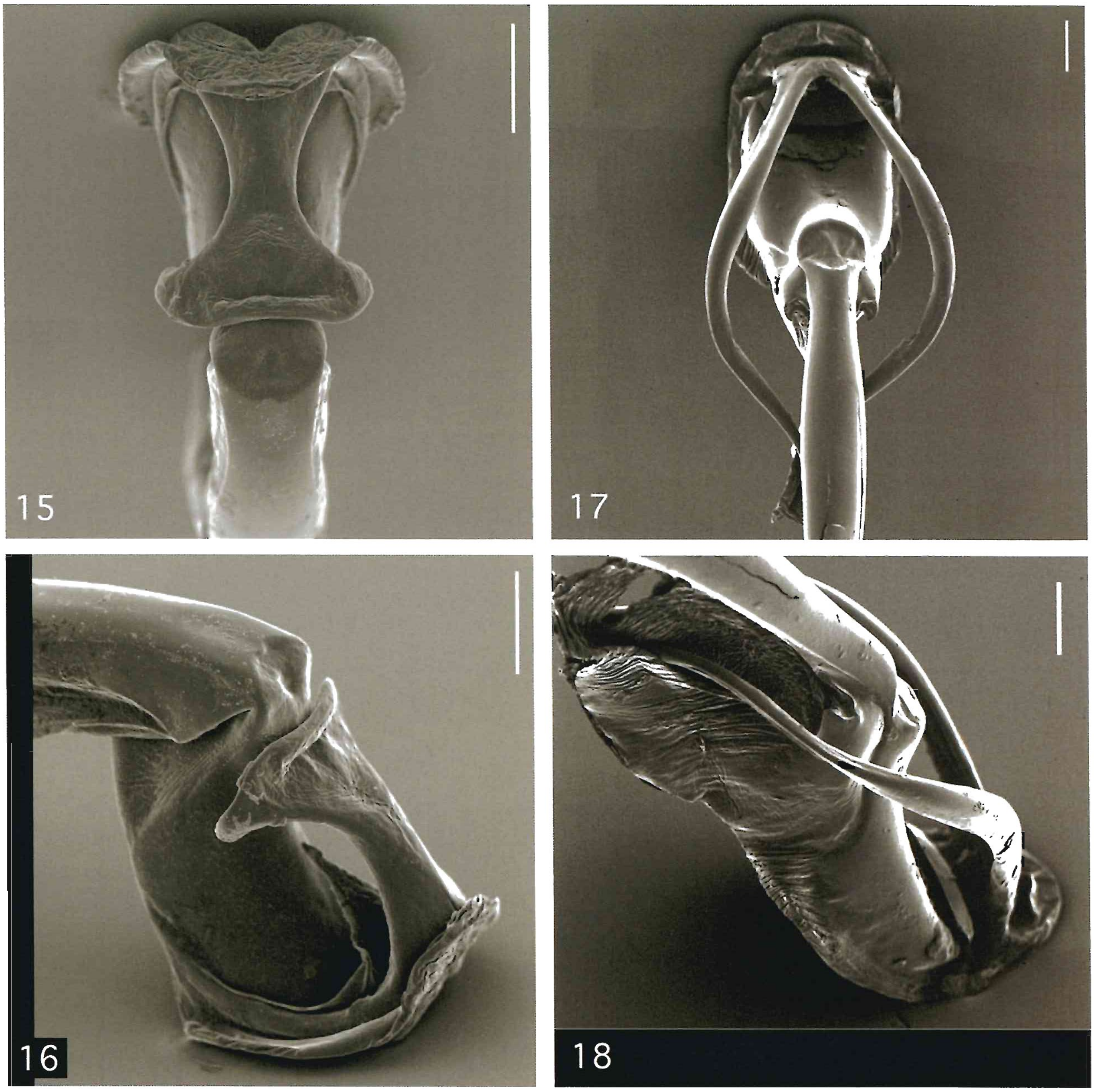
Figs. 3-6: Ligulae of ♂♂ in ventral (3, 5) and lateral view (4, 6): 3-4, *Asthenocnemis stephanodera*; 5-6, *Calicnemia eximia*. Scale bars 100 µm



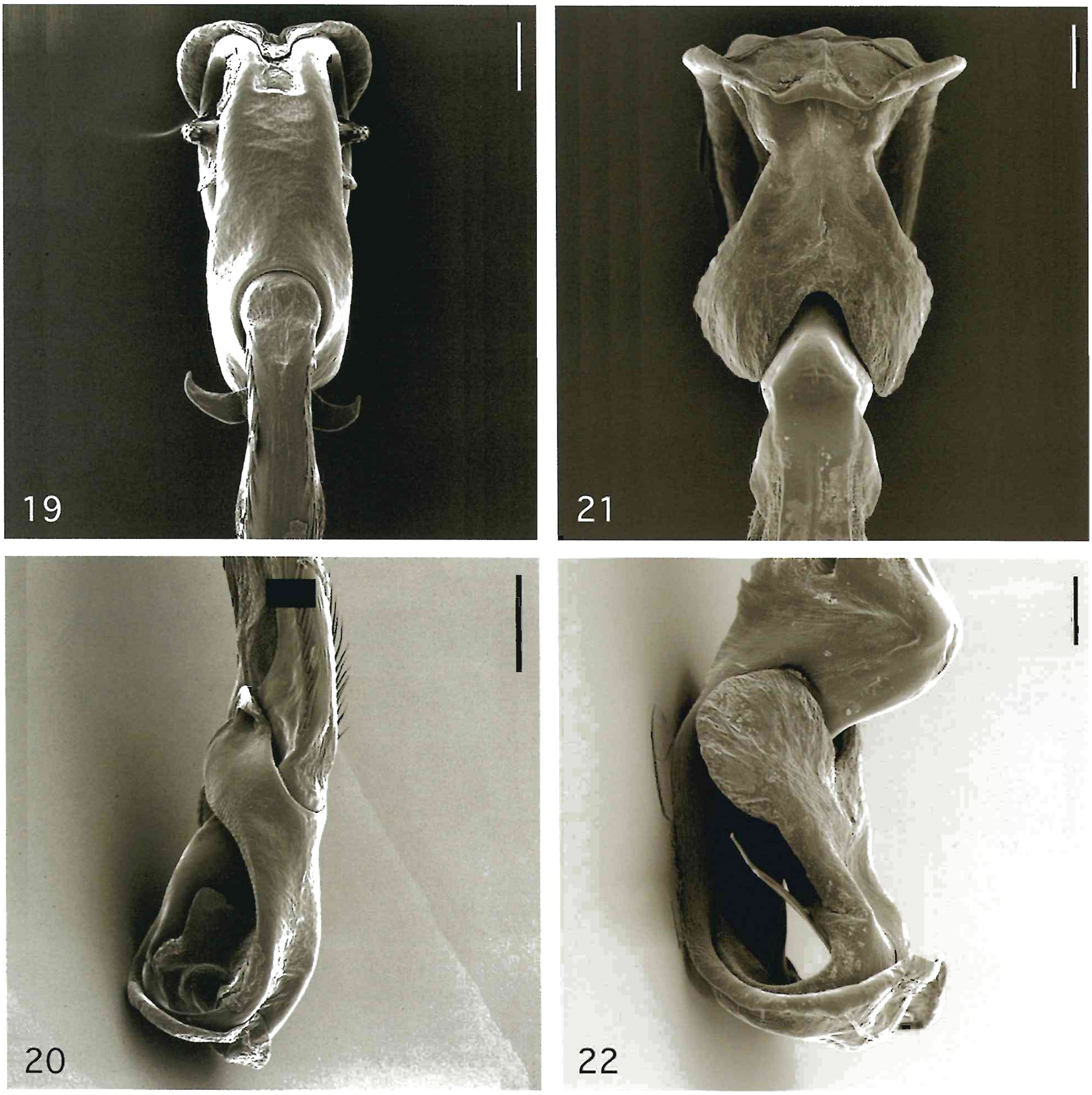
Figs. 7-10: Ligulae of ♂♂ in ventral (7, 9) and lateral view (8, 10): 7-8, *Coeliccia membranipes*; 9-10, *Copera marginipes*. Scale bars 100 µm.



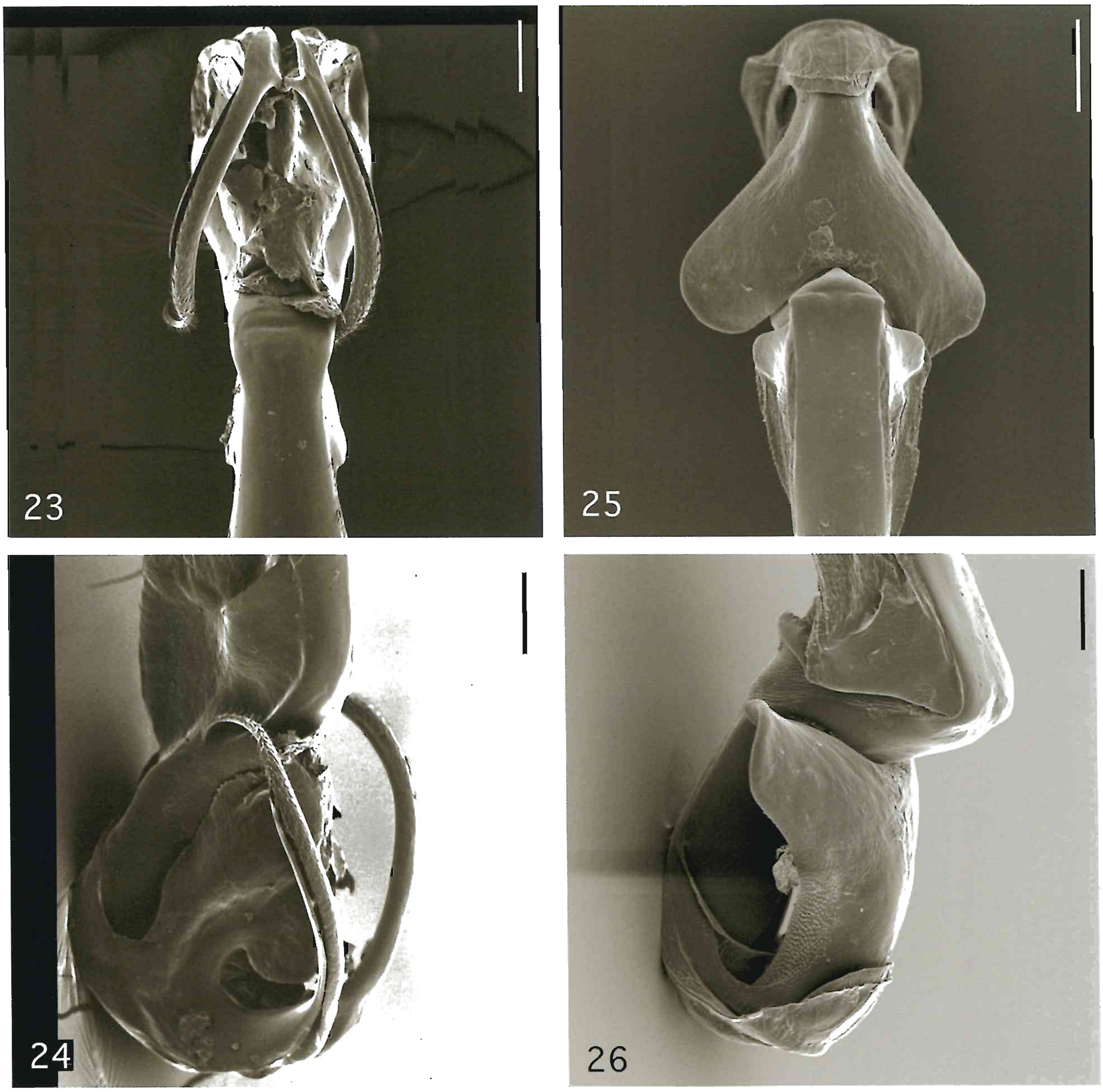
Figs. 11-14: Ligulae of ♂♂ in ventral (11, 13) and lateral view (12, 14): 11-12, *Cyanocnemis aureofrons*; 13-14, *Idiocnemis polhemi* (from alt. 700 m). Scale bars 100 µm.



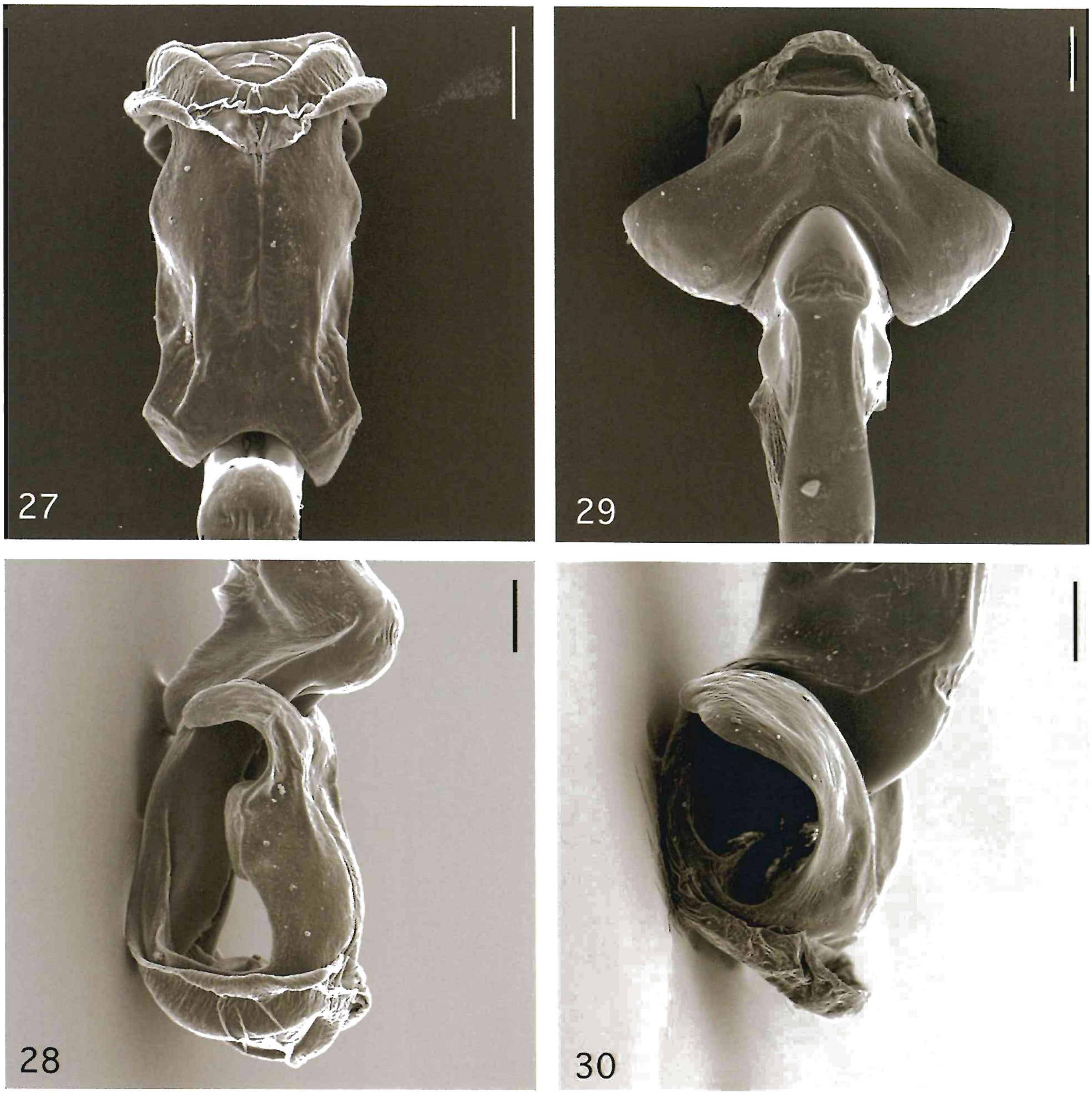
Figs. 15-18: Ligulae of ♂♂ in ventral (15, 17) and lateral view (16, 18): 15-16, *Idiocnemis zebrina sufficiens*; 17-18, *Indocnemis orang*. Scale bars 100 µm.



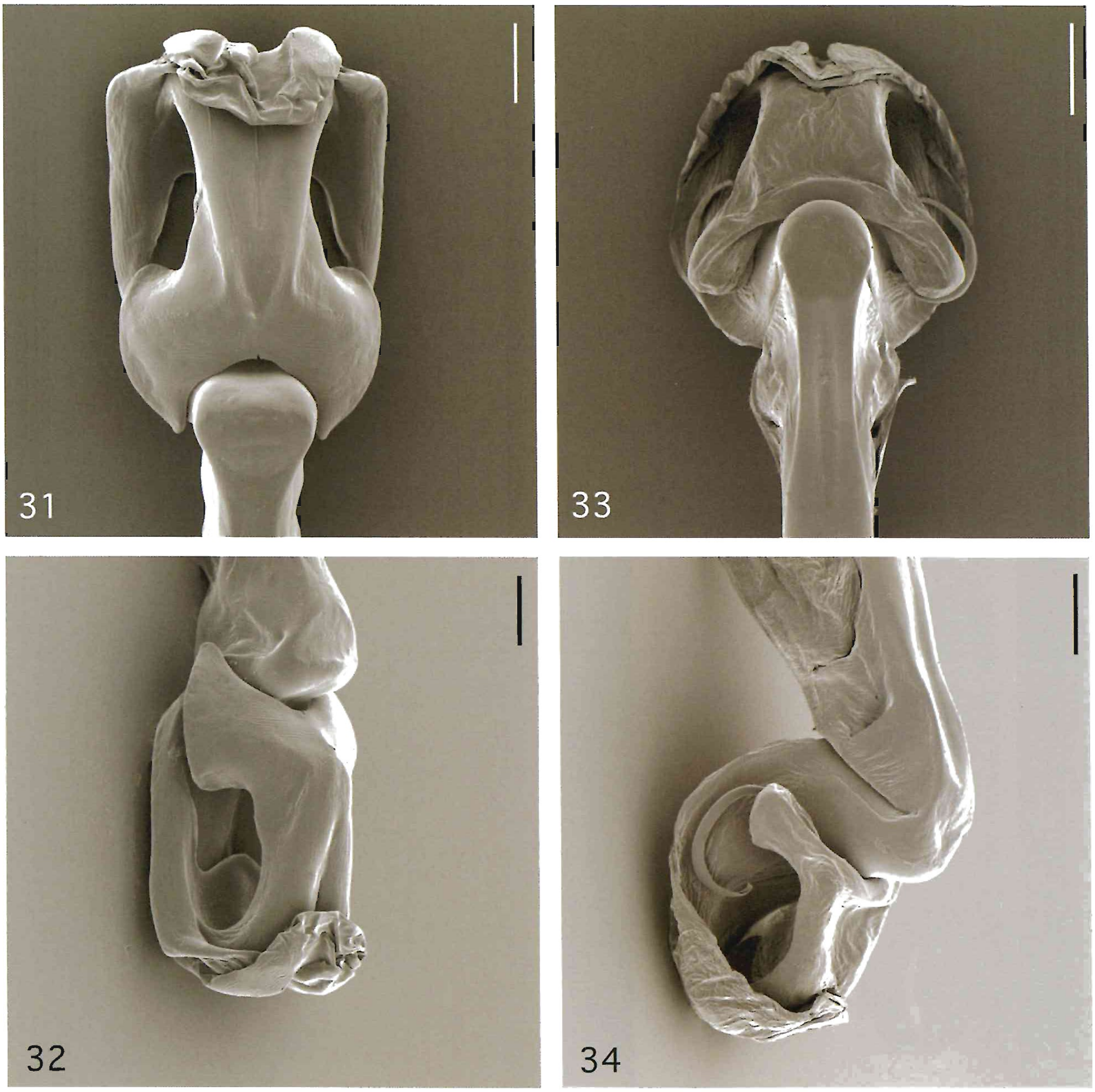
Figs. 19-22: Ligulae of ♂♂ in ventral (19, 21) and lateral view (20, 22): 19-20, *Leptocnemis cyanops*; 21-22, *Lochmaeocnemis malacodora*. Scale bars 100 µm.



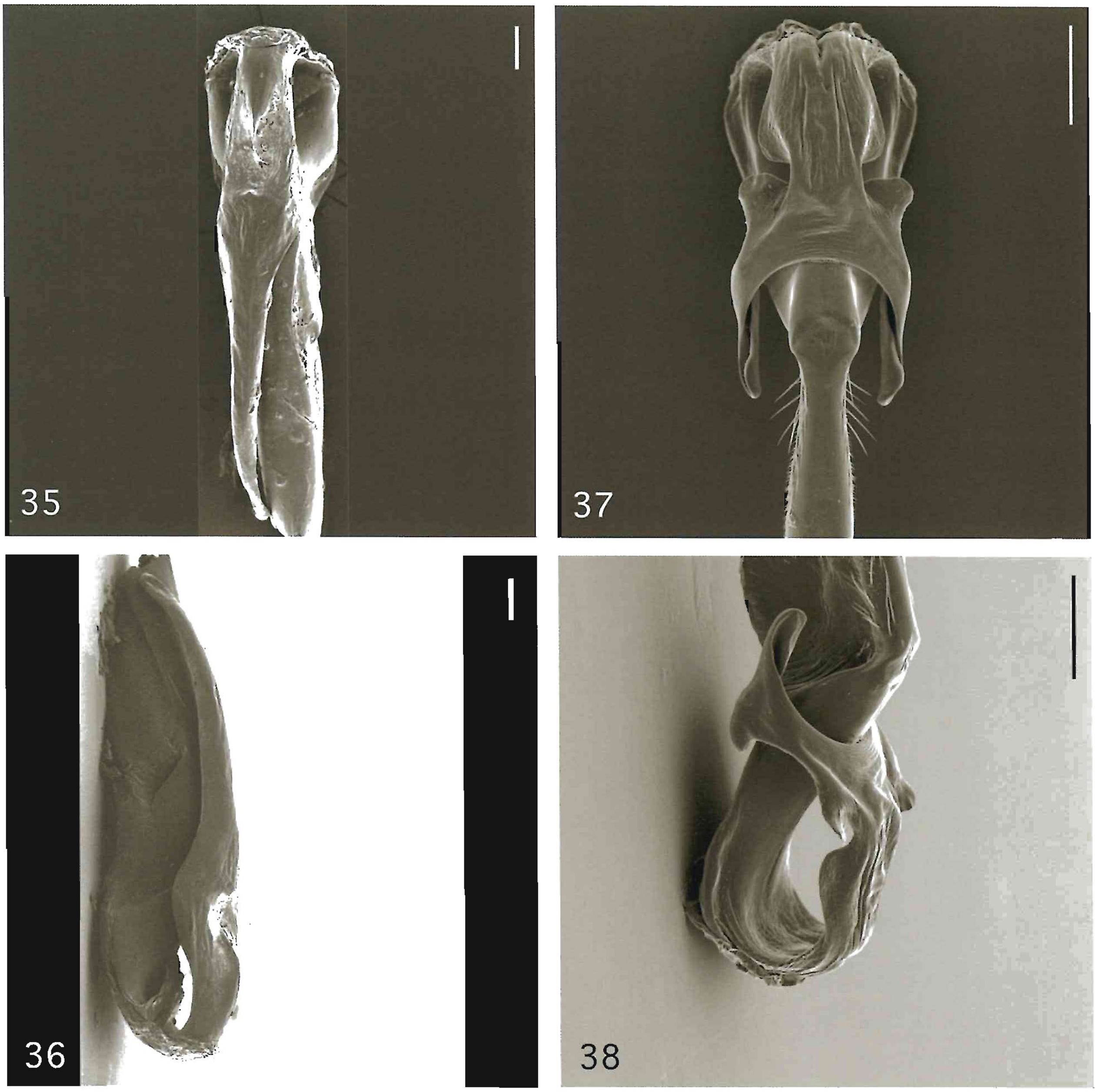
Figs. 23-26: Ligulae of ♂♂ in ventral (23, 25) and lateral view (24, 26): 23-24, *Mesocnemis singularis*; 25-26, *Paramecocnemis erythrostigma*. Scale bars 100 µm.



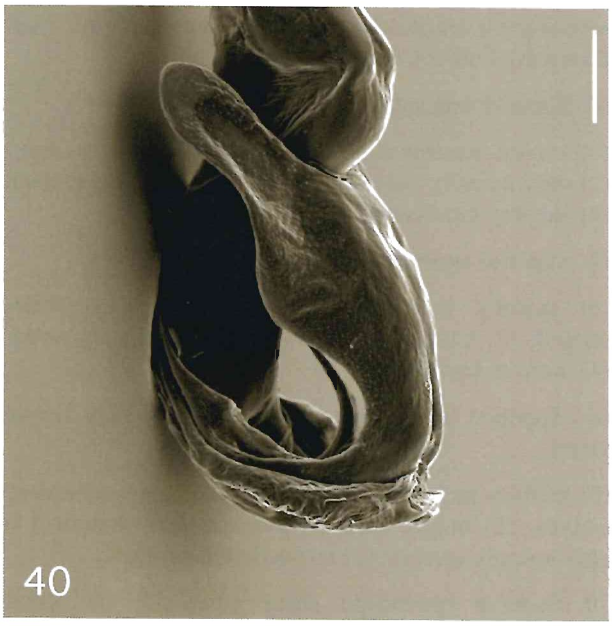
Figs. 27-30: Ligulae of ♂♂ in ventral (27, 29) and lateral view (28, 30): 27-28, *Rhyacocnemis leonorae*; 29-30, *Risiocnemis atropurpurea.* Scale bars 100 µm.



Figs. 31-34: Ligulae of ♂♂ in ventral (31, 33) and lateral view (32, 34): 31-32, *Risiocnemis appendiculata*; 33-34, *Risiocnemis gracilis*. Scale bars 100 μm.



Figs. 35-38: Ligulae of ♂♂ in ventral (35, 37) and lateral view (36, 38): 35-36, *Stenocnemis pachystigma*; 37-38, *Thaumatagrion funereum*. Scale bars 100 µm.



Figs. 39-40: Ligulae of ♂♂ in ventral (39) and lateral view (40): 39-40, *Torrenticnemis filicornis*, Scale bars 100 µm.

In the taxa concerned, the caudal end of abdomen is inflating dorsoventrally and/or laterally from segment 7 or segment 8 onwards.

55. Length ratio abdomen/hindwing.

(0) 1.4 ; (1) 1.5; (2) 1.6; (3) 1.7; (4) 1.8; (5) 1.9; (6) 2.1.

The length ratio of wing length and abdomen length is considerably constant within species; in cases where some variation occured, mean values were calculated.

Anal appendages

56. Length ratio inferior/superior anal appendages.

(0) about 3.0 times; (1) about 1.5 times; (2) 0.9 to 1.0 times; (3) 0.7 to 0.8 times; (4) 0.5 to 0.6 times; (5) 0.3 to 0.4 times; (6) 0.1 to 0.2 times.

For measuring the length of both inferior and superior appendages, curvation of appendages was taken into account as far as possible.

57. Length ratio superior appendages/abdominal segment 10.

(0) about half the length; (1) subequal; (2) about 1.3 times the length; (3) about 1.5 times the length; (4) about 1.75 times the length; (5) twice the length; (6) about 3 times the length.

To avoid measurement errors, the character states were only scored for those species with straight superior appendages.

58. Subbasal process.

(0) absent; (1) present.

In most of the taxa studied, there is a process situated more or less close to the base of superior appendage (Figs. 41-42, 44-45); it varies considerably in shape and length among the species (see below).

59. Subbasal process: shape.

(0) elongate, slender; (1) blunt, subtriangular; (2) acute, short; (3) hook-like, short; (4) long, flattened; (5) broad, flattened; (6) robust, rounded (Figs. 44-45); (7) protruding into a large extension; (8) short, slender; (9) notched squarish process; (10) broadly rounded.

60. Subbasal process: length.

(0) long; (1) of medium length; (2) short.

This character and the next were scored for Risiocnemis (Igneocnemis) species only because of both their good recognizability and discriminatory value in those species.

61. Subbasal process: position (in lateral view).

(0) Partly covered by posterior margin of abdominal segment 10 (in lateral view); (1) just distal to posterior margin; (2) moved further distally.

62. Inner median process.

(0) absent; (1) present.

The superior appendage of four species of the *Idiocnemis bidentata* species-group is furnished with an inner median process which is situated between subbasal and subdistal process; in *Idiocnemis bidentata*, the median process is almost fused with the subdistal one (cf. GASSMANN 2000: figs. 14-17).

63. Inner subdistal process.

(0) absent (Figs. 44-45); (1) small hook; (2) small tubercle; (3) finger-shaped hook; (4) slender hook; (5) blunt medium-sized hook; (6) tubercular protuberance, directed inwards; (7) subtriangular, hooked (Figs. 41-42); (8) large bulge.

64. Subdistal process: base.

(0) not prolonged; (1) moderately prolonged; (2) extensively prolonged.

In some (mainly *Lieftinckia*) species, the base of the subdistal process (hook) is considerably prolonged. Alternatively, the resulting elongate protuberance could also be interpreted and thus homologized as a distally moved subbasal process. However, its specific quality and position renders this alternative less plausible.

65. Superior appendage: second minute spine proximal to subdistal process.

(0) absent; (1) present.

66. Superior appendage: additional spines.

(0) absent; (1) present.

With an additional inner dorsal spine and a second inner baso-ventral spine, the superior appendage of *Lochmaeocnemis malacodora* is of far more complex built than that of other Calicnemiinae.

67. Superior appendage: curvature in lateral view.

(0) curved somewhat dorsad; (1) more or less straight; (2) only apically curved downwards; (3) sickle-shaped; (4) halfway incurved to right angle.

68. Superior appendage: curvature in dorsal view.

(0) apically incurved, tips converging; (1) sickle-shaped; (2) moderately incurved; (3) slightly incurved; (4) more or less straight.

69. Superior appendage: shape inner side (in dorsal view).

(0) halfway kinked outwards; (1) base bulgy, otherwise convex; (2) bulged out; (3) more or less straight; (4) only apically convex; (5) no such modifications.

70. Superior appendage: shape outer side (in dorsal view).

(0) slightly concave, kinked; (1) slightly convex; (2) bulged out; (3) more or less straight; (4) straight, distal part bent outwards; (5) no such modifications.

71. Superior appendage: shape of apex.

(0) rounded; (1) broadly rounded, somewhat flattened (Figs. 41-43; 44-46); (2) sharp; (3) complex, with inner plate; (4) notched; (5) subquadrangular.

72. Inferior appendage: shape in lateral view.

(0) straight, or slightly curved up; (1) strongly curved dorsad; (2) nearly plate-like, straight.

73. Inferior appendage: shape of apex.

(0) distinctly kinked inwards (Figs. 41-43); (1) slightly bent inwards; (2) not kinked inwards (Figs. 44-46).

In *Coeliccia membranipes* and *Indocnemis orang*, the apex of inferior appendage is distinctly kinked inwards as well as slightly bent downwards. *Calicnemia eximia* and *Allocnemis leucosticta* show the same feature, but less distinct.

74. Superior appendages: colour.

(0) black; (1) mainly black, with some yellow areas; (2) reddish; (3) reddish-brown; (4) yellow-brown; (5) yellow-orange; (6) yellow-white; (7) blue.

Ligula

75. Ligula: lateral hooks (cf. GASSMANN 2000).

(0) absent; (1) present (Fig. 12).

Cyanocnemis aureofrons and the species of the *Idiocnemis bidentata* - group exhibit more or less distinct lateral emarginations at the ligula head.

76. Ligula: distal median cleft (cf. GASSMANN 1999).

(0) absent; (1) present; (2) only slightly developed.

77. Ligula: flagella at ligula head.

(0) present (Figs. 5-6, 7-8, 17-18, 23-24, 33-34); (1) absent.

78. Ligula: terminal lobes.

(0) long, broad, apically subrectangular (Figs. 13-14); (1) of median length and width (Figs. 33-34, 39-40); (2) reduced (Figs. 11-12); (3) short, spatulate (Figs.15-16; Figs. 31-32); (4) long, broad, apically rounded; (5) long, very broad (Figs. 29-30); (6) very long, semi-acute (Figs. 35-36); (7) long, broad, apically hooked (Figs.19-20); (8) broad, of median length, subrectangular (Figs. 25-26, 27-28); (9) leaf-shaped, of median length (Figs. 21-22); (10) very broad, of median length; (11) very long, slender.

79. Ligula head: degree of folding.

(0) not folded; (1) slightly folded; (2) moderately folded; (3) strongly folded.

80. Ligula head: width.

(0) broad (Figs. 7-8, 15-16, 31-32, 33-34); (1) elongate, narrow (Figs. 13-14); (2) stout, as wide as long (Figs. 29-30); (3) elongate, subtriangular, widening distally.

81. Ligula: medio-lateral protrusion.

(0) absent; (1) present (Figs. 8, 28, 40).

82. Ligula head: inner protrusion.

(0) absent; (1) present (Figs. 4, 22, 28).

83. Ligula: apical ridge/plate.

(0) absent; (1) intermediate ridge (Figs. 15-16); (2) ridge (Figs. 33-34); (3) plate (Figs. 7-8).

84. Ligula: inner lamina/flagellum.

(0) lamina; (1) intermediate between lamina and flagellum (Fig. 16); (2) flagellum (Figs. 22, 40); (3) reduced to short process.

85. Ligula: incision between terminal lobes: shape.

(0) rounded (Figs. 5-6, 11-12, 13-14, 15-16, 17-18, 19-20, 21-22, 25-26, 27-28, 31-32, 33-34, 39-40); (1) arc-shaped; (2) slightly arc-shaped (Figs. 29-30); (3) sharp; (4) very sharp (Figs. 7-8, 23-24); (5) straight.

Female characters:

86. Female pronotal tubercles.

(0) distinct, high (Fig. 50); (1) distinct, of moderate height; (2) only sightly raised (Fig. 48), or bulgy.

The female pronotal tubercles can be flat up to slightly raised (Fig. 48), or extended into high conical processes (Fig. 50) which are mostly pointed apically.

87. Female posterior pronotal lobe.

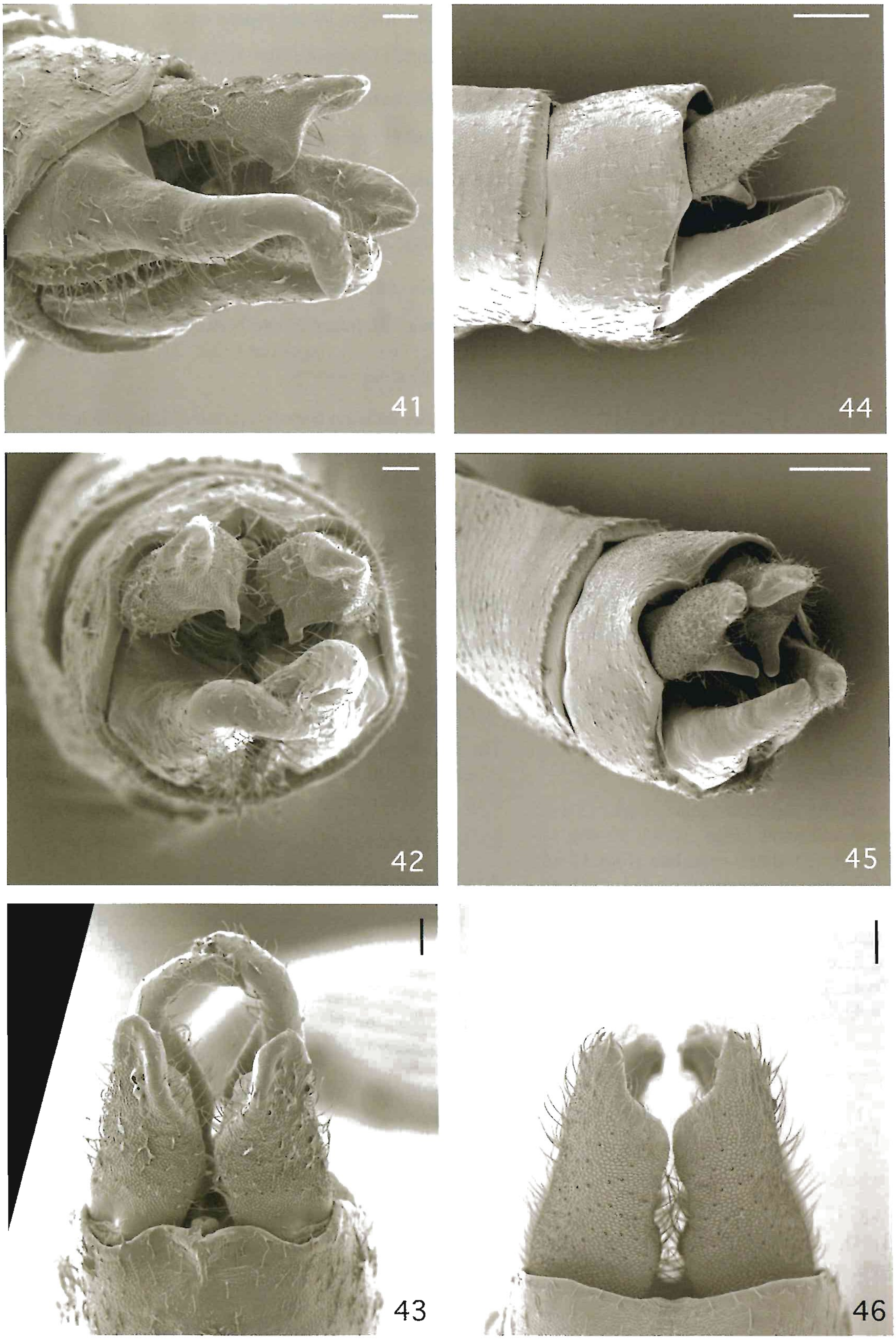
(0) trilobate; (1) undivided.

All species of genus *Risiocnemis* have the posterior pronotal lobe divided into a broad median lobe and a pair of narrow lateral lobes (Fig. 49). However, the character state 'trilobate' also circumscribes a condition where either the median lobe is completely lost or at least distinctly reduced.

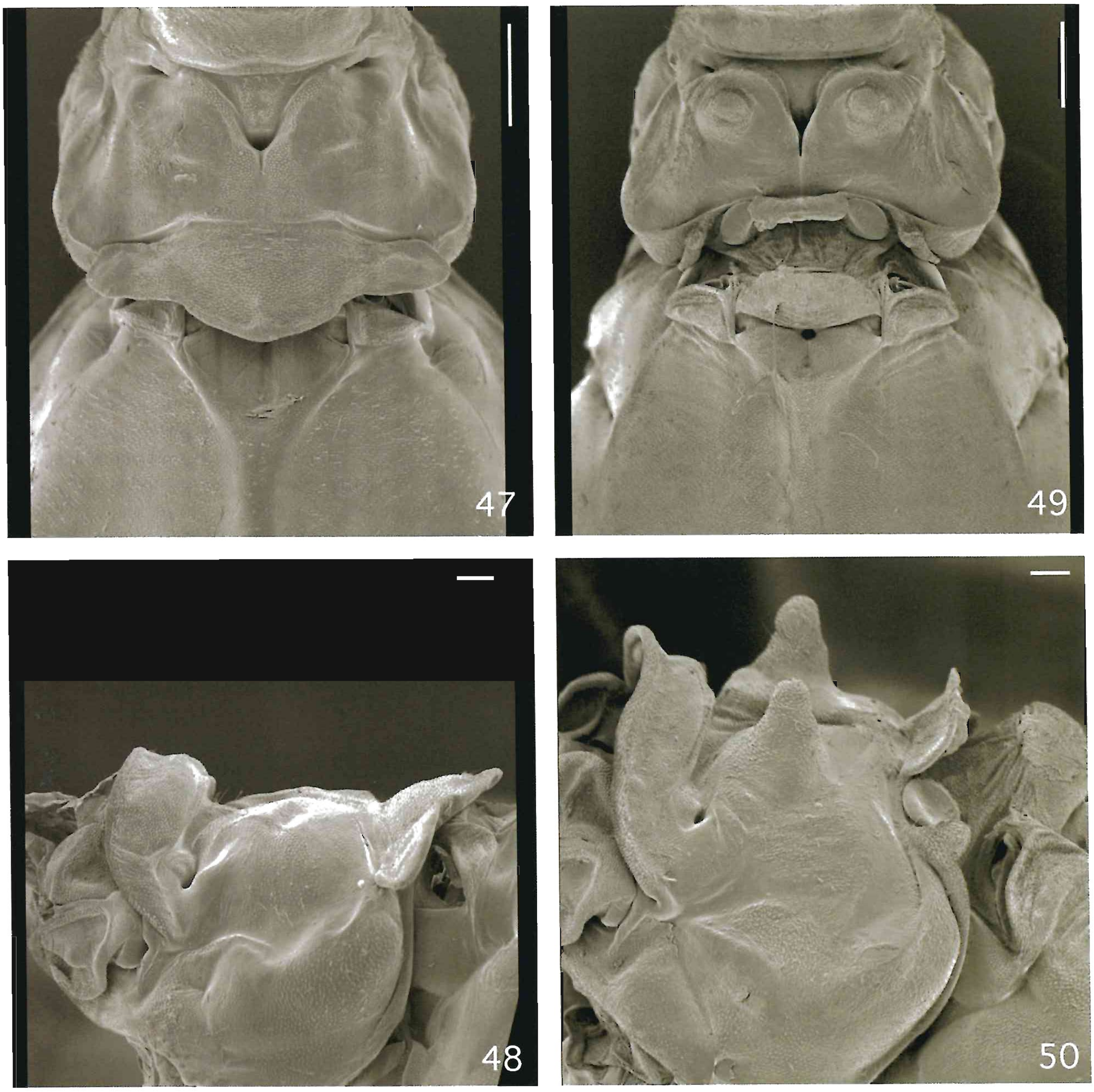
88. Female posterior pronotal lobe: elevation.

(0) directed anteriorly; (1) strongly elevated; (2) distinctly elevated (Fig. 50); (3) halfway elevated; (4) not or only slightly elevated (Fig. 48).

In case of species with trilobate posterior pronotal lobe, only the elevation of the median part (lobe) was determined.



Figs. 41-43: Anal appendages of *Coeliccia membranipes*, ♂, in lateral (41), posterior (42) and dorsal (43) view. **Figs. 44-46:** Anal appendages of *Risiocnemis elegans*, ♂, in lateral (44), posterior lateral (45) and dorsal (46) view. Scale bars 300 µm (44, 45), 100 µm (41-43, 46).



Figs. 47-50: Prothorax of *Idiocnemis mertoni*, ♀ (47, 48) and *Risiocnemis elegans*, ♀ (49, 50) in dorsal (47, 49) and lateral (48, 50) view. Scale bars 300 µm (47, 49), 100 µm (48, 50).

3. RESULTS

3.1. Monophyly of Platycnemididae and Calicnemiinae

Within the scope of the present study, it was not possible to thoroughly test the hypothesis of monophyly for the family Platycnemididae and/or the subfamily Calicnemiinae; several families of Coenagrionoidea and even other superfamilies would have to be included in such an analysis. However, the morphological studies revealed putative synapomorphies which apparently have not been mentioned by other authors, and which could, however, be considered in future studies of higher-level phylogeny. For the Platycnemididae these are the only moderately kinked arculus (which is not nearly right-angled, as in at least some coenagrionides), and the comparatively long legs (femora of hind legs distinctly reaching beyond posterior margin of synthorax). In the present analysis, the Calicnemiinae turn out to be monophyletic with regard to the Platycnemidinae (*Copera* and *Platycnemis*); however, all apomorphic character states at the ingroup node experience one or more subsequent reversals or transformations in the ingroup; thus, there is no synapomorphy uniting all calicnemiines based on the present data set.

3.2. Phylogeny

The parsimony analysis resulted in 732 equally parsimonious cladograms (721 steps; consistency index: 0.406, retention index: 0.717, rescaled c.i.: 0.292), of which the strict consensus is shown in Figure 51. The strict consensus cladogram is largely resolved at the species level for the New Guinean *Idiocnemis* and the Philippine *Risiocnemis*. The monophyly of both genera as well as that of the smaller Papuan genera *Arrhenocnemis* and *Paramecocnemis* is confirmed. *Rhyacocnemis* forms a monophyletic group together with *Idiocnemis leonorae* which therefore is transferred to that genus (see below). The three representative species of the Oriental genera *Calicnemia, Coeliccia* (*C. membranipes*, Plate 1a) and *Indocnemis* also cluster together in the strict consensus. At the base of the cladogram, we find an unresolved assemblage consisting of all Afrotropical genera examined. The ingroup node is well supported (d=3). We find *Arrhenocnemis* (New Guinea) in a reasonably well supported but unresolved clade (d=2) together with the genera *Risiocnemis* (Philippines), and single species of *Lieftinckia* and *Salomocnemis* (Solomon Islands); at a higher level, this clade is part of a polytomy comprising *Asthenocnemis*, the smaller Papuan genera and the *Idiocnemis* clade. At the next higher level, the African taxa join into a polytomy also involving the *Coeliccia-/Indocnemis-/Calicnemia* - clade.

Idiocnemis Selys

The relationships among the *Idiocnemis* species turn out to be nearly fully resolved in the strict consensus cladogram. The *I. inornata* species-group (GASSMANN 1999) is monophyletic, leaving the *I. bidentata* - group (GASSMANN 2000) paraphyletic. The latter one shows a largely pectinate topology except for the two sister species *I. inaequidens* Lieftinck (Plate 1d) and *I. pruinescens*. Not surprisingly, *I. dagnyae* represents the "link" between the two species-groups; this species combines traits of both species-groups. The *I. inornata* - group is well supported (d=3); its subclades only partly reflect the preliminary subgroupings recognized by GASSMANN (1999): leaving aside group I which only consists of one single species, *I. inornata*, we find that group II (northern New Guinea) is distributed across two clades which are, however, not sister clades. Instead, most members of group III (eastern Papuan archipelagos) are united with the western representatives of the northern New Guinea species in one clade, while the northeastern New Guinea species, together with a single southern species, *I. australis* Gassmann (Plate 1c), are the sister group to the remaining clade.

Risiocnemis Cowley

The Philippine genus *Risiocnemis* as well as both of its subgenera turn out to be monophyletic. While subgenus *Risiocnemis* is reasonably well supported (d=2), the basal node of subgenus *Igneocnemis* is even more strongly supported with the highest decay index (d=5) of all clades. Within subgenus *Risiocnemis*, the mainly northern Philippine *R. serrata* - species-group (Plate 1f: *R. serrata*) is well supported (d=3). The sister group relationship of *R. rolandmuelleri* and *R. seidenschwarzi*, distributed in the West Visayans, is confirmed and thus the monophyly of the *R. rolandmuelleri* - species-group, although only weakly supported (d=1). Independent from the still uncertain position of *R. erythrura* and *R. praeusta*, the predominantly southernly distributed *R. appendiculata* - group can be considered clearly paraphyletic, with *R. kiautai* representing the sister taxon of the *R. serrata* - group, and *R. confusa* being the sister taxon of the *R. rolandmuelleri* - group. *R. arator*, the only representative of the fourth species-group defined by HÄMÄLÄINEN (1991a), is the most basal taxon of the group.

In subgenus *Igneocnemis*, *R. atripes* is the most basal species, followed by *R. rubricercus*; both species are from Mindanao. Proceeding further on, we find two distinct clades which are each, however, weakly supported (d=1). The first one comprises only species from the eastern Philippines (e.g. *R. kaiseri*, Plate 1e), except for *R. fuligifrons* which is distributed across northwestern Mindanao (Zamboanga Peninsula). The second one mainly contains a mixed assemblage of species from Mindanao and Luzon, but also from the West and East Visayan islands. There is little hierarchical structure and only weak support within both these clades, except for the well supported sister group relationships of *R. calceata/R. siniae*, and *R. flammea/R. odobeni*.

3.3. Preferred phylogenetic hypothesis

A survey of all equally parsimonious cladograms revealed that there are two different positions *Asthenocnemis* takes: either basal to a clade containing all Papuan representatives, or just in between the Papuan taxa. Here, the latter alternative is considered less favourable, because it would mean that reversals in at least four important structural characters would have taken place in *Asthenocnemis*: from a denticulate wing margin back to a smooth one, the reversal from an inner flagellum to a lamina as well as the increase in postquadrilateral cells in both fore- and hindwing. If we filter the (resolved) trees showing *Asthenocnemis* in a basal position out of the entire set of trees, we obtain 70 trees which only differ in minor details of inner-generic relationships. To reconstruct character evolution, one tree out of this subset was chosen as the preferred phylogenetic hypothesis (Fig. 52). According to this clado-

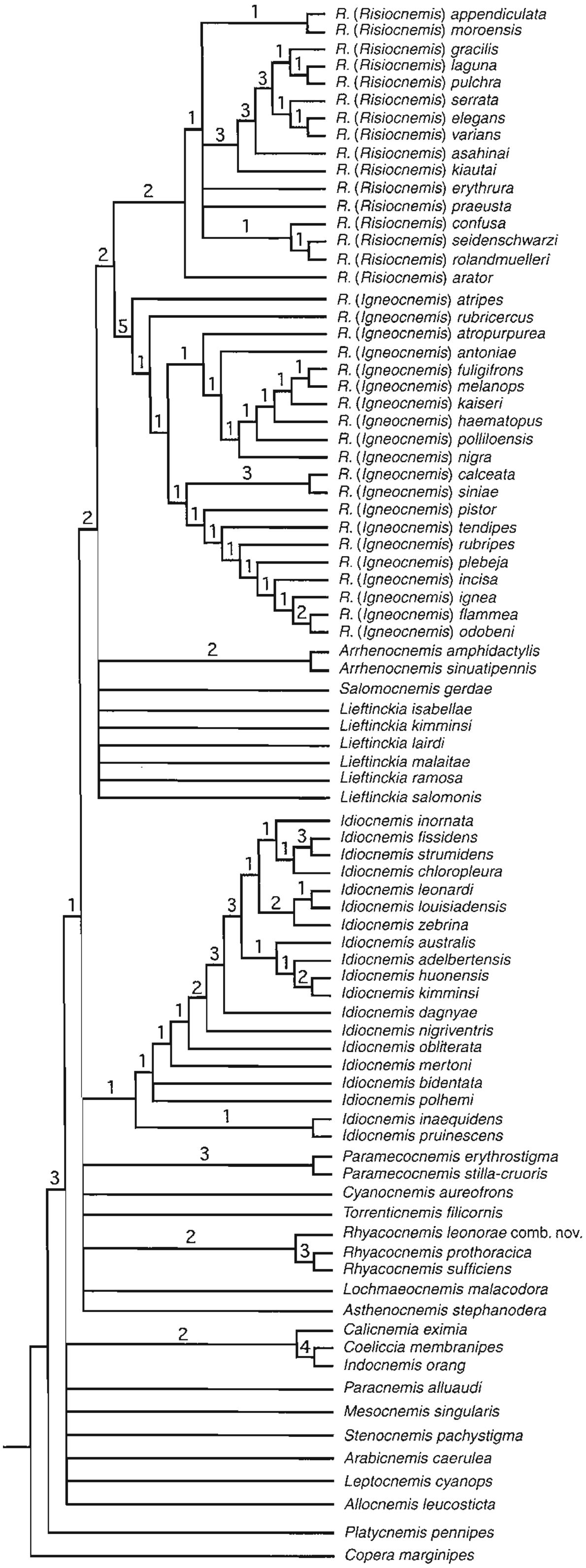
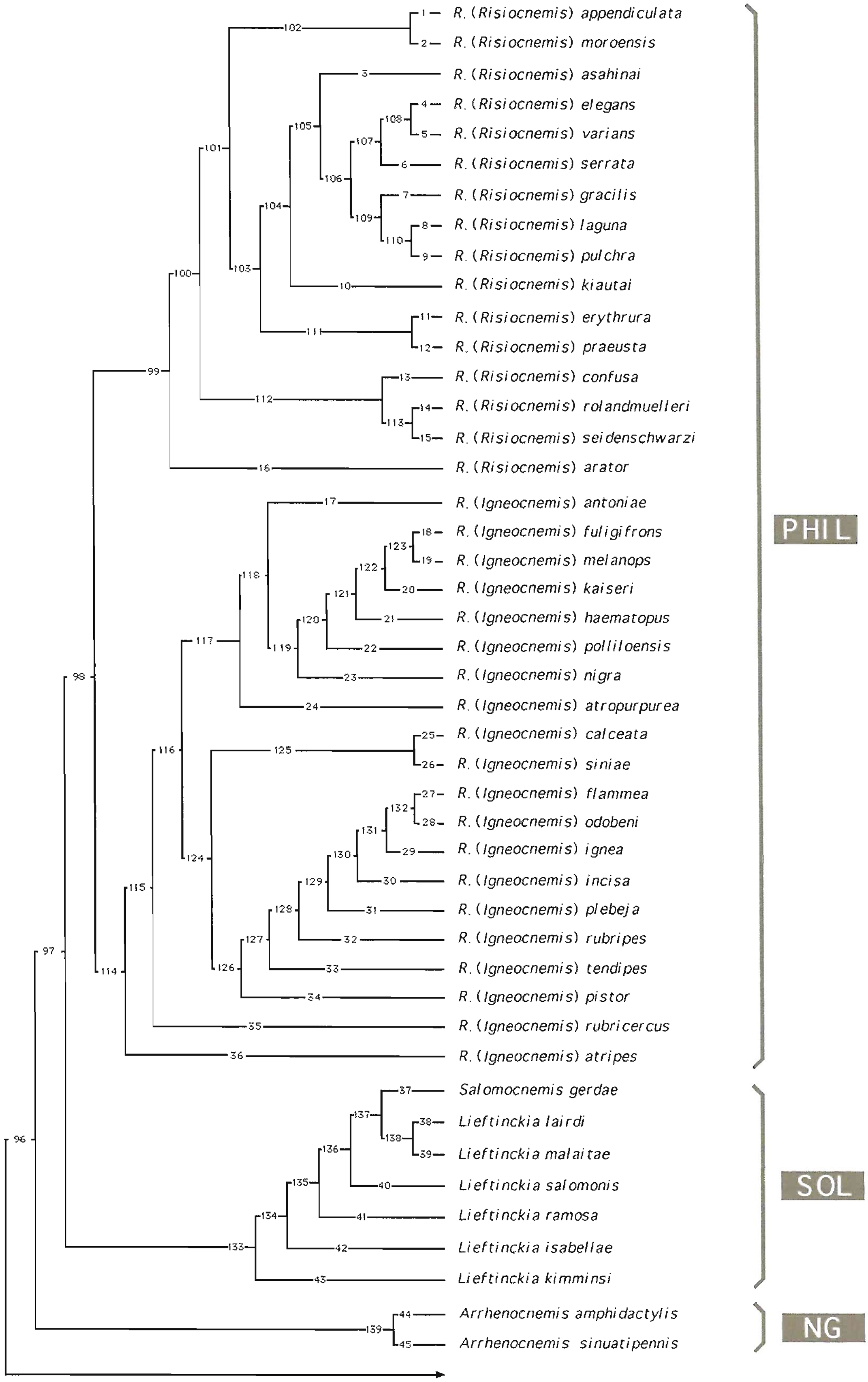


Fig. 51: Strict consensus cladogram derived from all 732 equally parsimonious trees. Decay indices (Bremer support values) are indicated on the branches.


1 R. (Risiocnemis) appendiculata
2 R. (Risiocnemis) moroensis
3 R. (Risiocnemis) asahinai
4 R. (Risiocnemis) elegans
5 R. (Risiocnemis) varians
6 R. (Risiocnemis) serrata
7 R. (Risiocnemis) gracilis
8 R. (Risiocnemis) laguna
9 R. (Risiocnemis) pulchra
10 R. (Risiocnemis) kiautai
11 R. (Risiocnemis) erythrura
12 R. (Risiocnemis) praeusta
13 R. (Risiocnemis) confusa
14 R. (Risiocnemis) rolandmuelleri
15 R. (Risiocnemis) seidenschwarzi
16 R. (Risiocnemis) arator
17 R. (Igneocnemis) antoniae
18 R. (Igneocnemis) fuligifrons
19 R. (Igneocnemis) melanops
20 R. (Igneocnemis) kaiseri
21 R. (Igneocnemis) haematopus
22 R. (Igneocnemis) polliloensis
23 R. (Igneocnemis) nigra
24 R. (Igneocnemis) atropurpurea
25 R. (Igneocnemis) calceata
26 R. (Igneocnemis) siniae
27 R. (Igneocnemis) flammea
28 R. (Igneocnemis) odobeni
29 R. (Igneocnemis) ignea
30 R. (Igneocnemis) incisa
31 R. (Igneocnemis) plebeja
32 R. (Igneocnemis) rubripes
33 R. (Igneocnemis) tendipes
34 R. (Igneocnemis) pistor
35 R. (Igneocnemis) rubricercus
36 R. (Igneocnemis) atripes
37 Salomocnemis gerdae
38 Lieftinckia lairdi
39 Lieftinckia malaitae
40 Lieftinckia salomonis
41 Lieftinckia ramosa
42 Lieftinckia isabellae
43 Lieftinckia kimminsi
44 Arrhenocnemis amphidactylis
45 Arrhenocnemis sinuatipennis
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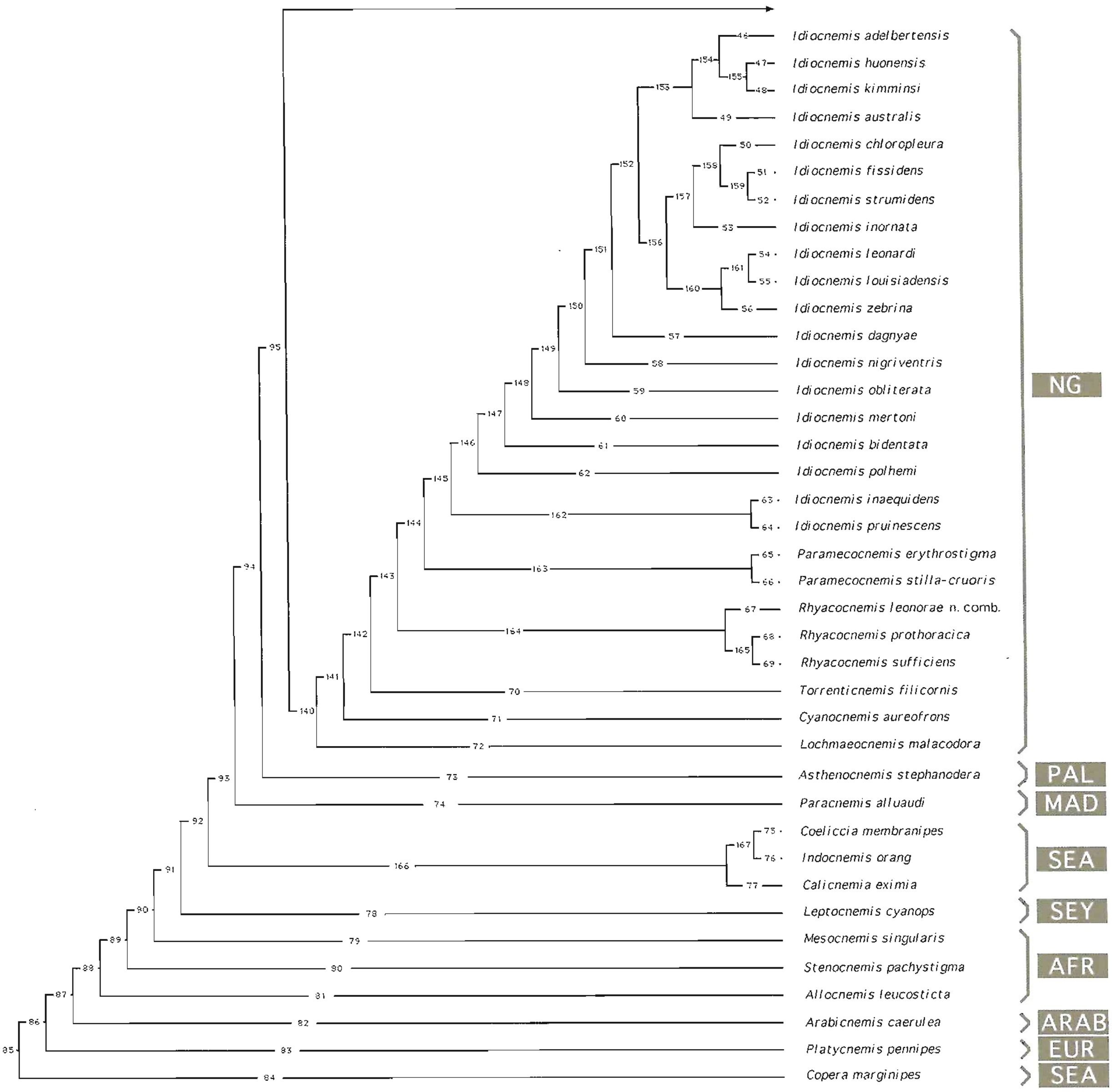

Fig. 52: Preferred tree out of 70 equally parsimonious trees showing *Asthenocnemis* in comparatively basal position. Branch numbers refer to the character changes listed in Appendix 3. Paraphyly of the outgroup taxa is due to the rooting method. Abbreviations: AFR = Africa; ARAB = Arabian Peninsula; EUR = Europe; MAD = Madagascar; NG = New Guinea; PAL = Palawan; PHIL = Philippines; SEA = (Mainland) Southeast Asia, Sundaland; SEY = Seychelles; SOL = Solomon Islands.

gram, a sister group relationship between the Philippine *Risiocnemis* and the Solomon-clade (*Lieftinckia-Salomocnemis*) is proposed, based on two synapomorphies: the absence of an antehumeral stripe and the shape of the terminal abdominal segments which are not inflated. This clade shares two synapomorphies with its sister group, *Arrhenocnemis*: the reduction of postquadrilateral cells in forewing from three to just two, as well as the reduction of a dorsal marking on segment 9; furthermore, two characters change along branch 96: the colour of superior appendages (from black to yellow-brown; strongly homoplasious character), and the shape of the terminal lobes of the ligula (from the reduced state to short, spatulate lobes). At the next higher level, that clade described above is united with all Papuan taxa in a monophyletic group, resulting in an 'Indo-Pacific clade'; the latter comprises all Papuan and Philippine taxa and is characterized by the reduction of the third postquadrangular cell in the hindwing (synapomorphy of all representatives) as well as the absence of a transverse stripe on vertex (with a reduction to an only diffuse stripe in *Arrhenocnemis*). The most remarkable apomorphic trait of the 'Indo-Pacific clade', however, is the distinctly crenulate wing margin; however, it is reduced to a smoothly sinuous condition in *Igneocnemis*; thus, the distinctly crenulate wing margin turns out to be plesiomorphic in subgenus *Risiocnemis*. The New Guinean clade (excluding *Arrhenocnemis*) is characterized by an basal apomorphic change (branch 140) from an inner lamina to an inner flagellum of the ligula, however, it cannot be considered an autapomorphy of the whole clade because two independent subsequent reversals into an intermediate state take place, as well as one into a rudimentary short process. Five further character changes occur at the base of the New Guinea clade, but all of them experience subsequent reversals.

The large Indo-Pacific (sub)genera and their group-defining characters are as follows: *Igneocnemis* species firstly are characterized by the smoothly sinuous wing apex. Other synapomorphies of *Igneocnemis* species are the subequal length of antennal pedicellus and scapus, the pointed (sharp) apex of the superior appendage and the stout ligula head. Thus, in total, *Igneocnemis* species are united by four synapomorphies. Subgenus *Risiocnemis* is characterized by three synapomorphies, i.e. the distal position of the arculus, a slight brownish breath on wings as well as the trilobate female posterior pronotal lobe. A pair of brown spots lateral to the ocelli is an autapomorphy of the most recent common ancestor of sg. *Risiocnemis* and is maintained in all species except for *R. appendiculata*. Compared to *Risiocnemis* and its subgenera, the monophyly of *Idiocnemis* is weakly supported (see above). However, the genus is characterized by the following autapomorphies (= synapomorphies of its species): coloration of legs (light to medium brown, darkened to a varying extent) and the shape of the terminal abdominal segments (not or only slightly inflated).

3.4. Consequences for classification

Idiocnemis leonorae Lieftinck is transferred to *Rhyacocnemis* Lieftinck:

Rhyacocnemis leonorae (Lieftinck, 1956) **comb. nov.**

The genus now comprises three species, characterized by four synapomorphies, most of them referring to the peculiar shape of the male appendages: superior appendage apically incurved, with tips converging; inferior appendages rudimentary (0.1 to 0.2 times the length of superiors); apex of superior appendage sharp (homoplasious character). A distinct apomorphic trait of the ligula in *Rhyacocnemis* is the inner protrusion of the ligula head (Fig. 28); however, the condition in *R. prothoracica* is not known.

Since the position of *Salomocnemis* within one clade together with *Lieftinckia* (Fig. 52) is not stable (cf. consenus cladogram: Fig. 51), synonymization of the former genus with the latter is not considered here.

4. DISCUSSION

4.1. General

The present study should be considered a first approach to the phylogeny of Calicnemiinae. However, some conclusions can be drawn with relative certainty, i. e. the confirmed monophyly of the larger Indo-Pacific genera, especially *Risiocnemis*; there can also be no doubt about the monophyly of each of its subgenera. Unfortunately, basal relationships within Calicnemiinae are not unambigiously resolved, a fact which might be due to taxon sampling in the Oriental and African taxa, as well as to the fact that genera of doubtful family status (e.g. *Mesocnemis*) have been included; these factors potentially introduce homoplasy. Generally it holds that a large number of taxa keeps the consistency index low (KITCHING et al., 1998); with a taxa/character ratio of 84/88, the comparatively low actual c. i. (= 0.406) was to be expected. However, it was the intention of the author to include as many representatives of Calicnemiinae as possible to thoroughly cover the (morphological) diversity of the group. The monophyly of the subfamily Calicnemiinae in its present form remains doubtful; no unique synapomorphy for all species currently included has been found in the analysis with regard to Platycnemidinae; however, REHN (2003) found one synapomorphic trait supporting his *Coeliccia-Indocnemis/Risiocnemis* - clade: the absence of a large, proximal hornlike sclerite on the posterior articular plate. Unfortunately, this character could no longer considered (and examined) here after REHN's paper had come out. Although REHN's taxon sampling is rather scarce, certainly structural traits of the wing articulation appear to be important characters to continue with.

Possibly, there are indeed comparatively distinct morphological characters which allow for the assumption of monophyly at least for the family Platycnemididae: i.e. the characteristic course of the MA and IR3 veins. However, these characters are somewhat more difficult to examine in taxa with comparatively short wings. In REHN's study (2003) Platycnemididae is rendered paraphyletic, and the old world Protoneuridae form a monophyletic group together with the subfamily Platycnemidinae. Since REHN included only very few platycnemidid taxa, the significance of his findings has to remain open to further study. So, there have been indications for both the monophyly of Platycnemididae and Calicnemiinae, but also against it; apparently, only the monophyly of the subfamily Platycnemidinae has never been doubted. A detailed phylogenetic analysis of at least Coenagrionoidea, if possible including Lestoidea (Megapodagrionidae) is urgently required.

Although the present study was not designed to clarify the family status of dubiously assigned taxa, some notes might be appropriate. The genus *Arrhenocnemis* was included here because it shares the distinctly crenulate wing apex with all other Papuan Calicnemiinae (except *Thaumatagrion*, see below) and, in terms of wing venation, mediates between *Lieftinckia* and *Risiocnemis*. It is not clear to the author why LIEFTINCK (1971; short note in type catalogue) placed this genus in the Megapodagrionidae, although he originally described it as a "platycnemine" (LIEFTINCK 1933). In 1965, he wrote in his account on the Odonata of Madagascar, referring to the genus *Arrhenocnemis*: "... Like *Tatocnemis*, this was originally placed in Platycnemididae, but it is quite evident that both should be removed therefrom." Another doubtful case is the New Guinean *Thaumatagrion*: possibly Lieftinck had already something different in mind when he named the genus by using the suffix *-agrion* instead of *-cnemis*. In any case, he placed it within the Platycnemididae (LIEFTINCK 1932), a decision which is strongly questioned here. The general wing shape and colour, the size, but most of all, the largely zigzagged course of the MA and IR3 veins and the distinctly kinked arculus make the author consider it to be a potential coenagrionide; the 'very faintly denticulate margin' of the wing apex (LIEFTINCK 1932) differs considerably from that of the other Papuan taxa. Beside that, the ligula structure is different from all other known calicnemiine taxa: the presence of spines attached to the ligula shaft (Figs. 37-38) suggests a closer relationship with the Papuan coenagrionide genus *Oreagrion*. BECHLY (1996) considered the absence of those spines to be an autapomorphy of the family Platycnemididae. And, finally, no internal lamina or filament seems to be present (Fig. 38). Based on these considerations, *Thaumatagrion* was excluded from the present analysis. Since REHN's study, also the status of *Allocnemis* within the Platycnemididae is in question. In his analysis, this African genus turned out to be a sister group of a clade which contained the Calicnemiinae on one side and a clade consisting of Platycnemidinae and old world Protoneuridae on the other. As REHN points out himself, the sister group relationship between *Allocnemis* and Platycnemididae/Protoneuridae is based only on a single homoplasious character, the extension of the premental cleft (REHN 2003). In the present analysis, *Allocnemis*, clusters quite 'logically' between the African platycnemidides.

4.2. Relationships between calicnemiine genera

With regard to previous ideas on phylogenetic relationships within Calicnemiinae, both confirming and surprising results arose from the analysis. SCHMIDT suggested a close relationship between some Papuan genera (*Thaumatagrion, Paramecocnemis*) and the African *Mesocnemis* and *Metacnemis* (SCHMIDT 1951); these hypotheses are not at all corroborated by the present results. However, FRASER's suggestion of a close relationship between the Oriental genera *Calicnemia, Coeliccia* and *Indocnemis* has been confirmed (FRASER 1932). While LIEFTINCK (1963), in the light of the present analysis, was very right to consider *Lieftinckia* and *Risiocnemis* closely allied, he was apparently not with regard to *Idiocnemis* and *Coeliccia*. Some of these considerations were founded on larval morphology; however, LIEFTINCK himself stated that those findings are not always reliable because of the difficulties of assigning larval to adult stages in the field (LIEFTINCK 1984).

Remarkably, the Madagascan genera *Leptocnemis* and *Paracnemis* are found at slightly displaced positions within the cladogram (Fig. 52): instead of splitting off from the first, *Paracnemis alluaudi* branches off from the Oriental taxa. It should be noted that for *Paracnemis*, a total of 13 character states are either unknown to the author or - as those of the uniquely shaped male appendages - inapplicable and therefore coded as missing values in the data matrix. Thus, it is possible that the position of *Paracnemis* in the cladogram represents an artefact; this will be taken into account for biogeographic conclusions (VAN TOL & GASSMANN, in prep.).

The ambigious position of *Asthenocnemis stephanodera* in the set of equally parsimonious trees (see above) can possibly be explained by taxon sampling. Preliminary results from work on the *Coeliccia* species of the Greater Sunda Islands and the Philippines have revealed that *Asthenocnemis* probably just represents an 'offshot' of one of two monophyletic radiations within the genus *Coeliccia*, one of them partly leading to the colonization of geological terranes which today constitute the western and southern Philippines. In this context, *A. stephanodera* apparently is the most 'apomorphic' species (DIJKSTRA & GASSMANN, in prep.). Thus, it is very likely that insufficient taxon sampling is the cause for the unresolved position of *A. stephanodera* in the resulting set of cladograms since the mediating morphological traits are lacking. Consequently, further phylogenetic analyses of the Southeast Asian Calicnemiinae should include the highly interesting West Malesian radiations of *Coeliccia*. This would also contribute to the ongoing work on the historical biogeography of the group (GASSMANN, in prep.; VAN TOL & GASSMANN, submitted).

4.3. Perspectives for further studies of calicnemiine phylogeny

The present study has resulted in a first estimate of the phylogeny of the damselfly subfamily Calicnemiinae. It is apparent that basal relationships are still unsatisfactorily resolved (Fig. 51), and that the addition of taxa from the Oriental complex of genera (and the Palawan genus *Asthenocnemis* should be included in this context) is required. Firstly, this would allow for testing the uncertain monophyly of genera as *Calicnemia* and *Coeliccia*, which partly have been defined on the base of variable (polymorphic) wing venational traits of which the group-defining properties very much depend on our definition of the character states concerned. Secondly, it is necessary to newly define the generic borders between *Coeliccia* and *Asthenocnemis*. Several new as well as described species should be transferred to the latter genus; distinct putative synapomorphies have been found (DIJKSTRA & GASSMANN, in prep.). Thirdly, by increasing the range of taxa and of both morphological (e.g. endosceletal) and molecular characters, the ambigious phylogenetic position of *Asthenocnemis* could possibly be resolved.

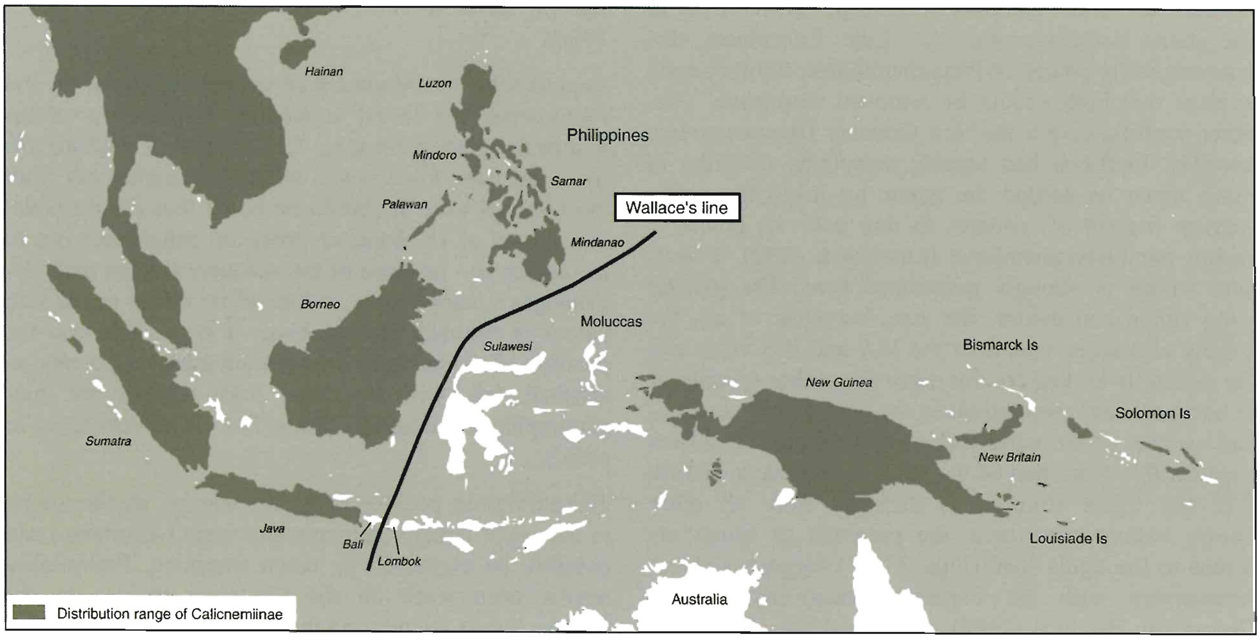

Fig. 53: Map of Malesia, with distribution range of Calicnemiinae indicated.

4.4. Implications for biogeography

As a group of insects occuring to the west and to the east of the Wallace line (Fig. 53), the Calicnemiinae are of special interest for biogeographical studies in the Indo-Australian transition zone. The phylogenetic hypothesis presented above allows for the postulation of active or passive dispersal events both into the East as well as, subsequently, back into the West (i.e. the Philippines). Since a detailed scenario for the distributional history of the group has been developed elsewhere in the context of the historical biogeography of the freshwater biota in Southeast Asia (VAN TOL & GASSMANN, submitted), the reader is referred to that forthcoming paper.

Acknowledgments. It is an honour to me to dedicate the present paper to the memory of Professor Clas M. Naumann (Zoological Research Institute and Museum Alexander Koenig Bonn, and University of Bonn/Germany), whom I owe a long lasting motivation and enthusiasm to work in the field of organismic biology; this as well as his support during the developing PhD thesis will be gratefully remembered. The present project is conducted under the direction of Prof. Dr. E. Gittenberger and J. van Tol (Leiden University and Natural History Museum, Leiden/Netherlands). I am grateful to Dr. H. Duffels (University of Amsterdam) for comments on the manuscript. I thank K.-D. Dijkstra (Leiden), Dr. M. Hämäläinen (Helsinki), Dr. A. Martens (Braunschweig) and Dr. J. Kuhn (Seewiesen) for information of different kinds, as well as Dr. H. Turner and C. Rüffler (Leiden) for general discussions. Most of curators and collection management staff of various collections I have either visited or received loans from have been acknowledged in previous papers. For additional specimens included here, I thank K.-D. Dijkstra, V. J. Kalkman (Leiden), Dr. W. Schneider (Hessisches Landesmuseum, Darmstadt) and Dr. G. Vick (Basingstoke, UK). I am grateful to Mrs. G. Lamers and Dr. W. de Priester (Institute of Biology, Leiden) for their permission to let me do my SEM studies; a minor part of the micrographs, however, has been made at the Natural History Museum Leiden, with thanks to J. Goud for assistance. Dr. John Michalski and Prof. Dennis Paulson (USA), Roland A. Müller (St. Gallen, Switzerland) and J. van Tol provided field photographs. For scanning of negatives and slides, I thank M. Brittijn and J. Meijvogel (IBL, Leiden).

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APPENDIX 1

Taxa included in the cladistic analysis and their distribution
(m = male, f = female; [*] = only literature data available; [-] = not known).

Allocnemis Selys, 1863				
		Allocnemis leucosticta Selys, 1863	m/f*	Southern Africa
Arabicnemis Waterston, 1984				
		Arabicnemis caerulea Waterston, 1984	m/f*	Arabian Peninsula: Oman, Yemen
Asthenocnemis Lieftinck, 1949				
		Asthenocnemis stephanodera Lieftinck, 1949	m/f	Philippines: Palawan
Arrhenocnemis Lieftinck, 1933				
		Arrhenocnemis amphidactylis Lieftinck, 1949	m/-	Central northern New Guinea
		Arrhenocnemis sinuatipennis Lieftinck, 1933	m/-	Northern New Guinea
Calicnemia Strand, 1928				
		Calicnemia eximia (Selys, 1863)	m/f	Mainland southern/southeastern Asia, Hainan (first record), Taiwan
Coeliccia Kirby, 1890				
		Coeliccia membranipes (Rambur, 1842)	m/f	Greater Sunda Islands: Java, Sumatra
Copera Kirby, 1890				
		Copera marginipes (Rambur, 1842)	m/f	Southern and southeastern Asia
Cyanocnemis Lieftinck, 1949				
		Cyanocnemis aureofrons Lieftinck, 1949	m/f	Central northern New Guinea
Idiocnemis Selys, 1878				
	bidentata species-group			
		Idiocnemis bidentata Selys, 1878	m/f	Western New Guinea: Bird's Head Peninsula; Batanta; Salawati; Waigeo
		Idiocnemis dagnyae Lieftinck, 1958	m/f	Western New Guinea: Bird's Head Peninsula and southwestern New Guinea; Misool
		Idiocnemis inaequidens Lieftinck, 1932	m/f	Northeastern and eastern New Guinea
		Idiocnemis mertoni Ris, 1913	m/f	Southern New Guinea; Aru Islands

		Idiocnemis nigriventris Lieftinck, 1937	m/f	Northern New Guinea
		Idiocnemis obliterata Lieftinck, 1932	m/f	Northern and central northern New Guinea
		Idiocnemis polhemi Gassmann, 2000	m/f	Southeastern central New Guinea
		Idiocnemis pruinescens Lieftinck, 1937	m/f	Papuan Peninsula
	inornata species-group			
		Idiocnemis adelbertensis Gassmann, 1999	m/f	Northeastern New Guinea: Adelbert Range
		Idiocnemis australis Gassmann, 1999	m/f	Southern central and southern New Guinea
		Idiocnemis chloropleura Lieftinck, 1932	m/f	Northern New Guinea
		Idiocnemis fissidens Lieftinck, 1958	m/f	West Papuan Islands: Waigeo
		Idiocnemis huonensis Lieftinck, 1958	m/f	Northeastern New Guinea: Huon Peninsula
		Idiocnemis inornata Selys, 1878	m/f	Western New Guinea: Bird's Head Peninsula
		Idiocnemis kimminsi Lieftinck, 1958	m/f	Bismarck Archipelago: New Britain, Mioko
		Idiocnemis leonardi Lieftinck, 1958	m/-	Louisiade Archipelago: Tagula (Sudest)
		Idiocnemis louisiadensis Lieftinck, 1958	m/f	Louis. Arch.: Misima, Rossel; Marshall Bennett Arch.: Woodlark
		Idiocnemis strumidens Lieftinck, 1958	m/f	Western New Guinea: Bird's Head Peninsula and southwestern New Guinea; Misool
		Idiocnemis zebrina zebrina Lieftinck, 1958	m/f	Northeastern and central Papuan Peninsula
[excluded, see GASSMANN (2000)]				
		Idiocnemis leonorae Lieftinck, 1949	m/f	Northeastern and southern central New Guinea
Indocnemis Laidlaw, 1917				
		Indocnemis orang (Förster in Laidlaw, 1907)	m/f*	Southern and southeastern Asia
Leptocnemis Selys, 1886				
		Leptocnemis cyanops (Selys, 1869)	m/f*	Seychelles
Lieftinckia Kimmins, 1957				
		Lieftinckia isabellae Lieftinck, 1987	m/-	Solomon Islands: Santa Ysabel
		Lieftinckia kimminsi Lieftinck, 1963	m/f	Solomon Islands: Bougainville
		Lieftinckia lairdi	m*/f*	Solomon Islands: Guadalcanal

		Lieftinck, 1963		
		Lieftinckia malaitae Lieftinck, 1987	m/f	Solomon Islands: Malaita
		Lieftinckia ramosa Lieftinck, 1987	m/-	Solomon Islands: San Jorge; ? Bougainville
		Lieftinckia salomonis Kimmins, 1957	m/f	Solomon Islands: Guadalcanal
Lochmaeocnemis Lieftinck, 1949				
		Lochmaeocnemis malacodora Lieftinck, 1949	m/f	Central northern New Guinea
Mesocnemis Karsch, 1891				
		Mesocnemis singularis Karsch, 1891	m/f	Western Africa
Paracnemis Martin, 1903				
		Paracnemis alluaudi Martin, 1903	m/f	Madagascar
Paramecocnemis Lieftinck, 1932				
		Paramecocnemis erythrostigma Lieftinck, 1932	m/f*	Northern New Guinea
		Paramecocnemis stilla-cruoris Lieftinck, 1956	m*/-	Northeastern New Guinea
Platycnemis Burmeister, 1839				
		Platycnemis pennipes (Pallas, 1771)	m/f	Western and central Europe
Rhyacocnemis Lieftinck, 1956				
		Rhyacocnemis prothoracica Lieftinck, 1987	m*/-	Northeastern New Guinea
		Rhyacocnemis sufficiens Lieftinck, 1956	m/-	D'Entrecasteaux Islands: Goodenough
Risiocnemis Cowley, 1934				
	Subgenus *Risiocnemis (Risiocnemis)* Cowley			
		Risiocnemis appendiculata (Brauer, 1868)	m/f	Philippines: Mindanao; Dinagat; Camiguin; Samar; Leyte; Panaon; Biliran; Bohol; Homonhon
		Risiocnemis arator Hämäläinen, 1991	m/f	Philippines: northern/central Luzon
		Risiocnemis asahinai Kitagawa, 1990	m/f	Philippines: southern Luzon; Mindoro
		Risiocnemis confusa Hämäläinen, 1991	m/f*	Philippines: southern Luzon; Catanduanes
		Risiocnemis elegans Kitagawa, 1990	m/f	Philippines: Luzon

	Risiocnemis erythrura (Brauer, 1868)	m/f	Philippines: eastern Mindanao; Siargao
	Risiocnemis gracilis Hämäläinen, 1991	m/f	Philippines: central Luzon
	Risiocnemis kiautai Hämäläinen, 1991	m/f*	Philippines: Sibuyan
	Risiocnemis laguna Hämäläinen, 1991	m/f	Philippines: southern Luzon
	Risiocnemis moroensis Hämäläinen, 1991	m/f	Philippines: central Mindanao
	Risiocnemis praeusta Hämäläinen, 1991	m/f	Philippines: Dinagat; Samar; Leyte; Panaon; Biliran
	Risiocnemis pulchra Hämäläinen, 1991	m/f	Philippines: southern Luzon
	Risiocnemis rolandmuelleri Hämäläinen, 1991	m/f	Philippines: Sibuyan; Panay; Negros; Masbate; Siquijor
	Risiocnemis seidenschwarzi Hämäläinen, 2000	m/f*	Philippines: Cebu
	Risiocnemis serrata (Hagen in Selys, 1863)	m/f	Philippines: Luzon; Polillo; Marinduque; Catanduanes
	Risiocnemis varians Hämäläinen, 1991	m/f	Philippines: central northern Luzon.
Subgenus *Risiocnemis* (*Igneocnemis*) Hämäläinen			
	Risiocnemis antoniae Gassmann and Hämäläinen, 2002	m/f	Philippines: northeastern/eastern Mindanao
	Risiocnemis atripes (Needham and Gyger, 1941)	m/f	Philippines: central/eastern Mindanao
	Risiocnemis atropurpurea (Brauer, 1868)	m/f	Luzon; Marinduque
	Risiocnemis calceata Hämäläinen, 1991	m/f	Dinagat; Panaon
	Risiocnemis flammea (Selys, 1882)	m/f	Philippines: Mindanao; Dinagat; Biliran; Homonhon; Panaon; Leyte; Samar
	Risiocnemis fuligifrons Hämäläinen, 1991	m/f	Philippines: western/northern Mindanao; Dinagat; Basilan; Panaon; Leyte
	Risiocnemis haematopus (Selys, 1882)	m/f	Philippines: southern Luzon; Catanduanes
	Risiocnemis ignea (Brauer, 1868)	m/f	Philippines: northern/northeastern Luzon
	Risiocnemis incisa Kimmins, 1936	m/f	Philippines: northern and central Luzon
	Risiocnemis kaiseri Gassmann and Hämäläinen, 2002	m/f	Philippines: Samar
	Risiocnemis melanops Hämäläinen, 1991	m/f	Philippines: Samar
	Risiocnemis nigra	m/f	Philippines: Samar

	Gassmann and Hämäläinen, 2002		
	Risiocnemis odobeni Hämäläinen, 1991	m/f	Philippines: southeastern Luzon; Catanduanes
	Risiocnemis pistor Gassmann and Hämäläinen, 2002	m/-	Philippines: southeastern Mindanao
	Risiocnemis plebeja Hämäläinen, 1991	m/f	Philippines: Sibuyan; Panay
	Risiocnemis polilloensis Hämäläinen, 1991	m/f	Philippines: southeastern Luzon; Catanduanes; Polillo
	Risiocnemis rubricercus Gassmann and Hämäläinen, 2002	m/-	Philippines: eastern Mindanao
	Risiocnemis rubripes (Needham and Gyger, 1939)	m/f	Philippines: eastern Mindanao; Dinagat
	Risiocnemis siniae Hämäläinen, 1991	m/f	Philippines: Leyte; Samar
	Risiocnemis tendipes (Needham and Gyger, 1941)	m/f	Philippines: Mindanao
Salomocnemis Lieftinck, 1987			
	Salomocnemis gerdae Lieftinck, 1987	m/f	Solomon Islands: Guadalcanal
Stenocnemis Karsch, 1899			
	Stenocnemis pachystigma (Selys, 1886)	m/f	Western Africa
Torrenticnemis Lieftinck, 1949			
	Torrenticnemis filicornis Lieftinck, 1949	m/f	Central northern New Guinea

APPENDIX 2

Data matrix for the cladistic analysis of Calicnemiinae

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	88888888
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678
Idiocnemis adelbertensis	2011400000	2200001355	321???0423	3200100221	0052100000	?00012?10?	?010002155	0025011101	00020218
Idiocnemis australis	2011400000	3200001355	321???0423	3200100221	0052100000	?00012?10?	?020002155	0025001200	00020219
Idiocnemis chloropleura	2011300000	2200001355	321???0423	3201101221	0072100000	?00013?10?	?010002155	0125011101	00020214
Idiocnemis fissidens	2011?00000	2200001355	??1????423	3201101221	0052101000	?00013?10?	?030002155	0025011133	000??219
Idiocnemis huonensis	2011400000	2200001355	321???0423	3202100221	0050?00000	?00012?10?	?010002255	0025011101	00020218
Idiocnemis inornata	2011300000	2200001355	321???0423	3201100221	0071200000	?00013?10?	?010002255	0025001401	0002021A
Idiocnemis kimminsi	2011400000	2200001355	321???0423	3202100221	0070?00000	?00012?10?	?010102255	0025011101	00020218
Idiocnemis leonardi	2011300000	4200001355	321???0423	3201100221	0070?01000	?00014?10?	?020002255	0025001201	00020???
Idiocnemis louisiadensis	2011300000	3200001355	321???0423	3201100221	0070?01000	?00012?10?	?020002255	0025001201	0002021C
Idiocnemis strumidens	2011300000	2200001355	321???0423	3201101221	0052100000	?00013?10?	?040002155	0025011133	000?0219
Idiocnemis zebrina	2011300000	3200001355	321???0423	3201100221	0070?01000	?00023?10?	?020002155	0025001300	0011021C
Idiocnemis bidentata	2011400000	22000013A0	3201040400	0223100021	0202300000	010013?11?	?150003155	0021101011	000?021B
Idiocnemis dagnyae	2011300000	2200001397	321???0423	32{02}0100221	0{01}72300000	010013?11?	?030003155	0025101011	000?021B
Idiocnemis inaequidens	2011300000	2200001000	1201040400	0223100021	0202300100	010014?12?	?050003255	0020101021	000?0210
Idiocnemis mertoni	2011300000	2200001334	3201040400	0223100021	0200?00000	010014?11?	?050003155	0025101011	000?021B
Idiocnemis nigriventris	2011300000	2200001363	32010?0403	0203100021	0212300000	010013?13?	?120003255	0025101021	000?0210
Idiocnemis obliterata	2011300000	2200001334	3201040400	0223100021	0212300000	010013?11?	?150003155	0025101011	000?0210
Idiocnemis polhemi	2011300000	2200001320	3201040401	1223100021	0202300000	010013?11?	?150003155	0020101011	000?0210
Idiocnemis pruinescens	2011300000	2200001040	3201040400	0223100021	0202300100	010023?10?	?050003255	0021101011	000?021D
Risiocnemis appendiculata	2011400000	4400011570	221???2423	2200100221	0070?0?000	?00022314?	?00?000255	0022001300	0000020?
Risiocnemis arator	2011400000	44000110B0	021????400	0300110021	0270?0?000	?00012114?	?00?001455	0020000?01	0000000?
Risiocnemis asahinai	2011400000	34000110C9	000101?400	0300110021	027201?000	?00023318?	?00?001455	0027000100	0020000?
Risiocnemis confusa	2021400000	4400011010	021????400	0300110021	0270?0?001	?00014113?	?00?001455	0022001300	0000020?
Risiocnemis elegans	2011400000	44000116C9	000011?400	0300111021	027201?000	011022116?	?00?001445	1027000100	0020000?
Risiocnemis erythrura	2011400000	44000111B0	021????400	0300110021	0270?0?001	?00032114?	?00?001455	0022001300	0000020?
Risiocnemis gracilis	2011400000	4400011123	101????400	0200110021	027202?000	011033110?	?00?001455	0027000100	0020000?
Risiocnemis kiautai	2011400000	44000116C9	800111?408	0300110021	0270?0?000	?00032114?	?00?001455	1027001300	0000020?
Risiocnemis aguna	2011400000	44000111C9	100111?400	0200110021	027201?000	011032118?	?060001445	0027000100	0020000?
Risiocnemis moroensis	2011400000	44000120B0	021????400	0200110021	0270?0?001	?00053314?	?00?001455	0023001300	0000020?
Risiocnemis praeusta	2011400000	44000110B0	021????400	0300110021	0270?0?001	?00032114?	?00?001455	1022001300	0000020?
Risiocnemis pulchra	2011400000	44000116C9	8001012400	0200110021	027202?000	011032118?	?060001445	0027000100	0020000?
Risiocnemis rolandmuelleri	2021400000	44000111B0	121????400	8300110021	027200?000	?00012113?	?00?001455	0020000300	0000020?
Risiocnemis seidenschwarzi	2021400000	44000110C0	021????400	030011?0?1	027200?000	?00024117?	?0??001455	002000030?	0000?20?
Risiocnemis serrata	2011400000	44000116C9	800011?400	0300111021	023201?000	011034113?	?00?001455	0027000100	0020000?
Risiocnemis varians	2011400000	44000110C9	000011?400	0300111021	027201?000	011022118?	?060001445	0027000100	0020000?
Risiocnemis antoniae	1011200000	4400001000	031????400	0000100071	0270?0?000	?000223100	100?001413	2022001502	0000021J
Risiocnemis atripes	1011200000	44000010B0	031????400	0000100001	0270?0?000	?000141151	000?001433	2021001502	0000021K
Risiocnemis atropurpurea	1011200000	4400001000	021????400	0000100080	0270?0?000	?000243162	000?001433	2021001502	0000221H
Risiocnemis calceata	1011200000	4400001000	031????400	{02}000100051	0270?0?001	?000233152	000?001434	2022001502	0000321J
Risiocnemis flammea	1011200000	4400001574	221???2425	5000100271	0070?0?000	?000343100	100?001400	2022001502	0000021E
Risiocnemis fuligifrons	1011200000	4400001070	031????420	2000100271	0070?0?000	?000345101	200?001411	2021001502	0000021H
Risiocnemis haematopus	1011200000	4400001000	031????400	0000100071	0270?0?000	?000343101	100?001411	2021001502	0000021H
Risiocnemis ignea	1011200000	4400001276	231???2422	2000100271	0070?0?000	?000255101	100?001433	2022001202	0000021H
Risiocnemis incisa	1011200000	4400001242	431???2422	2000100271	0070?0?000	?0002{34}3101	000?001433	2022001502	0000021J
Risiocnemis kaiseri	1011200000	4400001000	031????400	2000100041	0270?0?000	?000444101	100?001411	2021001502	0000021E

APPENDIX 2 (CONTINUED)

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	88888888
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678
Risiocnemis melanops	1011200000	4400001042	031????400	2000100271	0070?0?000	?000343101	100?001411	2021001502	0000021H
Risiocnemis nigra	1011200000	4400001000	021????400	0000100011	0270?0?000	?000343100	100?001400	2021001502	0000021E
Risiocnemis odobeni	1011200000	4400001{02}8{06}	{02}31???241{02}	{02}000100271	0070?0?001	?000245100	100?001400	2021001502	0000021J
Risiocnemis plebeja	1011200000	4400001542	331???2422	2000100271	0070?0?000	?000242102	000?001433	2024001502	00000217
Risiocnemis pistor	1011200000	4400001000	031????400	0000100271	0270?0?000	?000343152	100?001433	2022001502	00001???
Risiocnemis polliloensis	1011200000	4400001000	021????400	0000100041	0270?0?000	?000343101	100?001410	2021001502	0000021H
Risiocnemis rubripes	1011200000	4400001245	231???2422	2000100271	0070?0?000	?000243152	100?001433	2022001502	0000121H
Risiocnemis rubricercus	1011200000	4400001040	021????400	0000100001	0270?0?000	?000143152	000?001422	2022001502	00001???
Risiocnemis siniae	1011200000	4400001000	031????400	0000100051	0270?0?001	?000245152	000?001434	2022001502	0000321J
Risiocnemis tendipes	1011200000	4400001000	031????420	2000100271	0270?0?000	?000253152	000?001433	2022001502	00000217
Paramecocnemis erythrostigma	2011200000	2210001720	7201070400	0203101211	022200?000	010165?0??	?08?004255	3020001801	00020210
Paramecocnemis stilla-cruoris	2011200000	22100?1800	6?0107?400	0203101011	020260?000	?00164?0??	?08?004355	3020?0???1	????????
Cyanocnemis aureofrons	2001231110	0001021028	010205?404	0200100001	027200?000	010103?11?	?071002255	0020101201	00030210
Torrenticnemis filicornis	2001231000	0000031000	4201062400	0203100001	020240?010	01010260??	?00?002255	0020021101	10020211
Idiocnemis leonorae	2011230000	010000184B	6201032400	0203100?11	0062?0?000	010106?11?	?050001055	2??0001801	110?0212
Lochmaeocnemis malacodora	2001232000	0000031020	021????400	0300100001	0202?0?000	010103?10?	?040012255	2020001901	01020210
Arrhenocnemis amphidactylis	2001410000	24000018E0	6000061300	0300100021	120200?000	?00113?0??	?00?001255	0024??????	????????
Arrhenocnemis sinuatipennis	2001410000	4400001660	8?0001??26	3?03100?21	020200?000	?0011220??	?032001355	0024001301	000?0???
Rhyacocnemis prothoracica	2011220000	10000?1820	5200032400	0303100011	02?2?0?000	010116?11?	?00?002055	2020001?01	??020???
Rhyacocnemis sufficiens	2011220000	1000011820	5201032400	0300100011	0202?0?000	010116?11?	?00?002055	2??0001101	11020???
Salomocnemis gerdae	2011200000	02000018EB	621????4??	?000101??1	0?72?0?000	?00021411?	?00?001455	2025001301	00110?10
Lieftinckia isabellae	2031200000	2000011001	020000?400	?000100?21	007??0?000	?0001411A?	?011101255	0024?0???1	?0??????
Lieftinckia kimminsi	2031200000	2300001001	020001?400	0300100021	02???0?000	?00022119?	?012001355	0021001201	00010213
Lieftinckia lairdi	2031400000	22000?1???	??1????4?3	330010?121	00???0?000	?000?120??	?00?001455	0025001300	00110?13
Lieftinckia malaitae	20314?0000	2200001271	221???2423	3500100221	007??0?000	?0001120??	?00?001455	0021?01??1	?0???213
Lieftinckia ramosa	2031400000	2200011271	221????4{02}0	0100100221	00???0?000	?0002210??	?012001355	0024?01??1	?0??????
Lieftinckia salomonis	20314?0000	2200011276	2?1???24?3	?400100121	007??0?000	?00011110?	?00?001455	2024001301	00110213
Coeliccia membranipes	0011232020	11010010C0	821???2100	0300000021	020200?000	011021119?	?070001455	1007000?00	1030410?
Asthenocnemis stephanodera	0011222020	22000016C0	8200002006	6203102221	000200?000	01011260??	?08?001355	3020001201	0100?115
Calicnemia eximia	0001232010	0001001348	4202052004	4300000061	020240?000	?00011119?	?00?001455	0015000??1	00000214
Indocnemis orang	0001232221	0101003020	021????100	0300000001	020250?000	011011219?	?070001455	1000000??1	?0000214
Arabicnemis caerulea	0100030000	00000007DA	7?1???2437	7200100281	0000?0?000	?00023110?	?00?001455	2117001A01	0000010?
Leptocnemis cyanops	1011232020	0001011320	121????200	0200100021	0242?0?000	??1024?10?	?00?002255	2120001701	0000020?
Allocnemis leucosticta	0010220000	2201131820	6201021400	0500100011	020270?000	111021?19?	?00?001255	0015??1B01	000?020?
Mesocnemis singularis	0101032221	0000001?30	12?????00	0500100011	0??2?0?200	211005110?	?00?001455	2020000??1	?000420?
Paracnemis alluaudi	0000232120	00010016B0	8200011000	??00100081	0202?0?000	011012010?	?00?00??55	52?000??01	000?0210
Stenocnemis pachystigma	0001130000	00000013A8	421???2000	4300100011	020270?000	111012410?	?00?001455	2120001601	0000?214
Copera marginipes	0000400000	0000000450	721???2000	0100000030	020270?000	111040?0??	?00?00??55	0016001201	0000?116
Platycnemis pennipes	0000200000	000000145A	7201022000	0300001080	020250?000	11100110??	?00?001455	4007000??1	000?510?

APPENDIX 3

List of unambigious character state changes along branches of the preferred most parsimonious cladogram (cf. fig. 52).

Branch 1: char. 18: 0→5; char. 19: B→7; char. 21: 0→2; char. 29: 0→2; char. 30: 0→3; char. 31: 0→2; char. 36: 1→0; char. 38: 0→2; char. 42: 2→0; char. 67: 1→0; char. 68: 4→2. Branch 2: char. 17: 1→2; char. 50: 0→1; char. 56: 2→3; char. 74: 2→3. Branch 3: char. 11: 4→3; char. 55: 3→2; char. 56: 2→3; char. 57: 1→3. Branch 4: char. 59: 8→6; char. 71: 0→1; char. 88: 1→2. Branch 5: char. 63: 0→6. Branch 6: char. 21: 0→8; char. 43: 7→3; char. 56: 2→4; char. 59: 8→3; char. 88: 1→4. Branch 7: char. 19: C→2; char. 20: 9→3; char. 23: 0→1; char. 56: 2→3; char. 59: 8→0. Branch 8: none. Branch 9: char. 21: 1→8. Branch 10: char. 21: 0→8; char. 30: 0→8; char. 71: 0→1. Branch 11: char. 18: 0→1. Branch 12: char. 71: 0→1. Branch 13: char. 19: B→1; char. 50: 0→1. Branch 14: char. 18: 0→1; char. 21: 0→1; char. 31: 0→8. Branch 15: char. 19: B→C; char. 55: 1→2; char. 59: 3→7. Branch 16: char. 74: 2→0; char. 77: 1→0; char. 86: 2→0. Branch 17: char. 22: 2→3; char. 56: 4→2. Branch 18: char. 29: 0→2; char. 57: 3→5; char. 61: 1→2. Branch 19: char. 20: 0→2; char. 88: 1→2. Branch 20: char. 39: 7→4; char. 55: 3→4; char. 57: 3→4. Branch 21: none. Branch 22: char. 39: 7→4. Branch 23: char. 39: 7→1; char. 69: 1→0. Branch 24: char. 39: 7→8; char. 40: 1→0; char. 85: 0→2. Branch 25: char. 56: 4→3. Branch 26: char. 57: 3→5; char. 88: 4→3. Branch 27: char. 18: 2→5; char. 20: 6→4; char. 22: 3→2; char. 30: 2→5; char. 31: 2→5; char. 55: 2→3. Branch 28: char. 19: 7→8; char. 29: 2→1; char. 50: 0→1; char. 74: 2→1. Branch 29: char. 56: 4→5; char. 78: 6→2. Branch 30: char. 21: 2→4. Branch 31: char. 18: 2→5; char. 21: 2→3; char. 57: 3→2; char. 74: 2→4. Branch 32: char. 61: 0→1; char. 85: 0→1; char. 88: 4→1. Branch 33: char. 56: 4→5. Branch 34: char. 55: 2→3; char. 61: 0→1; char. 85: 0→1. Branch 35: char. 69: 3→2; char. 70: 3→2; char. 85: 0→1. Branch 36: char. 22: 2→3; char. 74: 2→1. Branch 37: char. 3: 3→1; char. 5: 4→2; char. 11: 2→0; char. 18: 2→8; char. 19: 7→E; char. 20: 1→B; char. 21: 2→6; char. 37: 0→1; char. 55: 1→2. Branch 38: char. 80: 1→0. Branch 39: char. 74: 5→1. Branch 40: char. 20: 1→6; char. 32: 0/3→4; char. 88: 4→3. Branch 41: char. 32: 0/3→1; char. 55: 1→2; char. 58: 1→0. Branch 42: char. 56: 2→4; char. 59: 0→A; char. 64: 2→1; char. 65: 0→1; char. 68: 3→2. Branch 43: char. 55: 1→2; char. 59: 0→9; char. 74: 4→1; char. 78: 3→2. Branch 44: char. 26: 1→6; char. 41: 0→1; char. 56: 2→3; char. 68: 3→2. Branch 45: char. 29: 0→2; char. 30: 0→6; char. 31: 0→3; char. 34: 0→3; char. 63: 0→3. Branch 46: none. Branch 47: none. Branch 48: char. 43: 5→7; char. 65: 0→1. Branch 49: char. 11: 2→3; char. 80: 1→0. Branch 50: char. 72: 0→1. Branch 51: char. 47: 0→1. Branch 52: none. Branch 53: char. 44: 2→1; char. 45: 1→2; char. 68: 1→2; char. 88: 4→1. Branch 54: char. 11: 3→4. Branch 55: none. Branch 56: char. 55: 1→2; char. 80: 1→0; char. 83: 0→1; char. 84: 2→1. Branch 57: char. 63: 2→3. Branch 58: char. 59: 1→3; char. 68: 1→2; char. 79: 1→2. Branch 59: none. Branch 60: char. 44: 2→0; char. 56: 3→4; char. 62: 1→0. Branch 61: char. 5: 3→4. Branch 62: char. 30: 0→1; char. 31: 0→1. Branch 63: char. 21: 3→1; char. 56: 3→4; char. 79: 1→2. Branch 64: char. 55: 1→2; char. 74: 0→1. Branch 65: char. 21: 6→7; char. 38: 0→2; char. 43: 0→2. Branch 66: char. 19: 2→0; char. 45: 0→6; char. 52: 1→0; char. 68: 2→3. Branch 67: char. 12: 0→1; char. 19: 2→4; char. 20: 0→B; char. 42: 2→0; char. 43: 0→6; char. 67: 2→1. Branch 68: char. 24: 1→0. Branch 69: char. 34: 3→0. Branch 70: char. 19: 2→0; char. 45: 0→4; char. 49: 0→1; char. 56: 3→2; char. 58: 1→0; char. 76: 0→2. Branch 71: char. 8: 0→1; char. 9: 0→1; char. 14: 0→1; char. 16: 0/3→2; char. 20: 0→8; char. 22: 2→1; char. 30: 0→4; char. 43: 0→7; char. 63: 0→7; char. 64: 0→1; char. 75: 0→1; char. 84: 2→3. Branch 72: char. 23: 0→1; char. 63: 0→4; char. 66: 0→1; char. 71: 0→2; char. 78: 2→A; char. 82: 0→1. Branch 73: char. 3: 0→1; char. 6: 3→2; char. 12: 0→2; char. 19: 2/B→C; char. 26: 1/5→0; char. 30: 0→6; char. 31: 0→6; char. 32: 3→2; char. 34: 0→3; char. 37: 0→2; char. 38: 0→2; char. 42: 2→0; char. 58: 1→0; char. 63: 0→8; char. 71: 0→3; char. 82: 0→1; char. 86: 2→1; char. 88: 4→3. Branch 74: char. 4: 1→0; char. 8: 0→1; char. 27: 2→1; char. 39: 2→8; char. 71: 0→5; char. 72: 0→2. Branch 75: char. 3: 0→1; char. 11: 0→1; char. 19: 2→C; char. 55: 1→2; char. 74: 0→7; char. 80: 1→0; char. 83: 0→3; char. 85: 0→4; char. 86: 2→1; char. 87: 1→0. Branch 76: char. 8: 0→2; char. 10: 0→1; char. 17: 1→3; char. 21: 8→0; char. 39: 2→0; char. 45: 0→5; char. 57: 1→2. Branch 77: char. 9: 2→1; char. 19: 2→4; char. 20: 0→8; char. 21: 8→4; char. 30: 0→4; char. 31: 0→4; char. 39: 2→6; char. 45: 0→4; char. 52: 1→0; char. 53: 1→0; char. 74: 0→5. Branch 78: char. 1: 0→1; char. 3: 0→1; char. 16: 0→1; char. 28: 0→2; char. 32: 3→2; char. 43: 0→4; char. 56: 1/2→4; char. 67: 1→2; char. 68: 4→2; char. 72: 0→1; char. 78: 2→8. Branch 79: char. 2: 0→1; char. 5: 2→0; char. 8: 2→0; char. 10: 0→1; char. 19: 2→3; char. 32: 3→5; char. 48: 0→2; char. 55: 1/2→0; char. 56: 1/2→5; char. 77: 1→0; char. 85: 0→4. Branch 80: char. 5: 2→1; char. 19: 2→A; char. 20: 0→8; char. 31: 0→4; char. 57: 1→4; char. 72: 0→1; char. 78: 2→7; char. 87: 0→1. Branch 81: char. 3: 0→1; char. 6: 3→2; char. 11: 0→2; char. 12: 0→2; char. 14: 0→1; char. 15: 0→1; char. 16: 0→3; char. 23: 1→0; char. 27: 2→1; char. 32: 3→5; char. 59: 0→9; char. 68: 4→2; char. 78: 2→C. Branch 82: char. 2: 0→1; char. 5: 2→0; char. 29: 0→3; char. 30: 0→7; char. 31: 0→7; char. 32: 3→2; char. 38: 0→2; char. 42: 2→0; char. 44: 2→0; char. 52: 1→0; char. 53: 1→0; char. 56: 1→3; char. 72: 0→1;

char. 78: 2→B. Branch 83: char. 23: 1→0; char. 37: 0→1; char. 45: 7→5; char. 73: 1→0; char. 77: 1→0. Branch 84: none. Branch 85: none. Branch 86: none. Branch 87: char. 6: 0→3; char. 35: 0→1; char. 40: 0→1; char. 58: 0→1. Branch 88: char. 39: 8→1; char. 86: 1→2. Branch 89: char. 4: 0→1; char. 73: 1→2. Branch 90: char. 7: 0→2; char. 9: 0→2. Branch 91: char. 14: 0→1; char. 39: 1→2. Branch 92: char. 21: 1→8; char. 71: 2→0; char. 87: 0→1. Branch 93: char. 18: 3→6. Branch 94: char. 14: 1→0; char. 53: 1→0; char. 54: 0→1. Branch 95: char. 1: 0→2; char. 9: 2→0; char. 28: 0→4. Branch 96: char. 7: 2→0; char. 52: 1→0; char. 74: 0→4; char. 78: 2→3. Branch 97: char. 43: 0→7; char. 54: 1→0. Branch 98: char. 23: 0→1; char. 44: 2→0; char. 68: 3→4; char. 74: 4→2. Branch 99: char. 5: 2→4; char. 16: 0→1; char. 36: 0→1; char. 87: 1→0. Branch 100: char. 80: 1→0. Branch 101: none. Branch 102: char. 32: 3→2; char. 57: 1→3. Branch 103: none. Branch 104: char. 19: B→C; char. 20: 0→9; char. 22: 2→0; char. 23: 1→0; char. 74: 2→7; char. 88: 4→3. Branch 105: char. 44: 0→2; char. 46: 0→1; char. 59: 4→8; char. 77: 1→0; char. 78: 3→1; char. 83: 0→2; char. 86: 2→0. Branch 106: char. 52: 0→1; char. 53: 0→1; char. 88: 3→1. Branch 107: char. 24: 1→0; char. 37: 0→1. Branch 108: char. 55: 3→2; char. 69: 5→4. Branch 109: char. 21: 0→1; char. 32: 3→2. Branch 110: char. 63: 0→6; char. 69: 5→4. Branch 111: char. 50: 0→1. Branch 112: char. 3: 1→2; char. 59: 4→3. Branch 113: char. 44: 0→2; char. 74: 2→0; char. 77: 0→1. Branch 114: char. 1: 2→1; char. 32: 3→0; char. 39: 2→0; char. 56: 2→4; char. 69: 5→3; char. 70: 5→3; char. 71: 0→2; char. 78: 3→6; char. 80: 1→2. Branch 115: char. 57: 1→3. Branch 116: char. 39: 0→7; char. 55: 1→2. Branch 117: char. 88: 4→2. Branch 118: char. 60: 2→0; char. 61: 0→1; char. 69: 3→1. Branch 119: char. 55: 2→3; char. 70: 3→0. Branch 120: char. 60: 0→1; char. 88: 2→1. Branch 121: char. 22: 2→3; char. 70: 0→1. Branch 122: char. 31: 0→2. Branch 123: char. 38: 0→2; char. 42: 2→0. Branch 124: char. 22: 2→3. Branch 125: char. 39: 7→5; char. 50: 0→1; char. 70: 3→4; char. 85: 0→3. Branch 126: char. 38: 0→2. Branch 127: char. 29: 0→2; char. 31: 0→2. Branch 128: char. 18: 0→2; char. 19: 0→4; char. 21: 0→2; char. 30: 0→2; char. 42: 2→0. Branch 129: char. 59: 5→0. Branch 130: char. 60: 2→1. Branch 131: char. 19: 4→7; char. 20: 2→6; char. 61: 0→1. Branch 132: char. 60: 1→0; char. 69: 3→0; char. 70: 3→0. Branch 133: char. 20: 0→1; char. 63: 0→1; char. 84: 0→1. Branch 134: char. 16: 0→1; char. 42: 2→0. Branch 135: char. 5: 2→4; char. 18: 0→2; char. 19: 0→7; char. 21: 0→2; char. 23: 0→1. Branch 136: char. 30: 0→3; char. 56: 2→1; char. 63: 1→0; char. 68: 3→4. Branch 137: char. 16: 1→0; char. 74: 4→5. Branch 138: char. 58: 1→0. Branch 139: char. 5: 2→4; char. 58: 1→0. Branch 140: char. 39: 2→0; char. 55: 1→0; char. 56: 2→3; char. 67: 1→2; char. 68: 3→2; char. 84: 0→2. Branch 141: char. 7: 2→1; char. 32: 3→2; char. 59: 0→1. Branch 142: char. 34: 0→3. Branch 143: char. 3: 0→1; char. 7: 1→0; char. 39: 0→1. Branch 144: char. 6: 3→0; char. 11: 0→2; char. 12: 0→2; char. 27: 2→0. Branch 145: char. 5: 2→3; char. 21: 6→3; char. 33: 0→2; char. 39: 1→2; char. 45: 0→3; char. 54: 1→0; char. 75: 0→1; char. 79: 0→1. Branch 146: char. 62: 0→1; char. 68: 2→1. Branch 147: none. Branch 148: char. 20: 0→4. Branch 149: char. 43: 0→1. Branch 150: char. 30: 0→3; char. 33: 2→0; char. 63: 5→2. Branch 151: char. 23: 0→1; char. 29: 0→2; char. 31: 0→3; char. 34: 3→0; char. 38: 0→2; char. 42: 2→0; char. 43: 1→7; char. 62: 1→0. Branch 152: char. 45: 3→1; char. 52: 1→0; char. 59: 1→0; char. 67: 3→2; char. 75: 1→0; char. 78: 0→1/2; char. 79: 1→0. Branch 153: char. 5: 3→4; char. 43: 7→5; char. 56: 3→2. Branch 154: char. 63: 2→1; char. 76: 0→1. Branch 155: char. 34: 0→2; char. 44: 2→0; char. 68: 1→2. Branch 156: char. 34: 0→1. Branch 157: char. 63: 2→1. Branch 158: char. 37: 0→1; char. 76: 0→1. Branch 159: char. 43: 7→5; char. 79: 0→3; char. 80: 1→3. Branch 160: char. 11: 2→3; char. 44: 2→0; char. 47: 0→1. Branch 161: char. 68: 1→2. Branch 162: char. 48: 0→1. Branch 163: char. 13: 0→1; char. 37: 0→1; char. 58: 1→0; char. 71: 0→3. Branch 164: char. 56: 3→6; char. 68: 2→0; char. 71: 0→2; char. 82: 0→1. Branch 165: char. 6: 3→2; char. 11: 0→1; char. 21: 6→5; char. 32: 2→3. Branch 166: char. 35: 1→0; char. 59: 0→9; char. 77: 1→0. Branch 167: char. 12: 0→1; char. 18: 3→0; char. 28: 0→1; char. 63: 0→7; char. 71: 0→1.

APPENDIX 4

For detailed information on specimens studied, the reader should refer to the 'material examined' sections in GASSMANN (1999), GASSMANN (2000) and GASSMANN & HÄMÄLÄINEN (2002). Additional taxa/specimens examined for the present study are listed in the following.

Collections:

BMNH = Natural History Museum: British Museum (Natural History), London.

HLMD = Hessisches Landesmuseum, Darmstadt.

ISNB = Institut Royal des Sciences Naturelles, Brussels.

RMNH = National Museum of Natural History (Naturalis; formerly: Rijksmuseum van Natuurlijke Historie), Leiden (including the former Roland Müller collection).

SMFD = Senckenberg-Museum, Frankfurt.

Allocnemis leucosticta: **South Africa, Cape Province**: 4♂, Natal, Durban, 8.iii.1939, RMNH. 2♂, Klein-Swartberge, Seweweekspoort Pass, 5.i.1951, Swedish S. Africa Exped. 1950-1951, RMNH.

Arabicnemis caerulea: **Arabian Peninsula, Oman**: 1♂, Wadi Al-Abyadh, appr. 21°32'N 56°18'E, 16.ix.1988, ex Oman Nat. Hist. Mus., HLMD-Od 226, HLMD.

Arrhenocnemis amphidactylis: **New Guinea, West Papua**: 1♂ (paratype), central New Guinea, above Bernhard Camp, 700 m, 29.iii.1939, RMNH.

Asthenocnemis stephanodera: **Philippines, Palawan Island**: 1♂, Quezon, Lamakan, Magmuni str, 27.v.-1.vi.1991, RMNH. 1♂, Quezon, Lamakan, Magmuni str, 1000 ft., 16-22.v.1991, RMNH. 1♀, Quezon, Magmuni str, 1000 ft., 16-22.v.1992, RMNH.

Calicnemia eximia: **China, Hainan**: 1♂, China, Central Hainan Island, Tongshi City, Tongshi Holiday Resort, 400 m, 28.vi.1993, RMNH. **India, Assam**: 1♂, Assam, Shillong, 25.vi.1974, RMNH. **India, West Bengal**: 1♀, Bom Busty, 1.vi.1976, RMNH. 1♂, 1♀, Gumpha, 6.vi.1976, RMNH. 1♂, Kapkot, 26.ix.73, RMNH. 1♂, Loharkhet, 26.ix.73, RMNH. **India, Sikkim**: 1♀, Kool-loo [Kooloo?], Carleton, ISNB. 1♂, ex Staudinger, acq. 1903, RMNH. 1♂, ex Mus. Ann Arbor (coll. Forster), acq. 1936, RMNH. **Nepal**: 1♂, Barabhise, Tibettan frontier, ca. 950 m, 4.vi.1973, RMNH. 2♂, Charnavati Khola/pine for., 1200 m, 15.ix.74, RMNH. 1♂, Kathmandu valley, Waterfall west Chaunica, 1400 m, 24.v.1973, RMNH. 14 (juv.), 1♀, Kodari, Tibettan frontier, ca. 1700 m, 4.vi.73, RMNH. 1♂, Rhedi, 1520 m, 14.ix.74, RMNH.

Coeliccia membranipes: **Indonesia, Java**: 1♂, W. Java, Salak, 800 m, 31.x.60 [1961?, different labels], ex coll. A. Heymer, RMNH. **Indonesia, Nias Island**: 1♂, Central Nias Island, Lahago, 4.ii.-10.iii.1896, RMNH. **Indonesia, Sumatra**: 1♂, Bambar Baru, 950 m, 12.xi.50, RMNH. 1♂, Fanangtalu, Ophir Distrikten, Pad. Bovenland, v.1915 [1914 ?]. 1♂, Fort de Kok, x.1913. 1♀, Moesa Kambangan, 10.ix.1927. 2♂, N. Sumatra, Atjeh, Sangir, 1200 m, 19.iii.1937. 1♂, N.E. Sumatra, Sibolangiti, 400 m, 17.xi.1950. 2♂, S. Sumatra, S.W. Lampoeng, Mt Tanggamoes, 3.i.35. 2♂, S. Sumatra, S.W. Lampoeng, Mt Tanggamoes, 24.xii.34, RMNH. 2♂, S. Sumatra, Wai Teboe, 500 m, 24.vi.1934. 1♂, Sumatra Sungai Kumbang (Kurintji), ix.1915, RMNH. 1♀, Sumatra, Serapai (Kurintji), vii.1915. 1♂, Sumatra, Bengkulen, Suban Ajam (Redjang), vii.1916. 1♂, Suban Ajam (Redjang) Bengkulen, vii.1916. 2♂, Weg B. Agoeng, grens Benkoelen, Ranaumeer, 2.i.1938, RMNH.

Copera marginipes: **Indonesia, eastern Java region**: 1♂, Kangean Island, 21.ix.54, Petafan, RMNH. **Indonesia, Bali**: 1♂, 1♀, ca. 2 km inland from Grokgak, 8°11'S 114°47'E", 150 m asl., 11.v.1991, RMNH.

Cyanocnemis aureofrons: **New Guinea, West Papua**: 5♂, 2♀, paratypes, Araucariakamp, 700-800 m, 8.-31.iii.1939, RMNH. All paratypes; Neth. Ind.-Amer. New Guinea Exped., RMNH.

Idiocnemis leonorae: **Papua New Guinea**: 3♂, 2♀, NE New Guinea, E. Highlands, Yonkie Dome, 11 mi. NE Kainantu, 1500 m, 18-20.x.1972, ex coll. Donnelly, RMNH.

Indocnemis orang: **SE Asia, Malayan Peninsula**: 2♂, Malaya, Selangor, Templer Park, K. L., 12-13 mi., 21.iii.1963, RMNH. 1♂, Malaya, S. Kedah, Bading, Badenoch Estate, 21.ii.1963, RMNH.

Leptocnemis cyanops: **Seychelles, Mahé island**: 1♂, banks of the Grand Bois R., 6.ii.1974, RMNH. 1♂, Bouin, 15.ii.1974 RMNH. 1♂, St. Louis R., 8.ii.1974, RMNH. **Seychelles, Praslin island**: 1♂, Vallée de Mai, 25.vii.1965, ex coll. Pinhey '66, RMNH.

Lieftinckia isabellae: 2♂ (1 def.), **Solomon Islands, Santa Ysabel island**, Maring distr., Ta Matahi, 2.vii.1960, ex BISH, RMNH.

Lieftinckia kimminsi: Paratypes: 1♂, **Solomon Islands, southern Bougainville**, west Kieta, Crown Prince Range, Kokorei (=Kokuze), 900 m, 12.vi.56, RMNH. 1♂, 1♀, west Kieta, Crown Prince Range, Kokorei (=Kokuze), 9.vi.56, RMNH.

Lieftinckia malaitae: Paratypes: 2♂ (1 juv., incompl.), 1♀ (semi-adult), **Solomon Islands, Malaita Island**, Dala, 50 m, 9-4.vi.1969, RMNH. 2♂ (1 semi-adult), Ngwaian, 1500 ft., 10.x.1967, RMNH.

Lieftinckia ramosa: Paratype: 1♂, **Solomon Islands, Bougainville island**, RMNH.

Lieftinckia salomonis: 2♂, 1♀, **Solomon Islands, Guadalcanal island**, Gold Ridge, 30.vi.1956, BMNH (no. BM 1956-712). 1♀, Sornolio R. [?], 30.vi.1956, BMNH (no. BM 1956-712). 1♀, Tenaligi R., 25.ix.65, "Dicht bos; juv., white", RMNH.

Lochmaeocnemis malacodora: 2♂, **New Guinea, West Papua**, Araucaria Camp, 800 m, iii.1939. 24, Lower Mist Camp, 1400-1600 m, i.1939. 6♂, 2♀, Rattan Camp, 1200 m, ii-iii.1939. All paratypes; Neth. Ind.-Amer. New Guinea Exped., RMNH.

Mesocnemis singularis: **East Africa**: 3♂, Rusinga Island, Lake Victoria, iii.1950, RMNH. 3♀, Jinja, Uganda, vi. 1949, RMNH. 1♀, Victoria Falls, 29.ix.1961, RMNH. 2♂, Ghana (Eastern Region), 31 km NW Koforidua: Birim R. at Bunso Waterworks. 6°16.0'N 0°28.3'W, 10.v.2000, RMNH.

Paracnemis alluaudi: **Madagascar**: 1♂, Fort-Dauphin, 17.ii.58, RMNH. 1♀, Soanierana-Ivongo, 10.xi.57, RMNH.

Paramecocnemis erythrostigma: **New Guinea, West Papua**: 4♂ paratypes, Hollandia, iv.-vi.1931 RMNH. 3♂, Hollandia, vii.1938, Dutch-Amer. New Guinea Exped. 1938-1939, RMNH.

Platycnemis pennipes: **Europe, France**: 1♂, Dampierre, bij Parijs, 19.vi.1966, RMNH. **Europe, Turkey**: 1♂, 1♀, Mugla, ca. 7 km SW of Köycegiz: Lamnan Çayi, near bridge SW of Hamitköy, 5 m asl, 1.vi.2000, RMNH.

Rhyacocnemis sufficiens: **Papua New Guinea, D'Entrecasteaux Islands**: 1♂ paratype, Goodenough I., 1600 m – Camp (4th Archbold New Guinea Exped.), 12.x.1953, RMNH. 1♂, Normanby I., Camp 2 (5th Archbold New Guinea Exped.), Mt Pabinama, 820 m, 8.v.1956, RMNH. Archbold Exped.

Risiocnemis appendiculata: **Philippines, Mindanao Island, Misamis Oriental Province**: 3♂, 1♀, Bal-ason, 2-3.iv.1960, RMNH. **Philippines, Mindanao Island, South Cotabato Province**: 2♂, Koronadal, Barrio 8, 4.ii.1994, RMNH. 1♂, Mt Matutum, 500-700 m, 16-19.ix.1993, RMNH. **Philippines, Mindanao Island, Surigao del Sur Province**: 1♂ (def.), Cotabato, Parang, 13.i.1954, RMNH. 3♂, Tandag, Hitaub Creek, 500-600 m, 16-19.iv.1995, RMNH. **Philippines, Leyte Island**: 1♂, Ormoc, 18.xi.1966, RMNH.

Risiocnemis arator: **Philippines, Luzon Island, Ifugao Province**: 1♂, Jacmal Bunhian, 24 km E Mayoyao, 800-1000 m, 7-8.iv.1967, RMNH. **Philippines, Luzon Island, Nueva Viscaya Province**: 1♂, 1♀, Sta Fe, Dalton Pass, 800-1200 m, 25-30.vi.1989, RMNH.

Risiocnemis asahinai: **Philippines, Mindoro Island**: 1♂, Barrio Luyang, Halcon Mts., 360-500 m, 14./17.v.1991, RMNH. 3♂, Mindoro Oriental Province, Calapan, Comonal, Mt Tarugin, ca. 350 m, 21./29.vi. & 17./26.vii.1990, RMNH. 2♂, 4♀, Mt Halcon, 1000-1500 m, 2-20.v.1994, RMNH.

Risiocnemis confusa: **Philippines, Catanduanes Island**: 1♂, Gigmoto, San Pedro, Tongao Creeks, 400-500 m, 20-30.vi.1996, RMNH.

Risiocnemis elegans: **Philippines, Luzon, Aurora Province**: 7♂, 1♀, Dinalungan, Mt Anaguao, Alebit R. area, 600-900 m, 9-14.iii.1997, RMNH. 2♂, Dinalungan, Mt Anaguao, Bolawan R., 800-1000 m, 11.iii.1997, RMNH.

Risiocnemis erythrura: **Philippines, Mindanao Island, Surigao Province**: 1♂, L. Mainit, 30.xi.1989, RMNH. **Philippines, Mindanao Island, Surigao del Sur Province**: 1♂, 1♀, Carmen, Upper Tandag R., km 9 Lanang Line, 500 m, 24.iv.1995, RMNH. 1♂, Tago, Meme R., 100-300 m, 12-18.vi.1996, RMNH.

Risiocnemis gracilis: **Philippines, Luzon Island, Nueva Ecija Province**: 1♂, 1♀, Caranglan, Batching R., 700-850 m, 11.vi.1991, RMNH. **Philippines, Luzon Island, Nueva Viscaya Province**: 1♂, 1♀, Sta Fe, Dalton Pass area, 900 m, 8-17. viii.1991, RMNH.

Risiocnemis kiautai: **Philippines, Sibuyan Island**: 1♂, paratype, Magdiwang, Katingas, 29.iii.1987, RMNH. 1♂, paratype, Magdiwang, Tampayan, Camp Ga-ong, 80-150 m, 1-12.iv.1987, RMNH.

Risiocnemis laguna: **Philippines, Luzon Island**, Laguna Province: 1♂, 1♀, paratypes, Paete, 29.vi.1916, SMFD.

Risiocnemis moroensis: **Philippines, Mindanao Island, Bukidnon Province**: 1♂, Philippines, Mindanao, Bukidnon, Mt Imbayo, 30.viii.1988, RMNH. 1♂, 2♀, Mt Kalatungan, Talakag, Brgy Mebadiang, Magamanason Creek, Sitio Olayan, 1000-1100 m, 5-18.viii.1995, RMNH. 1♀, Philippines, Mindanao Id, Bukidnon, Mabadiang, Olayan, Mt Kalatungan, Muntian Creek, 1200-1400 m, 24./25.xi.1995, RMNH. 2♀, Philippines, Mindanao Id, Bukidnon, Mebadiang, Dumatap, Mt Kalatungan, Mansabilan Creek, 1000-1300 m, 24.xi.1995, RMNH. 1♂, Mt Katanglad, Impasugong, Brgy Impalutao, Gantongan Creek, 800-900 m, 19-29.viii.1995, RMNH.

Risiocnemis praeusta: **Philippines, Dinagat Island**: 1♂, Loreto, Balitbiton, Mt Canbinlio, vii.1989, RMNH. **Philippines, Leyte Island**: 1♀, (Mt Balocaue ?), 20.i.1989, RMNH. **Philippines, Panaon Island**: 1♂, San Francisco, Gabing Gamay, big river, x.1988, RMNH. 1♂, 1♀, San Francisco, Batong Lapad, viii.1988, RMNH.

Risiocnemis pulchra: **Philippines, Luzon Island, Bataan Province**:1♂, paratype, Luzon, Limay, 21.x.1913, SMFD. **Philippines, Luzon Island, Zambales Province**: 6♂, 2♀, Masinloc, Mt Coto, Tal-tal, 400-700 m, 1-8.iv.1997, RMNH.

Risiocnemis rolandmuelleri: **Philippines, Negros Island**: 9♂, 1♀, Silay, Patag, Cuyong R., Dumalabdab Falls, 700-750 m, 22.v.1996, RMNH.

Risiocnemis seidenschwarzi: **Philippines, Cebu Island**: 4♂, paratypes, Tabunan, 500 m, 19.xi.1998 & 9.ii.1999, RMNH.

Risiocnemis serrata: **Philippines, Catanduanes Island**: 3♂, 1♀, Gigmoto, San Pedro, Simohe Creeks, 300-500 m, 20-30.vi.1996, RMNH. **Philippines, Luzon, Bataan Province**: 2♂ (1 def.), Los Baños, 15.v.1977, RMNH. 22, Los Baños, 50 m, 28.v.1949, RMNH.

Risiocnemis varians: **Philippines, Luzon Island, Nueva Viscaya Province**: 1♂, Dalton Pass, Sta Fe, Atbo, 500-900 m, 13.ii.1989, RMNH. 1♂, Dalton Pass, Sta Fe, Torner, 500-900 m, 12.ii.1989, paratype, RMNH. 2♀, Dalton Pass, Sta Fe, Zigsag, 500-900 m, 16.ii.1989, paratype, RMNH. 3♂, 3♀, Sta Fe, Barrio Lohong, Mounts east of Dalton Pass, 900-1000 m, 10-23.i.1993, RMNH. 2♂, Sta Fe, Dalton Pass, 800-1200 m, 25./30.vi.1989 & 5./18.vi.1990, Paratype, RMNH. 1♀, Sta Fe, Atbo R., 550-800 m, 10.vi.1991, RMNH. 1♂, Sta Fe, Dalton Pass area, 900 m, 8./17.viii.1991, RMNH. **Philippines, Luzon Island, Quirino Province**: 1♂, 1♀, Maddela, Sulong R., 500-650 m, 26./27.iv.1991, RMNH.

Salomocnemis gerdae: **Solomon Islands, Guadalcanal**: 1♂, Komugelea, forest, 1200 ft., 22.ix.1965, RMNH. 1♀, Komugelea, Guadalcanal, open brook, 1200 ft., 22.ix.1965, RMNH.

Stenocnemis pachystigma: **Western Africa, SW Cameroon**: 1♂, Meme, Nyasoso, Mt Kupe, R. Nyesosoh, water catchment, 920 m, 30.iii.1997, RMNH. 1♀, Tombel, Nyasoso, Mt Kupe, Shrike Trail, 920 m, 5.iv.1995, RMNH.

Thaumatagrion funereum: **Northern New Guinea**: 6♂, paratypes, Hollandia, iii.1931, RMNH. 1♂, 1♀, Hollandia, 24.i.1933, RMNH.

Torrenticnemis filicornis: **Central northern New Guinea**: 5♂, paratypes, Lower Mist Camp, 1400-1600 m, i.1939, RMNH. 5♂, 1♀, paratypes, Sigi Camp, 1500 m, ii.1939. Neth. Ind. - Amer. New Guinea Exped., RMNH.