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TEPUIBASIS GEN. NOV. FROM THE PANTEPUI REGION OF VENEZUELA, WITH DESCRIPTIONS OF FOUR NEW SPECIES, AND WITH BIOGEOGRAPHIC, PHYLOGENETIC AND TAXONOMIC CONSIDERATIONS ON THE TEINOBASINAE (ZYGOPTERA: COENAGRIONIDAE)

J. DE MARMELS
Museo del Instituto de Zoología Agrícola *Francisco Fernández Yépez*, Facultad de Agronomía,
Universidad Central de Venezuela, Apartado 4579, Maracay 2101-A, Venezuela
demarmjc@gmail.com

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The new genus *Tepuibasis* includes 7 spp., all endemic to Pantepui; – 4 are new to science, viz.: *T. garciana* sp. n. from the Serranía de Maigualida, *T. nigra* sp. n. from Cerro Yutajé and Cerro Yaví, *T. rubicunda* sp. n. from Cerro Guanay, and *T. thea* sp. n., also from Cerro Guanay. *T. chimantai* (De Marmels, 1988), comb. n., *T. fulvum* (Needham, 1933), comb. n. and *T. neblinae* (De Marmels, 1989) comb. n. are transferred to *Tepuibasis* from *Aeolagrion* Williamson, 1917. The new genus falls within Teinobasinae Tillyard, 1917 (= Amphicneminae Fraser, 1957 syn. n. = Nehalenniinae De Marmels, 1984 syn. n), and herein within Teinobasini, because of the presence of an articulated ventrobasal spur on the male cercus. Other noticeable features of *Tepuibasis* are a bifid apical penis segment, and a spiny, auricle-like process directed proximad, at the base of each of the lobes forming bifid tip. *Tepuibasis* evolved out of ancestral teinobasine stock with considerable morphogenetic potential reflected by the large number of recent genera present in cratonic S. America, which is equaled only by insular SE Asia. Taxogeny of *Tepuibasis* was triggered by the uplift of the Guyana shield, and the vicariant species are the result of secondary isolation through fracturing and partial erosion of these highlands.

INTRODUCTION

The complex relationships between several genera or species clusters of Coenagrionidae, all apparently related to *Telebasis* Selys, 1865 are still not fully understood. In some cases the relevant characters or character states (synapomorphies), which cladistic philosophy requires for supporting the currently accepted taxonomic arrangements, have yet to be identified. Such is the case of *Helve-*

ciagrion Machado, 1980 (see BICK & BICK, 1995), or of some species ascribed to *Aeolagrion* Williamson, 1917, viz. "*Aeolagrion*" *flammeum* (Selys, 1876) (see DUNKLE, 1991; DE MARMELS & GARRISON, 2005). Some authors do indeed recognize relevant characters, but refrain from drawing the taxonomic conclusions. DUNKLE (1991: 243) for instance observed a key character in the penis of "*Aeolagrion*" *flammeum*, namely the "chitinized tips on the lateral lobes" of the apical penis segment, a feature which at once separates this species from *Aeolagrion* sensu stricto, and from *Telebasis*, instead placing it closer to the species considered in the present paper as members of a new genus, described below. The same penile character was recognized by DE MARMELS (1985, 1988, 1989) in the three species then known of this new genus, but he nevertheless decided to let remain all three species in *Aeolagrion*. Fortunately, DUNKLE (1991) succeeded in definitively resolving the taxonomic status of *Aeolagrion* sensu stricto, on the basis of two synapomorphies, admitting in *Aeolagrion* only three species. Of those species excluded by Dunkle, three, viz. "*Aeolagrion*" *fulvum* Needham, 1933, "*Aeolagrion*" *chimantai* De Marmels, 1988, and "*Aeolagrion*" *neblinae* De Marmels, 1989, together with four hitherto undescribed species, are placed here in a new genus, *Tepuibasis* gen. nov. All seven species share an exclusive combination of several key characters, but neither of these characters isolated is exclusive ("synapomorphous") to them (see below). Additional characters further support their generic status. Ecologically, these species are found on histosols, and hence are probably adapted to peat bogs. Geographically, this genus is restricted to the higher reaches of the mountain systems of the Guyana Shield known as "Pantepui" (MAYR & PHELPS, 1967). An introduction to the geographical, physical and botanical features of Pantepui and comments on each of these mountains can be found in STEYERMARK et al. (1995).

MATERIAL AND METHODS

Specimens are preserved dry in standard cellophane envelopes with collection data entered onto an enclosed card, with the exception of one specimen, stored in 70% alcohol. All drawings were made with the help of a camera lucida coupled with a Wild M8 stereo microscope. Measurements are given in millimeters. Total length and length of abdomen include caudal appendages; length of pterostigma refers to costal edge of forewing pterostigma; terminology: FW = forewing, HW = hindwing; px = postnodal cross-veins; numbers between parentheses refer to right wing; discal cell = quadrangle. Wing vein nomenclature follows RIEK & KUKALOVÀ-PECK (1984), hence "anal crossing" = CuP (Cubitus posterior); genital ligula = penis. Quotation marks in the cases of "*Aeolagrion*" *flammeum* and "*Ceriagrion*" *tenellum* indicate dubious generic affiliation. Most specimens, including holotypes of new species are deposited in the Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépez" (MIZA) of the Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela. Some specimens of South Asian and Pacific genera were loaned by Jan van Tol, of the National Museum of Natural History, Leiden, The Netherlands. Distributional data were obtained from ASKEW (1988), BELYSHEV (1973), CANNINGS & STUART (1977), KOSTERIN (2005), LIEFTINCK (1954), MANOLIS (2003), NEEDHAM (1930), SCHNEIDER & DUMONT (1997), TARBOTON & TARBOTON (2005), TSUDA (1991), WESTFALL & MAY (1996), and WATSON et al. (1991). A panbiogeographic approach was used to reconstruct the phylogeny and evolution of *Tepuibasis* [CROIZAT (1964), CRAW et al. (1999)].

TEPUIBASIS GEN. NOV.

Type-species: *Aeolagrion fulvum* Needham, 1933, by present designation.

Etymology. – The name refers to the distributional range of this new genus, the Pantepui region (Guyana Highlands), and to its similarity with *Telebasis* Selys, 1865.

Head brassy black above; frons obtusely angulate to rounded; occipital lobes not bulging posteriorly; postocular spots absent; a pale dash between each lateral ocellus and corresponding antenna, and a pale occipital line behind vertex, present. Mesepisternum brassy black, broadly coppery along median carina, and metallic green along brown humeral stripe. Female mesokatepisternum lacking tubercle at dorsal end; mesanapleural suture straight dorsally.

Legs short; tibial spines as long or longer than intervals separating them; tarsal claws with well-developed subapical tooth. Wings hyaline to weakly infumated; pterostigma a parallelogram, from slightly shorter to slightly longer than underlying cell; petiolation ceasing at CuP.

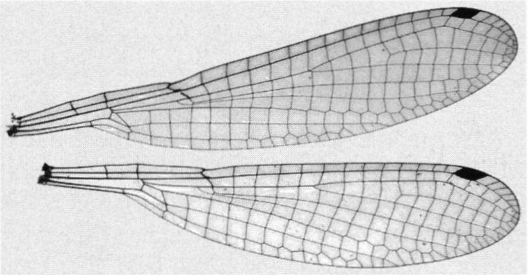


Fig. 1. Right pair of wings of male *Tepuibasis fulva*.

Abdomen in male either red or almost black with no conspicuous markings on apical segments. Male cercus directed rearwards, or bent downwards in distal half, armed with strongly chitinized swelling or tooth at or near tip (one species has short subapical ventral branch); a fleshy to moderately chitinized ventrobasal spur, articulated to a membranous area at base of cercus, and hence independent from sclerotized outline of dorsal branch of cercus proper, is present in all species; paraproct long, cylindrical, straight, directed caudad or slightly raising towards tip, and ending with chitinized hooklet curved inwards (paraproct abruptly bent dorsad in distal half in one species). Distal margin of segment 10 dorsally produced into a short, bifid or blunt median process (absent in one species). Penis with small to minute internal fold, and variably developed terminal fold; apical segment moderately to deeply bifid; a small to moderately long, auricle-like process directed proximad and armed marginally with minute, chitinized spinules is present ventro-laterally at base of each lobe conforming the bifid tip (vestigial in on species); penis shaft rarely with scattered soft setae. Female tergum of segment 10 deeply cleft; vulvar spine absent; ovipositor surpassing end of segment 10.

Larva unknown.

The genus *Tepuibasis* currently includes seven species, four of which are new to science:

T. chimantai (De Marmels, 1988) comb. nov.
T. fulva (Needham, 1933) comb. nov. (Type-species)
T. garciana sp. nov.
T. neblinae (De Marmels, 1989) comb. nov.
T. nigra sp. nov.
T. rubicunda sp. nov.
T. thea sp. nov.

TEPUIBASIS CHIMANTAI (DE MARMELS, 1988) COMB. NOV.

Figures 2, 11, 19, 27, 35, 46

Aeolagrion chimantai DE MARMELS (1988: 1; 1990a: 336); TSUDA (1991: 18); BRIDGES (1994: VII.49) (Catalogue).
"*Aeolagrion*" *chimantai*: DUNKLE (1991: 243).

Material (4 ♂, 1 ♀). – 2 ♂, 1 ♀ (type series): VENEZUELA, Bolívar State, Chimantá-Tepuí, 2200 m elevation, aprox. 5°18'N, 62°10'W, 10-X-1986, B. Bechině leg.; 2 ♂, 11-X-1990, J. Manzanilla leg.

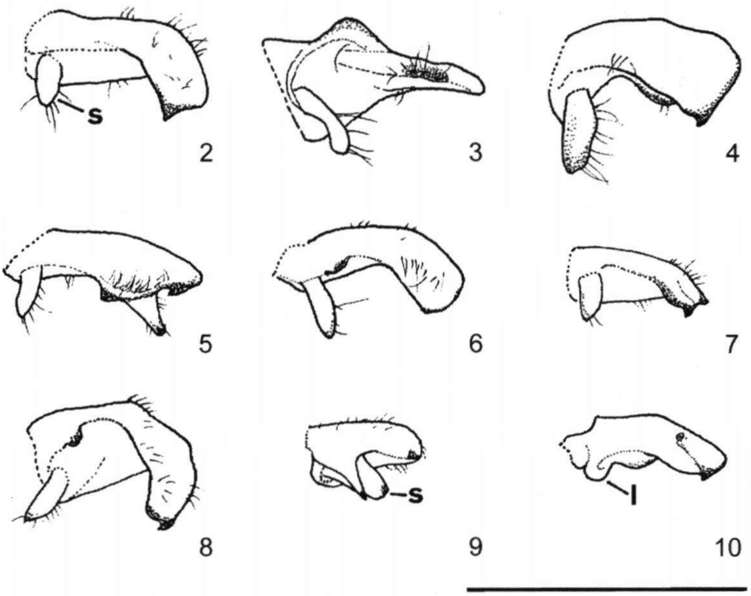
DESCRIPTIVE NOTES. – There is little to add to the original description by DE MARMELS (1988). The two additional males are fully mature and have a bright vermilion abdomen. Venational variation of these males fits within the figures given for males and the single female of the type series. It may be mentioned that one or several cells in the costal field after pterostigma are subdivided in both males collected in 1990, and both have four antenodal cells in discal field of FW after the quadrangle, and three in HW. The pterostigma is orange rather than "hellbraun" (pale brown), as quoted in the original description, and the legs, including tarsi, are also orange, not "beige".

Measurements (mm). – Abdomen 26-27; HW 18.

HABITATS AND HABITS. – Flying over low bank vegetation along small rivulets of the swampy plateau (observation by the collector, Jesús Manzanilla).

DISTRIBUTION. – Endemic to the summit of the Chimantá-Tepuí, a table-top mountain in southeastern Venezuela (Fig. 46). A thorough study of the Chimantá-Tepui has been published by HUBER (1992).

REMARKS. – This species has the habitus of a middle-sized *Telebasis* Selys, 1865. Structurally, the cercus is quite similar to that found in *Telebasis limoncocha* Bick & Bick, 1995 (BICK & BICK, 1995: figs 10, 18), and *T. salva* (Hagen, 1861), except that in *Tepuibasis chimantai* the distal third of the cercus is strongly arched ventrad. The paraproct is also strikingly similar in the three species. Within the group of species of *Tepuibasis* with red abdomen in the male sex, *T. chimantai* is the smallest. A particularity of *T. chimantai* is the notably proximal position of the pterostigma and, consequently, the large number of poststigmal cells in the costal space, in all wings.



Figs 2-10. Lateral internal view of male cercus in *Tepuibasis* and related genera (l = ventrobasal lobe; s = ventrobasal spur): (2) *T. chimantai*; – (3) *T. fulva*; – (4) *T. garciana* (paratype); – (5) *T. neblinae*; – (6) *T. nigra* (paratype); – (7) *T. rubicunda* (paratype); – (8) *T. thea (*holotype); – (9) *Nehalennia minuta*; – (10) *Telebasis limoncocha*. – [Scale = 1.0 mm]

TEPUIBASIS FULVA (NEEDHAM, 1933), COMB. NOV.

Figures 1, 3, 12, 20, 28, 36, 44, 46

Aeolagrion fulvum NEEDHAM (1933: 5), RACENIS (1953: 24), DAVIES & TOBIN (1984: 78), DE MARMELS (1989: 84), DE MARMELS (1990a: 336), TSUDA (1991: 18), BRIDGES (1994: VII.94) (Catalogue).
"Aeolagrion" fulvum: DE MARMELS (1985: 89, 90a), DUNKLE (1991: 243).

Material (6 ♂, 2 ♀). – 4 ♂, 1 ♀: VENEZUELA, Amazonas State, Mt Duida, 2110 m elevation, 3°18'N, 65°37'W, 20-XI-1991, R. García leg.; 1 ♂, 1 ♀, Mt Marawaka, 2600 m elevation, 29/30-III-1983, K. Jaffé leg.; 1 ♂, Sima (Marawaka), 3° 43' N, 65° 31' W, 1140 m elevation, 3/10-III-1985, A. Chacón leg.

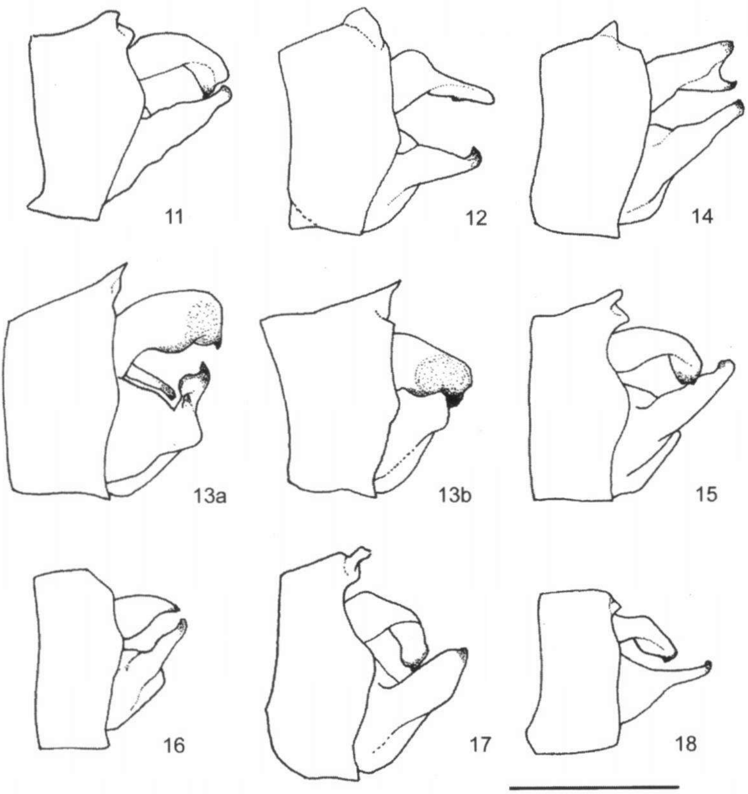
DESCRIPTIVE NOTES. – The original description of this species by NEEDHAM (1933) is adequate, but does not include any reference to the penis, nor illustrations of any kind. Male head, caudal appendages and penis were for the first time figured by DE MARMELS (1985). Frons rather rounded. Pronotal hindlobe in female not raised, shallowly undulate in dorsal view. Mesepimeral black stripe with metallic violet reflections. Three antenodal cells after quadrangle in discal field of FW, two in HW: 13-16 px in FW, 12-13 in HW; RP2 originating at px 6 in FW, between px 4 and 5 in HW; IR1 at px 10-11 in FW, at px 9 or 10 in HW. Abdomen in male bright red, in female rufous brown with small, pale, lateral marks at base of segments 3-7.

Measurements (mm). – Abdomen (both sexes) 32-33; HW 22-24.

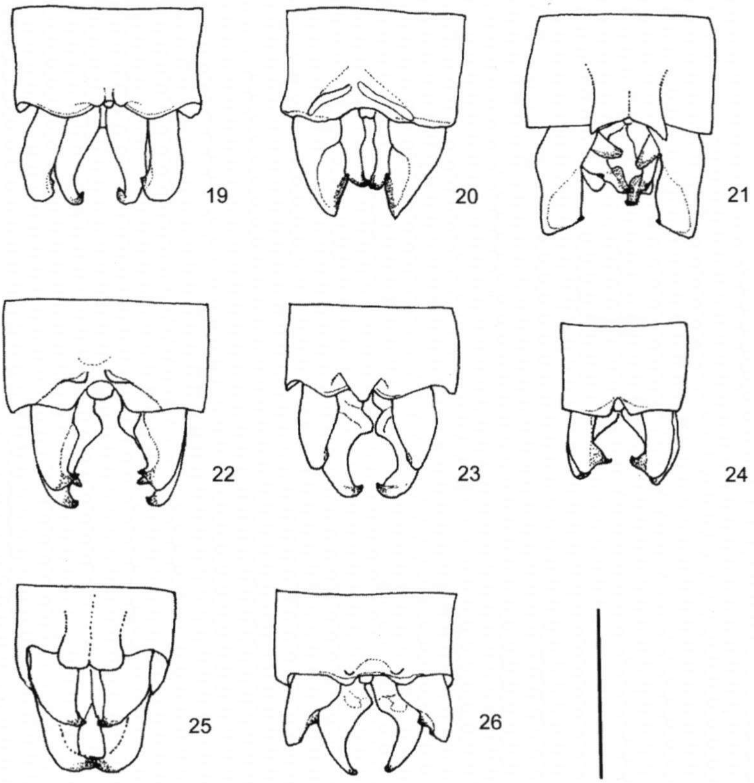
HABITATS AND HABITS. – The specimens collected at the southern extremity of Mt Duida were flying over peat bogs (Rafael García, pers. comm.).

DISTRIBUTION. – Endemic on Mt Duida and the neighbouring Mt Marawaka, between 1140 and 2600 m elevation (Fig. 46). Short papers dealing with the geology, flora and fauna of Mt Marawaka have been published by FUNDACIÓN TERRAMAR (1985), and see also STEYERMARK et al. (1995).

REMARKS. – The habitus of *T. fulva* with its all-red abdomen in the male sex



Figs 11-18. Abdominal segment 10 with caudal appendages of male *Tepuibasis* and *Telebasis limoncocha* (left lateral view): (11) *T. chimantai* (holotype); – (12) *T. fulva*; – (13a) *T. garciana* (paraproct exposed) (paratype); – (13b) same, with cercus in natural position (holotype); – (14) *T. neblinae* (holotype); – (15) *T. nigra* (holotype); – (16) *T. rubicunda* (holotype); – (17) *T. thea* (holotype); – (18) *Telebasis limoncocha*. – [Scale = 1.0 mm]



Figs 19-26. Abdominal segment 10 with caudal appendages of male *Tepuibasis* and *Telebasis limoncocha* (dorsal view): – (19) *T. chimantai* (holotype); – (20) *T. fulva*; – (21) *T. garciana* (paratype); – (22) *T. neblinae*; – (23) *T. nigra* (holotype); – (24) *T. rubicunda* (holotype); – (25) *T. thea* (holotype); – (26) *Telebasis limoncocha*. – [Scale = 1.0 mm]

is that of a large *Telebasis*. Within *Tepuibasis*, *T. fulva* has the deepest cleft apical penis segment, and the auricle-like, spiny process at the base of each lobe of the bifid tip is longest in this species (Fig. 28). The distal half of the male cercus is straight and apically tapering; a little-developed chitinized tooth is present internally, much anterior to tip.

TEPUIBASIS GARCIANA SP. NOV.

Figures 4, 13A-B, 21, 29, 37, 42A-B, 46

Material (3 ♂, type series). – **Holotype ♂**: VENEZUELA, Amazonas State, Átures Department, Serranía de Maigualida, 2170 m elevation, 5°30'N, 65°15'W, at a small left-side affluent of the

Caño Iguana, 25-XI-1989; – **Paratypes** 1 ♂, same data as holotype; 1 ♂, 28-II-1991, all Rafael García leg.

Etymology. – The new species is named in honor of my former graduate student, Rafael García Peña, Caracas (now Hamburg, Germany), who collected this and other highly interesting species during short visits to some almost inaccessible mountain tops in Pantepui, as well as to acknowledge Dr José Luis García, a hymenopterist, who secured several specimens of yet another new species described below.

MALE (**Holotype**). – Head. – Frons rather rounded; labium pale, labrum brown with free margin pale, clypeus and top of head black; ocellar marking and occipital line brown; antenna brown black; rear of head pale brown.

Thorax. – Pronotum black dorsally on middle lobe, anterior and posterior lobe, as well as a spot laterally on middle lobe, pale brown; hind lobe laterally erect and curved wave-like downwards to central portion, which is slightly emarginated posteriorly at middle (Figs 42A, B); mesostigmal lamina small, unconspicuous. Mesepisternum and mesepimeron black with metallic reflections, a brown humeral stripe present; mesokatepisternum black in dorsal half, pale ventrally; metepisternum mostly pale, but dorsally partly black continuous to mesepimeral black; metepimeron pale, its ventral extreme and metasternum dark brown (Fig. 37). Legs black, but tibiae pale brown externally; tibial spines of hind legs as long as, or slightly longer than spaces separating them; coxae pale.

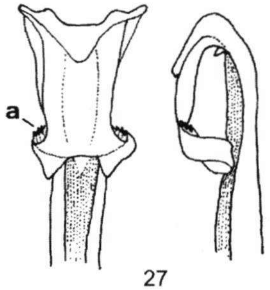
Wings hyaline, pterostigma brown encircled by narrow yellow border, shorter than underlying cell; venation black; costal edge of FW quadrangle slightly longer than proximal edge; three cells after quadrangle in discal field of FW, two in HW. 11 px in FW, 10(11) in HW; RP2 originating after px 4 (before) in FW, before px 3 in HW; IR1 originating at px 8 in FW, at px 7 in HW; there are 6-7 cells after pterostigma in costal space.

Abdomen. – Brown black, darker towards tip of each segment; last three segments almost entirely black. There are indefinite, paler areas laterally on segments 1 and 2, and a pale basal ring on segments 3-7, which is interrupted dorsally at middle. Distal border of segment 10 with a pair of diverging horns dorsally. Cercus straight in lateral view, broadening distalwards with truncate to slightly emarginated tip. Cercus in natural position slightly slanting to rearwards (Fig. 13B). Paraproct turned dorsad sharply in distal half, and ending in a spatulate, strongly chitinized tip (Fig. 13A).

Measurements (mm). – Total length 35.1; abdomen 27.1; cercus 0.6; HW 18.1; pterostigma 0.7.

MALE (**Paratypes**). – Very similar to holotype. One male has 12(13) px in FW,

Figs 27-34. Penis of *Tepuibasis* and of "*Aeolagrion*" *flammeum* (a = spiny, auricle like process at base of each apical lobe, p = proximal auricle-like process, v = vestigial auricle-like process; left = ventral view, right = lateral view): (27) *T. chimantai*; – (28) *T. fulva*; – (29) *T. garciana* (paratype); – (30) *T. neblinae*; – (31) *T. nigra* (paratype); – (32) *T. rubicunda* (paratype); – (33) *T. thea* (holotype); – (34) "*Aeolagrion*" *flammeum*. – [Scale = 0.5 mm]



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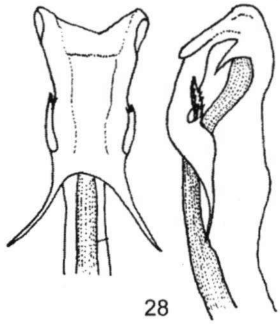

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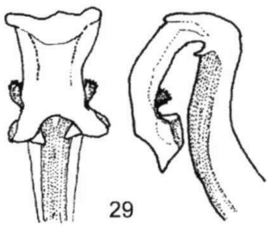

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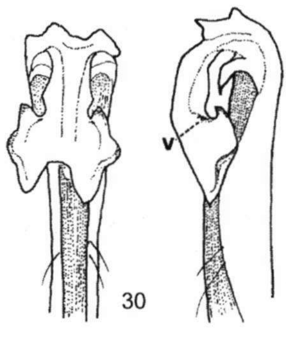

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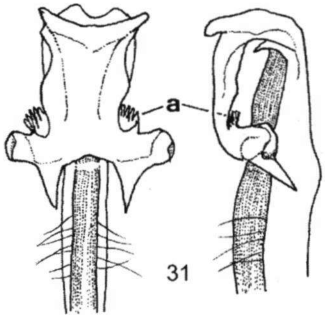

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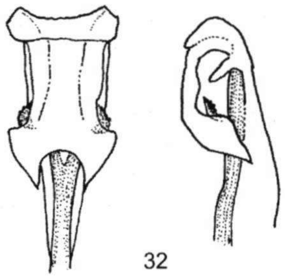

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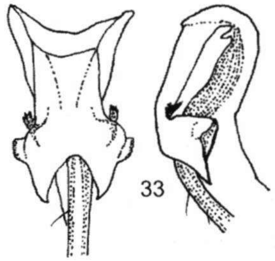

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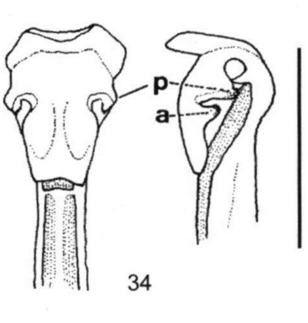

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12(11) in HW; R3 originates after px 4 or near px 5 in FW and after px 3 in HW; IR2 originates at px 7-9 in FW, and at px 9 in HW. Penis as in Figure 29.

Measurements (mm). – Total length 34.5-35; abdomen 27-27.6; cercus 0.5-0.6; HW 18.5-19; pterostigma 0.6.

FEMALE. – Unknown.

HABITATS AND HABITS. – According to the collector, the specimens were secured over small ponds in a peat bog crossed by tiny streams. Besides such herbaceous habitats, exposed granitic rocks and small interspersed pockets of forest are typical of the area. A plant genus found at the site and endemic to it is *Huberopappus* Pruski, 1992 (Asteraceae).

DISTRIBUTION. – Probably endemic in the Serranía de Maigualida (Fig. 46).

REMARKS. – The highly modified male pronotal hind lobe is unique. Another striking autapomorphy is the distally sharply dorsad curved paraproct. Additionally, the male cercus is not arched downwards distally as in the other two species with black abdomen. A colour slide taken from a live male in lateral view shows a compound eye which is black above, light blue below; the pale parts of the thorax are creamy white, with traces of bluish white pruinosity on lateral parts of pronotum, metepisternum, metepimeron, and on coxae.

TEPUIBASIS NEBLINAE (DE MARMELS, 1989) COMB. NOV.

Figures 5, 14, 22, 30, 38, 46

Aeolagrion neblinae DE MARMELS (1989: 83; 1990a: 336; 1990b: 194), TSUDA (1991: 18), DE MARMELS (1992: 62), BRIDGES (1994: VII.162) (Catalogue).
"*Aeolagrion*" *neblinae*, DUNKLE 1991: 243.

Material (10 ♂, 3 ♀). – 1 ♂, VENEZUELA, Amazonas State, Cerro de La Neblina, Camp X, 1690 m elevation, 0°54'40"N, 66°02'30"W, 12-II-1985; 2 ♂, 13-II-1985, all W. Steiner leg. (type series); 4 ♂, 2 ♀, Mt Arakamuni, 1415 m elevation, 1°32'N, 65°49'W, 24/30-X-1987, A. Chacón leg.; 2 ♂, 1 ♀, Sierra de Unturán, 900-1000 m elevation, 01°25'N, 65°18'W, 15/17-II-1989; 1 ♂, Serranía de Tapirapecó, Tamacuari, 1300 m elevation, 01°13'N, 64°41'30"W, 19/21-III-1989, all J. De Marmels leg.

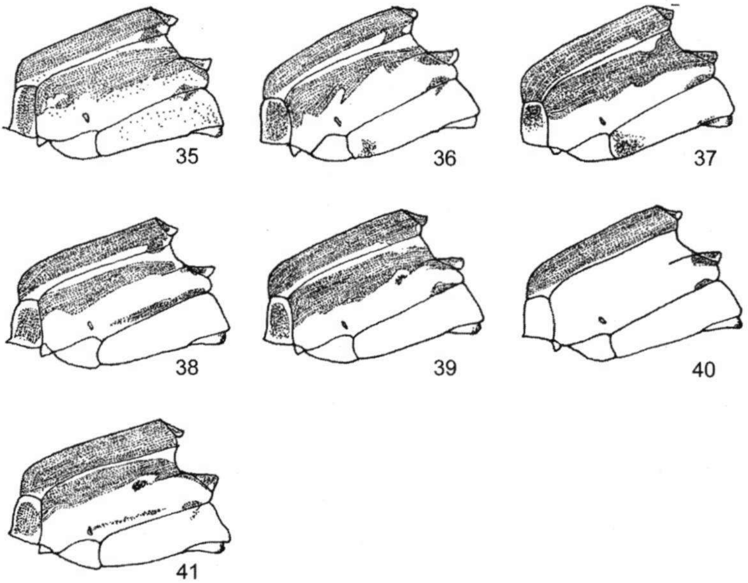
DESCRIPTIVE NOTES. – The original description by DE MARMELS (1989) is extensive and includes illustrations of head, thorax, tip of FW, penis and caudal appendages. However, the illustrations of the penis given in that paper are somewhat misleading: the proximal angle of the apical lobe is actually slightly sclerotized, but does not bear any spinules; instead, the auricle-like process which bears the spinules in the other species of this genus, is vestigial in *T. neblinae*, and the few minute spinules present are placed directly on the surface of the penis itself, being concealed below the inner margin of the base of the apical lobe (Fig 30).

Pronotal hindlobe of the females examined here is broadly rounded posteriorly rather than "straight" as indicated in the description of the allotype female. The "anteriorly directed triangular projection" mentioned in the original description refers to a jag of orange colour at middle of hind margin of pronotum; hind margin itself slightly raising near lateral angle, remainder of hind lobe flat. Mesostigmal lamina with small swelling near lateral angle, mesepisternum with shallow depression behind mesostigmal lamina, this depression closed mesally by small knob or swelling. There are three cells after quadrangle in discal field of FW, two in HW. Colour slides and descriptive notes of live male and female from Unturán show the following: (Male) compound eye brown black above (red brown posteriorly), pale blue below; pale parts of metepisternum and metepimeron grey green; abdomen dark red troughout, except for segment 1, which is orange brown; (female) compound eye dark brown above, pale blue below; abdominal segments 1 and 2 pale brown, rest dark red brown, last three segments brown black, segments 3-7 with pale brown basal ring.

Measurements (mm). – Abdomen (both sexes) 31.5-34.7; HW 20.5-24.0.

HABITATS AND HABITS. – At the Tamacuari site a male was caught at a large patch of terrestrial tank bromeliads on an open slope, while the specimens from Unturán were found in a boggy forest, not far from a small mountain stream (DE MARMELS, 1992). The collector of the specimens from Mt Arakamuni took them over a pond in an open peat bog (A. Chacón, pers. comm.).

DISTRIBUTION. – Known from four mountain systems covering a fairly extensive area in the extreme south of Venezuela (Fig. 46).



Figs 35-41. Thoracic pattern in male *Tepuibasis* (left lateral view): (35) *T. chimantai* (holotype); – (36) *T. fulva*; – (37) *T. garciana* (holotype); – (38) *T. neblinae* (holotype); – (39) *T. nigra* (holotype); – (40) *T. rubicunda* (holotype); – (41) *T. thea* (holotype). – [Schematized, not to scale]

REMARKS. – Resembling a large, red *Telebasis*, this is the only species within *Tepuibasis*, in which the spinous, auricle-like process at the basis of each apical lobe of the penis is vestigial. *T. neblinae* is also unique in having a postmedian ventral branch on the male cercus.

TEPUIBASIS NIGRA SP. NOV.

Figures 6, 15, 23, 31, 39, 46

Material (6 ♂, 4 ♀; type series). – **Holotype** ♂: VENEZUELA, Amazonas State, Cerro Yaví, 2150 m elevation, 5°43'08"N, 65°53'52"W, 24/28-II-1995, J.L. García leg.; – **Paratypes**: 4 ♂, 1 ♀, same data as holotype; 1 ♂, 1 ♀, Cerro Yutajé, 1750 m elevation, 5° 45' 35" W, 66° 08' 03" W, J.L. García leg.; 2 ♀, 12/19-II-1995, J. Clavijo leg.

Etymology. – The specific epithet refers to the mostly black body colouration in the male ("nigra": Latin for "black").

MALE (**Holotype**). – Head. – Frons obtusely angled; labium and mandible pale, labrum brown with free margin pale; clypeus black, top of head brassy black; ocellar marking and occipital line pale brown, the latter narrow and interrupted at middle, antenna black; rear of head black, except for a narrow, white area below gena along ventral margin of compound eye, and a narrow yellow area below occiput.

Thorax. – Pronotum mostly brassy black dorsally, but anterior half of anterior lobe, posterior margin of hind lobe, and lateral parts, pale brown; hind lobe flat, shallowly emarginated at middle. Mesepisternum and mesepimeron mostly brassy black, separated by brown humeral stripe (Fig. 39); mesokatepisternum brassy black surrounded by pale brown along borders; metepisternum and metepimeron mostly pale greenish grey; metasternum pale.

Legs black, tibiae pale-lined externally; tibial spines longer than spaces separating them; coxae, trochanters pale.

Wings hyaline; pterostigma dark brown with paler margins, as long as cell below it (slightly longer than underlying cell in right HW); venation black; three cells after quadrangle in discal field of FW, two in HW; 13 px in FW, 12(11) in HW; RP2 originating almost at px 6 in FW, at px 5 in HW; IR1 originating at px 9 in all wings; four cells in costal space after pterostigma (five in right HW).

Abdomen. – Black dorsally, paler lateroventrally; segments 3-8 with pale blue or creamy basal ring, which is interrupted on middorsum by black. Distal border of segment 10 with more or less triangular, undivided mediodorsal process. Cercus strongly arched downwards at distal two fifths of its length, blunt, with minute apical tubercle or tooth directed laterad. Paraproct longer than cercus, straight in lateral view, directed rearwards and slightly upwards; in dorsal view robust with tip curved mesad and ending in a strongly chitinized hooklet (Figs 15, 23).

Measurements (mm). – Total length 40; abdomen 32; cercus 0.5; HW 21; pterostigma 1.

MALE (**Paratypes**). – As holotype. Some specimens have incomplete brown stripe over part of second lateral suture below the black spot at dorsal end of same suture. Venational variations: 13 px in both HW (one male); RP2 originating after px 5 in FW; IR1 originating at px 8 in all wings (one male), at or before px 8 in HW, or at px 7 in all wings (one male each). Penis as in Figure 31.

Measurements (mm). – Abdomen 32.5-34.5; HW 21.2-22.5.

FEMALE (**Paratypes**). – Black colour less extended than in male. Vertical surface of frons, base of postclypeus and dorsolateral areas of frontal rim, pale brown. Pronotal hind lobe as in male; mesostigmal lamina small, unspecialized. Legs pale, except for dorsal surface of femora, area around femuro-tibial articulation, anterior dorsal line on fore tibiae, and tip of all tibiae, black. Wings as in male, but pterostigma paler, yellow brown. 12-16 px in FW and 12-14 in HW. Abdomen brown dorsally, each side with darker lateral line separating dorsal brown from much paler lateroventral area of tergites; these dark lateral lines broadly connected at apex across dorsum (some females have tergites uniformly dark dorsally). Segment 1 entirely pale brown; segments 2 and 3 with yellow or brown mediodorsal apical spot, lying within dark apical cross connection described above; segments 8-10 mostly dark dorsally; cercus shorter than segment 10, conical. Valves of ovipositor finely serrate along ventral margin, reaching to, or slightly surpassing, tip of cerci.

Measurements (mm). – Total length 37-40; abdomen 29-32; HW 21.6-24.

HABITATS AND HABITS. – On Cerro Yaví the species was found around a large pond within a peat bog, in open vegetation. On Cerro Yutajé it occurs in open, boggy gallery forest bordering a small stream (GARCÍA, 2003; J. Clavijo, pers. comm.).

REMARKS. – See comments under *T. thea* (below).

TEPUIBASIS RUBICUNDA SP. NOV.

Figures 7, 16, 24, 32, 40, 43, 46

Material (2 ♂, 1 ♀; type series). – **Holotype** ♂: VENEZUELA, Amazonas State, Cerro Guanay, 1250 m elevation, 05°52'04"N, 66°23'03"W, 5/12-II-1995, J. Clavijo leg.; – **Paratypes**: 1 ♂, 1 ♀, same data as holotype.

Etymology. – The term "rubicunda" (Latin) means "red", for the reddish abdomen in the male sex.

MALE (**Holotype**). – Head. – Frons obtusely angled; labium pale, labrum yellow, rest of face, antenna, ocellar mark and occipital line, orange; top of head brassy black, rear of head whitish.

Thorax. – Pronotum brassy black dorsally, anterior border of anterior lobe, depression between it and median lobe, lateral angle of median lobe, hind border of hind lobe, and lateral parts of prothorax, orange. Entire mesepisternum vividly metallic; rest of thorax orange, except for small, metallic green dash at antealar carina of metepisternum, and a black spot at upper end of second lateral suture (Fig. 40); metasternum pale. Legs orange, tibial spines black, longer than intervening spaces.

Wings hyaline, venation black; pterostigma pale orange brown, margined yellow, shorter than cell below it. Costal edge of FW quadrangle almost 1.5 times as long as proximal edge; three cells after quadrangle in discal field of FW, two in HW. 14 px in FW, 13(12) in HW; RP2 originating at px 6 (FW), at px 5 (HW); IR1 originating at px 8 (FW), at px 8(9) in HW; there are 3-4 cells in costal space after pterostigma.

Abdomen. – Long and slender, orange red dorsally, yellow orange laterally, tip of segments 4-7, and dorsum of segments 8-10, slightly darker; distal border of segment 10 without median dorsal process. Cercus straight, but sharply tapering to tip in lateral view, internally with large subapical tooth directed mesad (Figs 16, 24). Paraproct of same length as cercus, straight, directed towards tip of cercus and ending in an apical hooklet curved mesad.

Measurements. – Total length 38.5; abdomen 32; cercus 0.5; HW 20; pterostigma 0.8.

MALE (**Paratype**). – Similar to holotype, but has only 13 px in all wings, and IR2 originates at px 9, also in all wings. Penis as in Figure 32.

Measurements (mm). – Total length 38.9; abdomen 32.4; cercus 0.6; HW 19.5; pterostigma 0.7.

FEMALE (**Paratype**). – As male, but abdomen pale ochreous; pronotal hind lobe low, shallowly undulated, almost straight at middle; mesepisternal fossa present immediately behind mesostigmal lamina (Fig. 43); there are 15 px in left FW, but venation otherwise as in male. Valves of ovipositor reaching to tip of cerci finely serrate along ventral border.

Measurements (mm). – Total length 37.5; abdomen 30.5; HW 20.

HABITATS AND HABITS. – The collecting site was described as an open peat bog with many small pools (pers. comm. from the collector).

REMARKS. – This is the most slender built species of the genus. It is the only species with large, mesad directed subapical tooth in male cercus, and well-defined mesepisternal fossae in female. It is also the only species with mesepimeral stripe missing. It shares with *T. garciana* the long costal edge of FW quadrangle (shorter than proximal edge in all other species).

TEPUIBASIS THEA SP. NOV.

Figures 8, 17, 25, 33, 41, 46

Material (1♂, 1♀; type series). – **Holotype** ♂: VENEZUELA, Amazonas State, Cerro Guanay, 1250 m elevation, 05°52'04"N, 66°23'03"W, 5/12-II-1995, J. Clavijo leg.; – **Paratype**: 1 ♀, same data as holotype.

Etymology. – "Theá" in Greek means "goddess". This new species is named in allusion to the sacred status (to the local Amerindian tribes) of the mountains of Pantepui.

MALE (**Holotype**). – Head. – Frons moderately angled: labium pale, bluish at middle, labrum black with free border pale, mandibles pale blue laterally with black spot at anterior border; anteclypeus obscure, bluish; postclypeus, frons and top of head, black; antenna brown black, ocellar mark brown, occipital line obsolete, reduced to narrow, brown line posteriorly along occipital rim, visible in posterior view only. Rear of head black, except for small yellow área below occiput; genae pale with black dash below base of antenna.

Thorax. – Pronotum black dorsally, anterior lobe brown laterally, hind lobe narrowly margined with brown, lateral parts of prothorax brown; pronotal hind lobe straight behind, slightly raised at middle. Mesepisternum and mesepimeron brassy black, separated by brown humeral line lying entirely on mesepimeron; mesokatepisternum brown black, margined with pale brown (Fig. 41). Metepisternum and metepimeron pale greenish or bluish grey, with some pruinosity near pale brown coxae, and along antealar ridge. Metasternum with bunch of densely set hairs posteriorly. Legs black, tibiae pale-lined externally; tibial spines longer than intervals separating them.

Wings hyaline, venation black; pterostigma dark brown black, paler along edges, and covering cell below it; there are four poststigmal cells in costal field; three cells after quadrangle in discal field of FW, two in HW; costal edge of FW quadrangle as long as (slightly shorter than) proximal edge; 16 px in FW, 14(15) px in HW; RP2 originating after px 6 in left FW, at px 6 in all other wings; IR1 originating at px 11 in all wings.

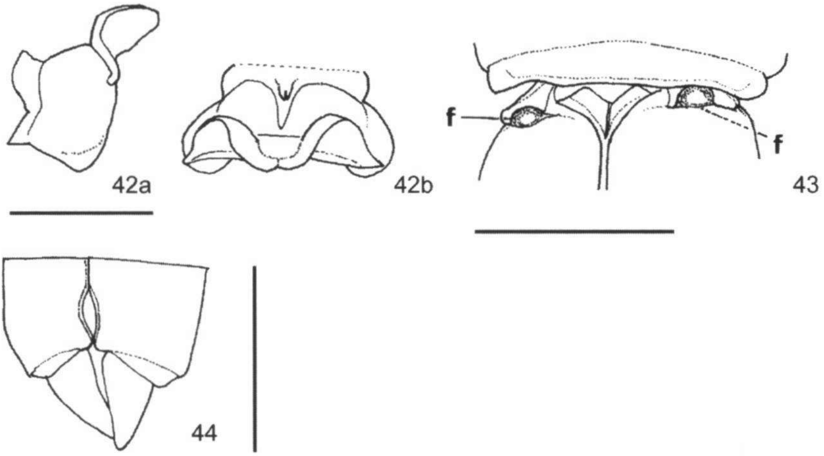
Abdomen. – Black dorsally, pale lateroventrally; segment 1 has blue distal dorsal rim, segment 2 is blue laterally; a pale basal spot laterally on segments 2-7. Penis as in Fig. 33. Cercus brown, claw-like, strongly arched ventrad after first third of its length, and with short apical tooth (Figs 17, 25); paraproct robust, pale blue ventrally at base, black in distal half, with tip arched mesad. Segment 10 with broad median dorsal process, slightly emarginated apically at middle.

Measurements (mm). – Total length 45; abdomen 36; cercus 0.7; HW 23; pterostigma 1.

FEMALE (**Paratype**). – Similar to male, with black on head and thorax less extended. Vertical part of frons brown; pale brown occipital line slightly better developed than in male. Pronotal hind lobe as in male. Brown humeral stripe much broader, occupying also part of mesepisternum adjacent to humeral suture. Femora ventrally pale brown, pale colour more extended dorsally on tibiae than in male. Pterostigma dark brown. 14 px in FW, 13 px in HW; RP2 originating at px 7 (between px 6 and 7) in FW, at px 6 in HW; IR1 originating at px 10 in all wings. Abdomen as in male, but pale blue to whitish basal rings better developed. Segments 9 and 10 predominantly brown dorsally. Cercus shorter than segment 10; ovipositor reaching to beyond tip of cerci, finely serrate along ventral border.

Measurements (mm). – Total length 40.2; abdomen 32; HW 22; pterostigma 1.

HABITATS AND HABITS. – *T. thea* was collected together with *T. rubicunda*. This is the only case so far of two species of *Tepuibasis* occurring sympatrically on the same mountain.



Figs 42-44. Morphological features in some species of *Tepuibasis*: (42A) prothorax showing raised pronotal hind lobe in male *T. garciana* (left lateral view); – (42B) same in dorsal view; – (43) anterior portion of mesothorax of female *T. rubicunda* showing mesepisternal fossae (f) (dorsal view); – (44) abdominal segment 10 with cerci of female *T. fulva*, showing dorsally cleft tergum (dorsal view, ovipositor omitted). – [Scale = 1.0 mm]

REMARKS. – *T. thea* is closely similar to *T. nigra*. The male cercus in *T. thea* is, however, more strongly and more proximally arched downwards, and the paraproct is considerably more robustly built. The middorsal apical process of segment 10 is truncate and slightly emarginate in *T. thea*, but convex in *T. nigra*. Females of these two species are also very similar, but the occipital line is well-marked in *T. nigra*, but obsolescent in *T. thea*. Pterostigma is dark brown in *T. thea*, but pale brown in *T. nigra*. Male and female *T. thea* have a dense bunch of closely set hairs on metasternum, while in *T. nigra* these hairs are more scattered.

KEY TO THE ADULTS OF *TEPUIBASIS*

1 Males 2
– Females* 8
2 Pronotal hind lobe erect, strongly undulate (Figs 42a, b); abdomen brown black; paraproct abruptly bent dorsad in distal half (Fig. 13a) .... ***garciana***
– Pronotal hind lobe neither erect, nor undulate; abdomen red or black; paraproct not sharply bent dorsad in distal half 3
3 Cercus with postmedian ventral branch (Fig. 14); abdomen red: auricle-like spiny process at base of apical lobes of penis vestigial (Fig. 30) .... ***neblinae***
– Cercus with no postmedian ventral branch; abdomen red or black; auricle-like spiny process at base of apical lobes of penis present 4
4 Usually more than seven poststigmal cells in costal field; HW with three postquadrangular cells

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* Female *T. garciana* unknown, but possibly it has modified pronotal hind lobe.

in discal field; abdomen red; cercus arched downwards in distal fifth ending in a pointed tooth (Fig. 11) .... ***chimantai***
– Usually less than seven poststigmal cells in costal field; HW with two postquadrangular cells in discal field (rarely three in one wing); abdomen red or black; cercus variable 5
5 Abdomen red; cercus in lateral view tapering towards tip, not strongly arched ventrad in distal half (Figs 12, 16) 6
– Abdomen almost black; cercus in lateral view not tapering towards tip, but strongly arched ventrad in distal half (Figs 15, 17) 7
6 Dark mesepimeral stripe absent; cercus in dorsal view with large subapical tooth internally (Fig. 24) .... ***rubicunda***
– Dark mesepimeral stripe present; cercus in dorsal view with no large subapical tooth internally (Fig. 20) .... ***fulva***
7 Cercus arched ventrad at about half its length; paraproct robust in lateral view (Fig. 17); mediodorsal process of segment 10 broad, emarginated at tip .... ***thea***
– Cercus arched ventrad in distal half of its length (Fig. 15); paraproct slender in lateral view: mediodorsal process of segment 10 convex, bluntly triangular .... ***nigra***
8 Dark mesepimeral stripe absent .... ***rubicunda***
– Dark mesepimeral stripe present 9
9 Usually more than seven poststigmal cells in costal field; HW with three postquadrangular cells in discal field .... ***chimantai***
– Usually less than seven poststigmal cells in costal field; HW with two postquadrangular cells in discal field (rarely three in one wing) 10
10 Ventral border of dark mesepimeral stripe with two or three decurrent jags (Fig. 36) .... ***fulva***
– Ventral border of mesepimeral stripe straight or little sinuate 11
11 Pronotal hind lobe slightly raised near lateral angle, flat at middle; mesostigmal lamina with small swelling near lateral angle; mesepisternum behind lateral angle of mesostigmal lamina with shallow, glabrous depression .... ***neblinae***
– Pronotal hind lobe flat laterally; mesostigmal lamina with no swelling near lateral angle; mesepisternum without shallow depression behind lateral angle of mesostigmal lamina 12
12 Pale occipital line well-defined; pterostigma pale brown; extreme distal margin of pronotal hind lobe not noticeably raised at middle; metasternum with a group of scattered hairs posteriorly .... ***nigra***
– Pale occipital line obsolescent; pterostigma dark brown; extreme distal margin of pronotal hind lobe noticeably raised at middle; metasternum with bunch of densely set hairs posteriorly ***thea***

ADDITIONAL TAXA OF TEINOBASINAE EXAMINED

Species examined of genera with articulated ventral branch of male cercus [the "(a) Chromagrion-Nehalennia-Teinobasis series" of KENNEDY (1920a)]

Amphicnemis Selys, 1863
A. mariae Lieftinck, 1940
* *Bromeliagrion* De Marmels, 2005
B. beebeanum (Calvert, 1948)
B. fernandezianum (Rácenis, 1958
Chromagrion Needham, 1903
C. conditum (Selys, 1876)
Melanesobasis Donnelly, 1984
M. corniculata (Tillyard, 1924)
M. flavilabris (Selys, 1891)
M. maculosa Donnelly, 1984
Nehalennia Selys, 1850
N. gracilis Morse, 1895
N. minuta (Selys, 1857)
N. speciosa (Charpentier, 1840)
Papuagrion Ris, 1913
P. occipitale (Selys, 1877)
P. prothoracale Lieftinck, 1935
Pericnemis Selys, 1863
P. stictica Selys, 1863

Plagulibasis Lieftinck, 1949
P. ciliata (Ris, 1913)
Pyrrhosoma Charpentier, 1840
P. nymphula (Sulzer, 1776)
Teinobasis Kirby, 1890
T. bradleyi Kimmins, 1957
T. filamentum Needham & Gyger, 1939
T. samaritis Ris, 1915
T. stigmatizans Lieftinck, 1938

Species examined of genera without articulated ventral branch of male cercus [the "(b) Ceriagrion-Telebasis-Metaleptobasis series" of KENNEDY (1920a)]

Aeolagrion Williamson, 1917
A. dorsale (Burmeister, 1839)
"A." flammeum (Selys, 1876)
Ceriagrion Selys, 1876
C. glabrum (Burmeister, 1839)
C. indochinense Asahina, 1967
C. melanurum Selys, 1876
"C." tenellum (de Villers, 1789)
Diceratobasis Kennedy, 1920
D. macrogaster (Selys, 1857)
Helveciagrion Machado, 1980
H. vulcanoae (Machado, 1980)
Hylaeonympha Rácenis, 1968
H. magoi Rácenis, 1968
Inpabasis Santos, 1961
I. machadoi Santos, 1961
Leptagrion Selys, 1876
L. perlongum Calvert, 1909
Metaleptobasis Calvert, 1907
M. brysonima Williamson, 1915
Minagrion Santos, 1965
M. ribeiroi Santos, 1962
M. waltheri (Selys, 1876)
Telebasis Selys, 1865
T. bastiaani Bick & Bick, 1996
T. boomsmae Garrison, 1994
T. brevis Bick & Bick, 1995
T. byersi Westfall, 1957
T. carmesina Calvert, 1909
T. carminita Calvert, 1909
T. corallina (Selys, 1876)
T. demararum (Williamson, 1917)
T. dominicana (Selys, 1857)
T. filiola (Perty, 1834)
T. griffini (Martin, 1896)
T. isthmica Calvert, 1902
T. limoncocha Bick & Bick, 1995
T. racenisi Bick & Bick, 1995
T. rubricauda Bick & Bick, 1995
T. salva (Hagen, 1861)
T. selaopyge De Marmels, 1989
T. simulata Tennessen, 2002
T. vulnerata (Hagen, 1861)
T. willinki Fraser, 1948

Genera of uncertain affiliation examined

Antiagrion Ris, 1904
A. antigone Ris, 1928
A. gayi (Selys, 1876)
** *Nesobasis* Selys, 1891
N. angulicollis Tillyard, 1924
N. brachycerca Tillyard, 1924
N. caerulecaudata Donnelly, 1990
N. longistyla (Selys, 1891)
N. campioni Tillyard, 1924
N. comosa Tillyard, 1924
N. erythrops (Selys,1891)
N. heteroneura Tillyard, 1924
N. leveri Kimmins, 1943
N. longistyla (Selys, 1891)
N. rufostigma Donnelly, 1990
N. selysii Tillyard, 1924
N. telegastra (Selys, 1891)

* Originally, I had included *Bromeliagrion fernandezianum* (sub *Leptagrion*) within the "Nehalenniinae" (= Teinobasinae) (DE MARMELS, 1985). Recently, I decided to again separate *Bromeliagrion* from this group (DE MARMELS & GARRISON, 2005), chiefly based on certain aspects of penis morphology. Male cercal morphology, however, suggests that *Bromeliagrion* is indeed a Teinobasinae (see below).

** DONNELLY (1990) mentions a few characters which seem to deny any possible relationship between *Nesobasis* and *Teinobasis*. The fact that *Teinobasis* is a close relative of *Melanesobasis* contradicts the affirmation made by Donnelly in the same paper (p. 91) that *Melanesobasis* "is clearly a close relative of *Nesobasis* (...)". Judging from the morphological characters of *Nesobasis* (frons, cerci, penis), this genus is not a Teinobasini, nor even clearly referable to Teinobasinae, and hence is unrelated to *Melanesobasis* (see below).

PHYLOGENETIC POSITION OF *TEPUIBASIS*

The new genus is referable to KENNEDY's (1920a) "Nehalennia-Telebasis Series", for which subfamily status (Nehalenniinae) was proposed by the late Dr Janis Rácenis (unpublished manuscript), based on a series of characters reviewed and expanded by DE MARMELS (1984). However, FRASER (1957: 48) had already proposed the name Amphicneminae to include a group of Old World genera, that also conform to Nehalenniinae (except *Archibasis* Kirby, 1890). The only two New World genera mentioned, viz. *Leptobasis* Selys, 1877, and *Antiagrion* Ris, 1904, should be excluded. Even earlier, TILLYARD (1917: 280) had introduced the "Tribe 4. Teinobasini". Teinobasinae should therefore be considered the valid name, while Amphicneminae and Nehalenniinae become junior synonyms. The mainly venational characters given by Fraser and by Tillyard to define the subfamily are phylogenetically uninformative within the Coenagrionidae (REHN, 2003), and none of the characters identified by DE MARMELS (1984) is strictly synapomorphous for Teinobasinae. O'GRADY & MAY (2003) reviewed traditional subfamily assemblages within the Coenagrionidae, but did not consider Nehalenniinae, nor did they discuss Amphicneminae or Teinobasini. They found the taxonomic characters commonly used in this family were continuously distributed, and concluded that "subfamilies should not be recognized within Coenagrionidae until well-supported subdivisions are demonstrated" (quoted from Abstract). It may be argued, however, that a unique combination of character states may safely identify a natural monophyletic group (NELSON & PLATNICK, 1981: 12; CRAW et al., 1999; HEADS, 1985, 2005).

KENNEDY (1920a: 28) divided his "Nehalennia-Telebasis series" (= Teinobasinae) into two subsets, viz. "(a) the Chromagrion-Nehalennia-Teinobasis series with appendages that have a large basal spine", and "(b) the Ceriagrion-Telebasis-Metaleptobasis series in which the appendages do not have a well developed basal spine". The series (a) is here considered to represent a tribe, Teinobasini, which is well identified by the apparent synapomorphy given by Kennedy. It should be emphasized, that this "basal spine" is not simply a basal ventral process springing from the dorsal branch of the cercus, as known from many genera of Zygoptera. Rather it is a movable spur articulated to the dorsal branch ventrobasally, at a membranous area, hence the spur is *not* continuous with the sclerotized outline of the dorsal branch (contra LIEFTINCK, 1987: 280). Therefore, the small ventrobasal lobule visible, for example, on the cercus of *Telebasis griffini* and *T. limoncocha* (Fig. 10) is not homologous with the ventrobasal spur of Teinobasini.

"Series (b)" of Kennedy, with the alternative character state, i. e. the articulated ventrobasal spur absent, remains a "paraphyletic" (but nevertheless "natural", see HERTING, 1993) entity until one or more synapomorphies of the genera included therein will be identified.

BIOGEOGRAPHY AND TAXOGENY OF TEINOBASINAE

In a panbiogeographic view (CRAW et al., 1999) the range of recent Teinobasinae as a whole largely reflects the total ancestral range of the group. Within the ancestral range the character state alternatives "articulated ventrobasal spur of male cercus present" or "absent", none of which necessarily being derived from the other ("synapomorphous"), are largely vicariant, the character state "present" following a track north of Tethys (Fig. 45A), the "absent" state one south of it (Fig. 45B) (see CROIZAT, 1964: 57 ff.). Of primary interest are those areas where both distributions coincide, especially northern South America and insular South East Asia and the West Pacific. These areas happen to hold important main massings, i. e. "greatest concentrations of taxonomic [here generic] diversity" (CRAW et al., 1999). No less than twelve genera of Teinobasinae, of which three are Teinobasini, are found in northern South America, including the Caribbean, while seven genera, six of them Teinobasini, are recorded from insular South East Asia. These two generic main massings, with tribe Teinobasini notably poor in South America and rich in SE Asia, are also massings at the species level: the neotropical genus *Telebasis* ["series (b)"] includes more than 30 species, while the Teinobasini genera *Amphicnemis* and *Papuagrion* of insular South East Asia each includes between 20 and 30 species, and *Teinobasis* of the same region has about 60.

The African continent is notably devoid of Teinobasini, except for the marginal presence of the palearctic *Pyrrhosoma* in Morocco, and *Seychellibasis* known from the east African coastal forests (to Malawi?), off-shore islands (Pemba, Zanzibar), Madagascar, and the Seychelles (Fig. 45A). This genus is closely related to the Southeast Asian-Pacific *Teinobasis* (absent from the Indian subcontinent and Ceylon), and both are considered synonymous by some authors (CLAUSNITZER, 2003). CLAUSNITZER (2003: 329) claims that the presence in Africa of *Teinobasis* (= *Seychellibasis*) "can be explained by trans-oceanic dispersal from Australasia (especially New Guinea, as well as Indonesia and the Philippines)", even though she recognizes that "the active dispersal potential of *Teinobasis* is very low to nil", because "species of this genus have a slow flight and stay in the dense undergrowth of swamp forests (...)". The supposed invasion of *Teinobasis* from Asia via the Seychelles into the Afrotropical region and to Madagascar "must therefore be passive by wind". Consequently, she blames the southeast or, alternatively, the northwest monsoon for sponsoring this "invasion". Her dilemma about the starting point for the "colonization" of Africa by *Teinobasis* is, however, futile, as the *Teinobasis* (Australasia)-*Seychellibasis* (East Africa)-link does not mirror any colonization event whatsoever, but is a standard biogeographic track across the Indian Ocean, well documented many years ago by CROIZAT (1958, 1968), and recently by CRAW et al. (1999, and references cited therein). It involves tectonics and vicariant form making rather than colonization flights, invasions or wind transport of these tiny damsels from New Guinea and the Philippines across the Indian Ocean into East Africa.- In any case, it is agreed that *Seychellibasis* is not a genuine "African" element. Therefore, if *Pyrrhosoma* and *Seychellibasis*, both Teinobasini, are dismissed, Africa holds only one single ge-

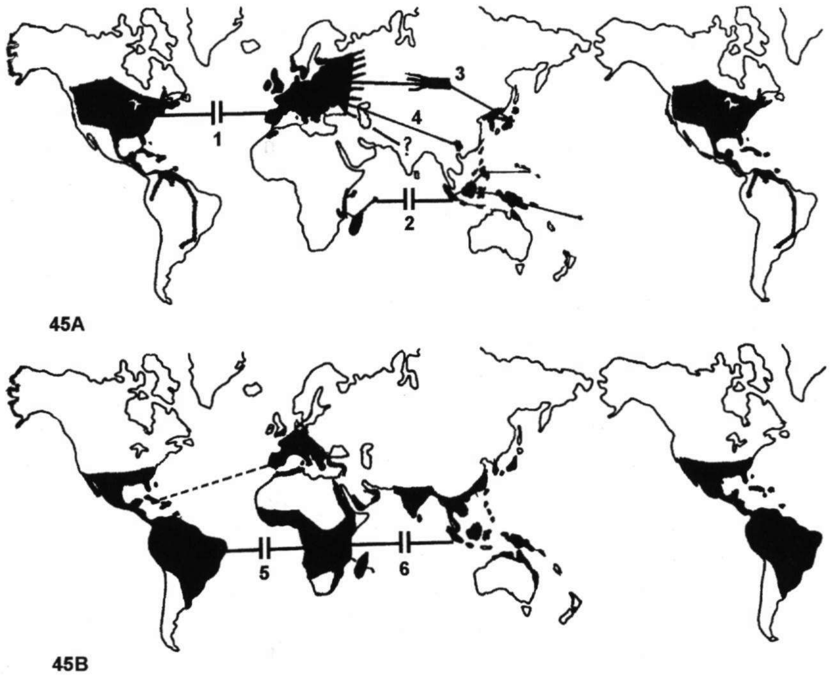


Fig. 45. Distribution of Teinobasinae. A: Distribution of Teinobasini (male cercus with articulated ventrobasal spur): 1 = Atlantic Ocean baseline sustained by the generalized track *Nehalennia gracilis* (eastern North America) – *N. speciosa* (Eurasia), and *Chromagrion* (eastern North America) – *Pyrrhosoma* (Europe to South West China); 2 = Indian Ocean baseline sustained by the track *Seychellibasis* (Seychelles, Madagascar, Zanzibar, Pemba, African east coast) – *Teinobasis* (insular South East Asia and western Pacific); 3 = northern Palearctic track connecting stations of *Nehalennia speciosa*; 4 = southern Palearctic track connecting *Pyrrhosoma nymphula* (Europe) with *P. tinctipenne* (South West China). – B: Distribution of "series (b)" Teinobasinae (male cercus without articulated ventrobasal spur): 5 = Atlantic Ocean baseline sustained by the track *Telebasis* (South America and the Caribbean) – *Ceriagrion* (South Central Africa); 6 = Indian Ocean baseline sustained by the track *Ceriagrion* (Africa) – *Ceriagrion* (South East Asia); broken line symbolizing track linking "*Ceriagrion*" *tenellum* (South West Europe to Near East, and Maghreb) with *Telebasis* and related genera (Caribbean and northern South America). Symbol for baseline taken from FORTINO & MORRONE (1997).

nus of Teinobasinae, viz. *Ceriagrion*, a "series (b)" Teinobasinae, which has one of its main massings (species level) on this continent (Fig. 45B). The other main massing of *Ceriagrion* lies, again, in south continental and insular South East Asia.

Australia is barely touched by Teinobasinae: the widespread *Teinobasis rufithorax* (Selys, 1877), a Teinobasini, occurs in extreme northeastern Australia, and *C. aeruginosum* (Brauer, 1869), a "series (b)" Teinobasinae, has been reported from extreme northern and northeastern Australia. Apart from these two records, Australia, New Zealand, New Caledonia, South Africa [except for the coastal margin inhabited by the widespread *Ceriagrion glabrum* (Burmeister, 1839)], and southwestern South America are notably devoid of Teinobasinae (Figs. 45A, B). Teinobasinae as a whole is absent from the subantarctic belt, or Notogea.

Both, Teinobasini and "series (b)" Teinobasinae reach America by seemingly different tracks, which nevertheless share an Atlantic Ocean baseline (CRAW et al., 1999). The Atlantic Ocean baseline is given, in the case of Teinobasini, by the track *Chromagrion* (eastern North America)-*Pyrrhosoma* (Europe to South West China), and *Nehalennia gracilis* (eastern North America)-*N. speciosa* (Europe-Siberia-Amurland, Korea, Japan). For "series (b)" Teinobasinae the transatlantic track connects *Ceriagrion* (South Central Africa) with *Telebasis* and allied genera (South America and the Caribbean).

The Indian Ocean baseline is given, for Teinobasini, by the *Teinobasis* (South East Asia)-*Seychellibasis* (East Africa)-track, and for the "series (b)" Teinobasinae by the *Ceriagrion* (South East Asia)-*Ceriagrion* (Africa) track.

The only "series (b)" Teinobasinae distributed north of Tethys is *Ceriagrion*. When omitting the three or so species present in eastern China and Japan, all of which are related to South East Asian forms, only "*Ceriagrion*" *tenellum* is left. This curious species ranges, in isolation from other *Ceriagrion*, from southwestern Europe and the Maghreb ["Tyrrhenis", cf. CROIZAT (1964, Fig. 20)] across the Balkans and Greece to Turkey, Syria and northern Israel (DUMONT, 1991), and factually sits at the western end of the classical sector of Tethys. The Tethys geosyncline is connected across the Atlantic with other geosynclinal belts in the Caribbean and the Americas (CROIZAT, 1964: 63, Fig. 16, p. 69). It comes, therefore, as no surprise that "*C.*" *tenellum* does not fit smoothly in the Old World *Ceriagrion*, but, instead, shares some characters with New World *Telebasis*. KENNEDY (1920b) even proposed a new genus (*Palaeobasis* Kennedy, 1920; see also COWLEY, 1935) for this single species. Unfortunately, the venational character on which Kennedy based the new genus is not useful for separating it from either *Ceriagrion* or *Telebasis*. Rather it is the extended brassy black colour of head and thorax, which approaches "*C.*" *tenellum* to *Telebasis*. The head of "*C.*" *tenellum* is less compact and has a less angled frontal ridge than have true *Ceriagrion*, but the frontal ridge itself is broader than in *Telebasis* and hence more similar to that found in true *Ceriagrion*. Based on penis or cercal morphology

Telebasis, *Ceriagrion* and "*C.*" *tenellum* are hardly separable at the generic level.

Another noteworthy genus is *Inpabasis* (three species) of the Amazon. This is the only "series (b)" Teinobasinae which recombines characters of South East Asian Teinobasini, (*Teinobasis*, *Papuagrion*), namely a male supra-anal plate, and toothless tarsal claws.

EVOLUTION OF *TEPUIBASIS*

Against the complex biogeographic background elucidated above for Teinobasinae, the evolution and taxogenesis of *Tepuibasis* may be assessed as follows. This genus arose from a core of teinobasine morphogenetic potential, located on the South American craton. Prior to Andean orogeny, the Guayana Shield was populated by some teinobasine ancestor, which was potential or actual bearer of both character state alternatives of the male cercus, viz. articulated ventro basal spur present or absent. The Andean uplift since the late Cretaceous triggered a simultaneous isostatic rise of large parts of the Guyana Shield "under the feet"

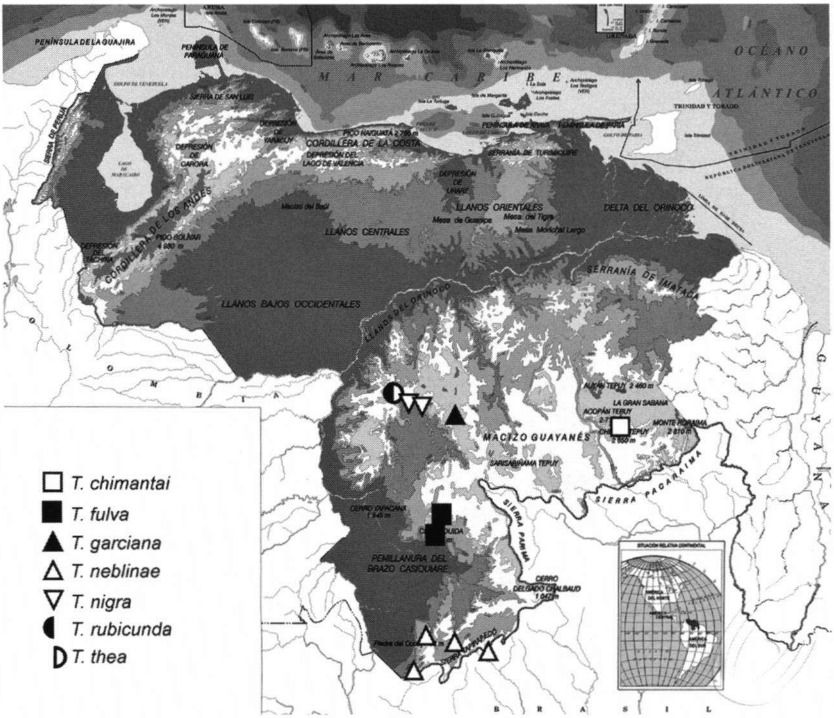


Fig. 46. Distribution of *Tepuibasis* in the Pantepui region of southern Venezuela.

(CROIZAT, 1964) of the local population of the teinobasine ancestor, which happened to locally recombine *some* of the ancestral character states now found in recent Teinobasini, and *some* of those associated rather with recent "series (b)" Teinobasinae, in this case, *Telebasis*. This segment of the ancestor was raised, together with the whole biota today known as 'pantepuyan', to considerable height – Mount Neblina, for instance, rises to 3000 m above sea level - and hence became isolated (vicariant) from the surrounding lowland populations and progressively adapted to high elevation conditions evolving into *Tepuibasis* stock (primary vicariance and taxogenic event). The uplift of the Guyana plateau provoked fractures and the resulting fragments were further dissected by erosion and reduced to what can be seen today as isolated remnant sierras and table-top mountains known as "tepuis" (se also CHAPMAN, 1931; TATE, 1938). This secondary vicariance and speciation event explains the presence in Pantepui of several vicariant species of *Tepuibasis* some of which probably still have to be discovered.

In spite of the apparent absence of any clear synapomorphy, *Tepuibasis* is well delimited by three morphological characters which are uniquely combined in this genus, although each of them can be found separately, in different combinations, in one or a few other Teinobasinae, or, isolated, even in more distantly related coenagrionid genera. These three key characters are: (1) the articulated ventrobasal spur of the male cercus, (2) the spiny, auricle-like process at the base of each apical lobe of the cleft apical penis segment, and (3) the apically cleft penis itself.

DISCUSSION OF THE KEY CHARACTERS

THE ARTICULATED VENTROBASAL SPUR OF THE MALE CERCUS

Among the Teinobasinae examined, I found a true ventrobasal spur, in addition to *Tepuibasis*, only in *Amphicnemis*, *Bromeliagrion*, *Chromagrion*, *Melanesobasis*, *Nehalennia*, *Papuagrion*, *Pericnemis*, *Plagulibasis*, *Pyrrhosoma*, *Seychellibasis* and *Teinobasis* (the "lower branch" of LIEFTINCK, 1987), but it may be present in a few additional Old World genera not examined, such as *Stenagrion* Laidlaw, 1915 and others, which then should be included within Teinobasini. When I reviewed *Nehalennia* (DE MARMELS, 1984), I obviously overlooked the ventrobasal spur in *N. gracilis* and in *N. speciosa*, but it is present in both, albeit small, knob-like in *N. gracilis*. The spur was recorded as "articulated ventral branch" in *Chromagrion* and *Pyrrhosoma* (DE MARMELS, 2002), and in *Bromeliagrion* (DE MARMELS & GARRISON, 2005).

THE SPINY, AURICLE-LIKE PROCESS AT THE BASE OF EACH APICAL LOBE OF THE APICAL PENIS SEGMENT

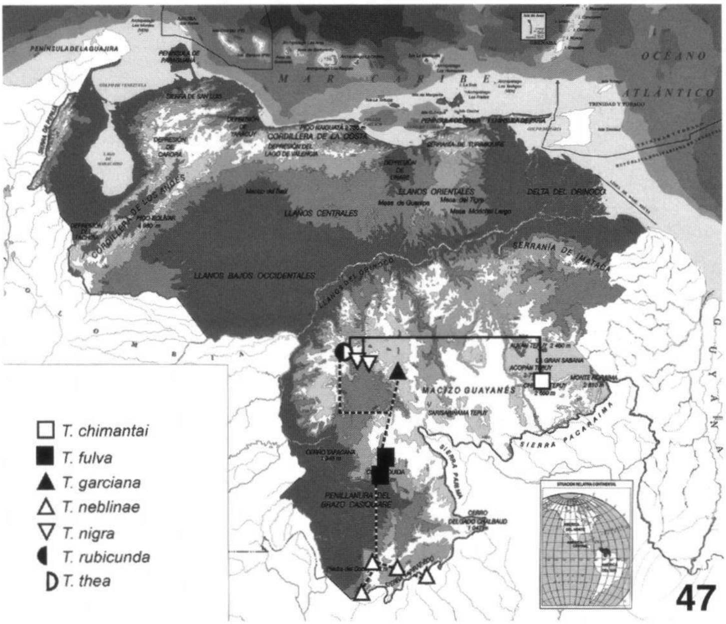
The only other Teinobasinae with similar processes, which I consider homologous, is "*Aeolagrion*" *flammeum*, but this species is referable to the "series (b)" Teinobasinae. True *Aeolagrion* lack these processes, while the "strange thoracic pattern" of "*A.*" *flammeum* (DUNKLE, 1991: 243) is reproduced in *Hylaeonympha magoi*, another "series (b)" Teinobasinae, with which "*A.*" *flammeum* co-occurs in southern Venezuela. Interestingly, "*A.*" *flammeum* has a second pair of similar processes, at a more proximal position on the apical penis segment (Fig. 34). These are absent in *Tepuibasis*, but probably homologous with the pair of chitinized processes at the same position in *Melanesobasis flavilabris* and related species from Fiji, and in the various species of *Teinobasis* examined (see above), perhaps also with the chitinized auricles of *Bromeliagrion*.

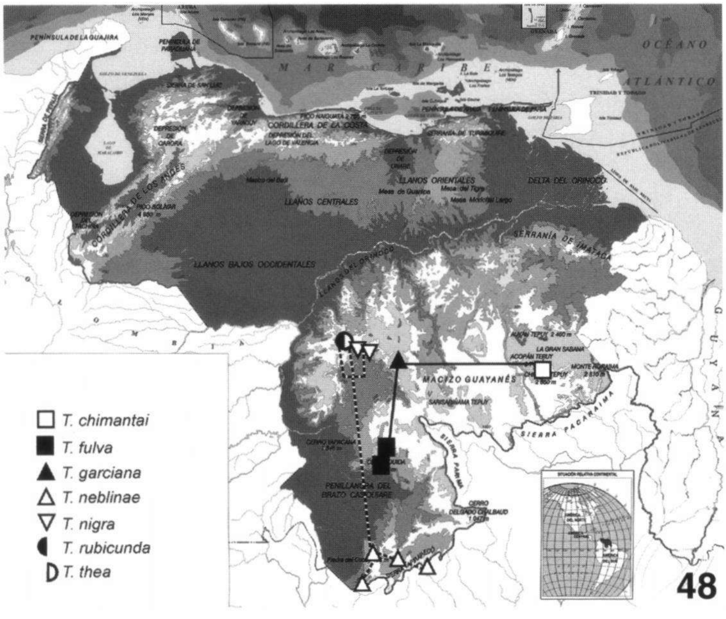
THE APICALLY CLEFT PENIS

A bifid apical penis segment is common across many genera of Coenagrionidae and beyond. However, it should be differentiated between an apical segment with its tip laterally expanded into lateral terminal lobes, and a truly cleft tip. Within Teinobasinae, a cleft apical segment is present, besides of *Tepuibasis*, in *Diceratobasis*, *Hylaeonympha*, *Inpabasis* and *Nehalennia*. In "*Aeolagrion*" *flammeum* a cleft condition is indicated by a clear emargination of the tip (Fig. 34).

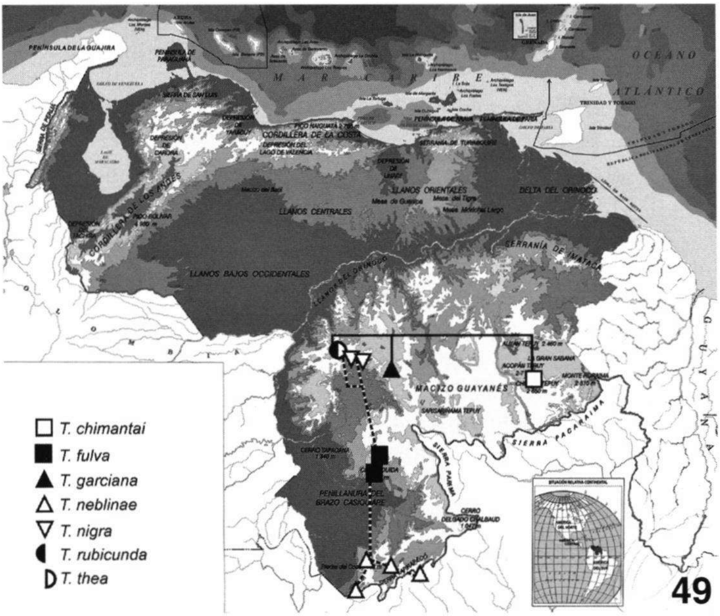
CHARACTER GEOGRAPHY IN *TEPUIBASIS*

Each of the seven species of *Tepuibasis* exhibits one or more character states which are exclusive to it. These may be considered autapomorphies, but some could be simply uniquely represented alternative ancestral character states. On the other hand, there are five character states each of which is present in several species, with an alternative state in the rest. These are mapped in Figures 47-50: (1) male cercus arched downwards, (2) frons rounded, (3) forewing pterostigma shorter than underlying cell, (4) rear of head pale, and (5) male abdomen black. The alternative states are: (1') male cercus straight, (2') frons angulate, (3') forewing pterostigma at least as long as underlying cell, (4') rear of head black, (5') male abdomen red. Which of these character states, if any, is 'synapomorphous' or 'symplesiomorphous' cannot be decided. It is known that in Coenagrionidae a bewildering array of character state alternatives exist which are scattered seemingly at random across widely separate genera, or across species within a genus. Identical states occurring 'in parallel' are then explained as 'homoplasies', but an identical character state may simply recombinate in different ways across the ancestral space, and hence become manifest in one or in another group, not caring





Figs 47-50. Character geography in *Tepuibasis*: (47) male cercus arched downwards (solid line) versus male cercus straight (dotted line); – (48) frons rounded (solid line) versus frons angulate (dotted line); – (49) FW pterostigma shorter than cell below, and rear of head pale (solid line) versus FW



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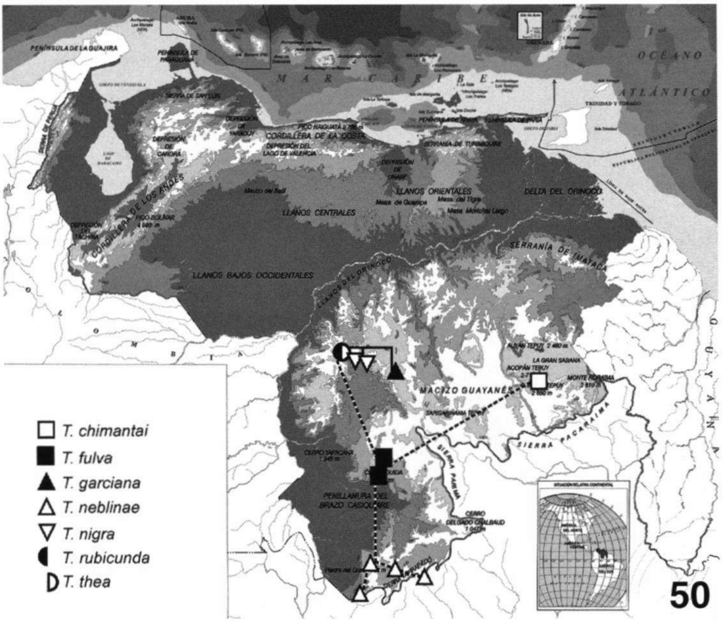

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pterostigma as long or longer than cell below, and rear of head black (dotted line); – (50) male abdomen black (solid line) versus male abdomen red (dotted line).

about 'clades'. This is because "characters have their own geographic and phylogenetic distribution and 'the group' can only be congruent with a limited number of characters" (HEADS, 2005: 104). The aim of cladists to polarize characters into primitive or derivative may be erroneous anyway, as "two characters may be alternative states, neither derived from the other" (HEADS, 2005: 75). The 'outgroup method' is problematic. HEADS (2005: 102) calls it "a more or less hopeful attempt at morphogenetic analysis. Nevertheless, character analysis cannot be simply 'probabilistic', as is so-called 'parsimony' analysis."

A glance at the maps (Figs 47-50) shows the following: *T. nigra* and *T. thea* are the most closely related, by sharing either one of the five depicted character states, or its alternative state. Indeed, these two species are very similar phenotypically, and close geographically. Beyond this fact, the five character states (or their alternatives) seem to be randomly distributed each connecting different species sets. This, however, is exactly what might be expected from the 'kaleidoscopic recombination' (HEADS, 2005: 102) of different character states actually or potentially present in a polymorphic ancestor submitted to vicariance processes.

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