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A cladistic revision of *Tortopus* Needham & Murphy with description of the new genus *Tortopsis* (Ephemeroptera: Polymitarcyidae)

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Abstract

The 12 species previously placed in *Tortopus* together with 3 species newly described here, are revised and included in a phylogenetic analysis. Based on synapomorphic characters on the nymphs and adults of both sexes, *Tortopus* is restricted to *T. igaranus* Needham & Murphy, *T. circumfluus* Ulmer, *T. harrisi* Traver, *T. zottai* (Navás), *T. bellus* Lugo-Ortiz & McCafferty, and *T. arenales* sp. nov., and the genus is defined by: female parastyli receptors with long furrows anterior to sockets; penes entirely flattened; male ninth abdominal sternum almost separated in two portions by a median notch; mesosternum with furcasternal protuberances contiguous only on basal corner; and nymphs with two subapical tubercles on mandibular tusks. *Tortopsis* is newly described for *T. bruchianus* (Navás), *T. limoncocha* sp. nov., *T. obscuripennis* (Domínguez), *T. parishi* (Banks), *T. primus* (McDunnough), *T. puella* (Pictet), *T. sarae* (Domínguez), *T. spatula* sp. nov., and *T. unguiculatus* (Ulmer). *Tortopsis* is characterized by: R sector of female fore wing without additional veins between R_2 and IR; female parastyli receptors C or V-shaped, with sockets opening towards median line; male gonopore associated with a claw-like structure; penes separated from the base; parastyli more than 5 times length of pedestals; parastyli curved in lateral view; nymphs with a single subapical tubercle on mandibular tusks.

The study of available type material permitted inclusion of comparative diagnoses, with figures and redescriptions as needed. The male imago of the type species of *Tortopus* (*T. igaranus* Needham & Murphy) is described for the first time, as are the female adults of *Tortopus bellus* Lugo-Ortiz & McCafferty and *T. harrisi* Traver. Three new Neotropical species based on male and female adults are described: *Tortopus arenales* and *Tortopsis limoncocha* from Ecuador, and *Tortopsis spatula* from Colombia. Keys to separate the adults and nymphs of the genera of Polymitarcyidae, and for male and female adults of all the species of *Tortopus* and *Tortopsis* are presented, as well as line drawings, pictures and SEM photographs of important structures.

Key words: Campsurinae, *Campsurus*, *Asthenopus*, mayfly, coupling apparatus, identification keys

Resumen

Se realiza un análisis filogenético y revisión taxonómica de las 12 especies previamente ubicadas en *Tortopus*, junto con 3 nuevas especies descriptas aquí. Sobre la base de caracteres sinapomórficos de ninfas y adultos de ambos sexos, *Tortopus* es restringido a *T. igaranus* Needham & Murphy, *T. circumfluus* Ulmer, *T. harrisi* Traver, *T. zottai* (Navás), *T. bellus* Lugo-Ortiz & McCafferty, y *T. arenales* sp. nov., y definido por: receptores de parastilo en hembras con largos surcos anteriores a los bolsillos; penes deprimidos; esterno abdominal IX del macho separado en dos porciones laterales por un surco mediano; mesosternum con protuberancias furcasternales contiguas sólo en la base; y ninfas con dos tubérculos subapicales en los colmillos mandibulares. El nuevo género *Tortopsis* es descripto para *T. bruchianus* (Navás), *T. limoncocha* sp. nov., *T. obscuripennis* (Domínguez), *T. parishi* (Banks), *T. primus* (McDunnough), *T. puella* (Pictet), *T. sarae* (Domínguez), *T. spatula* sp. nov., y *T. unguiculatus* (Ulmer). *Tortopsis* se caracteriza por: sector R en ala anterior femenina sin venas adicionales entre R_2 e IR; receptores de parastilo en hembras con forma de C o V, con bolsillos abriéndose hacia la línea media; gonoporo masculino asociado a una estructura en forma de garra; penes separados desde la base; parastilos con una longitud cinco veces mayor a la de los pedestales; parastilos curvados en vista lateral; ninfas con un solo tubérculo subapical en los colmillos mandibulares. El estudio del material tipo de todas las especies disponibles permitió la inclusión de diagnosis comparativas, con las figuras y redescripciones necesarias. El macho imago de la especie tipo de *Tortopus* (*T. igaranus* Needham & Murphy) es descripto por primera vez, así como las hembras adultas de *Tortopus bellus* Lugo-Ortiz & McCafferty y *T. harrisi* Traver. Se describen tres nuevas especies neotropicales sobre la base de adultos de ambos sexos: *Tortopus arenales* y *Tortopsis limoncocha* de Ecuador, y *Tortopsis spatula* de Colombia. Se ofrecen claves para separar los adultos y ninfas de los géneros de Polymitarcyidae y para los machos y hembras de las especies de *Tortopus* y *Tortopsis*, así como dibujos, fotos y fotografías de microscopía electrónica para las estructuras consideradas de interés sistemático.

Introduction

Mayflies in general are short-lived insects in the adult stage (eg, Brittain 1982), but adults of the subfamily Campsurinae (Polymitarcyidae) are among the shortest lived of all winged insects. Except for the male forelegs (used in copula), the adults do not have functional legs, only small motionless vestiges, and have reduced their life to a short, exclusively aerial period (Needham et al. 1935). New information (Molineri, unpublished) has corroborated the fact that the subimaginal moulting is done entirely in flight, as suggested by the absence of functional legs.

This interesting biology does not end here, since the nymphs, large sediment burrowers as other ephemeroid mayflies, are extremely active bioturbators that filter their food using a sophisticated basket of setae on the head and fore legs (Sattler 1967, Scott et al. 1959, Molineri 2008). The nymphs even produce silky secretions in the Malpighian tubules that are used to coat their tunnels (Sattler 1967) or to build soft cases fixed to rocks (Molineri & Emmerich in press). The nymphs of *Tortopus* burrow in relatively hard clay banks of rivers and streams (Scott et al. 1959, Knight & Cooper 1989, Molineri 2008) but their biology is little studied.

Male and female adults of *Tortopus* have a special, secondary coupling apparatus (McCafferty & Bloodgood 1989) formed by a pair of parastyli in the base of male forceps and a pair of sockets (parastylus receptors) on female abdominal sternum VIII. *Tortopus* has been characterized (Ulmer 1932, Traver 1950, Lugo-Ortiz & McCafferty 1996, Kluge 2004, Molineri 2008) by the following presumed apomorphies (no phylogenetic analysis is known for Campsurinae) in the adults: sexual dimorphic wing venation (thick veins in female, normal in male), all legs except fore legs of male weak and distorted, male styliger plate modified to form a pair of parastyli (some authors interpret these structures as modifications of the forceps bases), forceps bisegmented with the short basal segment bearing a ventral knob; and in the nymph: a single subapical tubercle is present in the medial margin of mandibular tusks, and the base of maxillae with a small finger-like gill.

Tortopus Needham & Murphy and its sister taxon *Campsurus* Eaton are known from the Americas and are the only members of the Campsurinae. Whilst *Campsurus* is known from 43 species, *Tortopus* presents only 12 species known from Argentina to Canada. The type species of the genus, *Tortopus igaranus* Needham & Murphy (1924) was known only from adult females and the lack of characters to distinguish it was an obstacle for further study in the group. Here, the male imago of *T. igaranus* is described for the first time. *Tortopus* is restricted to the type species, *T. igaranus* Needham & Murphy, and their closest relatives; whilst *Tortopsis* gen. nov. is described for *T. unguiculatus* Ulmer (type species), and related taxa. All the species in both genera are revised, illustrated and discussed. Generic and specific diagnoses, together with a key to the male and female adults are given. These taxonomic changes are based on the first morphological phylogenetic analysis of this group of mayflies. Additionally a key to the adults and nymphs of the genera of Polymitarcyidae is presented.

Material and methods

Terminology for morphological structures including wing veins is those traditionally used in mayflies, some are from Kluge (2004). All the material was fixed and preserved in alcohol, except otherwise stated.

Scanning electron microscope (SEM) photographs were obtained with a JEOL 35CF SEM at 25 kV. The studied structures were dehydrated in a graded ethanol series, dried by critical point-method (using CO_2 in a Bomar apparatus), mounted with double-sided tape on SEM stubs, and sputter coated with gold.

Material is deposited in the following Institutions: CUIC (Cornell University Insect Collection, Ithaca, NY), FAMU (Florida A&M University, Tallahassee, FL), IML (Instituto Miguel Lillo, Tucumán), MACN (Museo Argentino de Ciencias Naturales, Buenos Aires), MECN (Museo Ecuatoriano de Ciencias Naturales, Quito), MUSENUV (Museo de la Universidad del Valle, Cali), RBINS (Royal Belgian Institute of Natural Sciences, Brussels) and ZMH (Zoologisches Museum Hamburg).

Phylogenetic analysis: a matrix was constructed (Table 1) including 21 taxa and 27 morphological adult characters. Six outgroup taxa were used to root the tree (*Ephoron* sp.) or to test the monophyly of the ingroup (*Asthenopus* sp., *Campsurus violaceous*, *C. albifilum*, *C. segnis* and *C. essequibo*, including the major morphological diversity of the family). The remaining taxa are the twelve species previously placed in *Tortopus* and three new species here described. Characters are almost exclusively from the morphology of the adult stage (two characters are from eggs), because the nymphal stage of the majority of the species remains undescribed. The list of characters and states is given in Appendix 1, all characters were treated as non-additive. Group support was addressed by frequency differences and absolute and relative Bremer supports (Goloboff et al. 2003). Frequency difference is an improvement of jackknifing and its value results from the difference between the frequency of the group and the frequency of the most common contradictory group. Bremer support was calculated from suboptimal trees. Searches were conducted in TNT (Goloboff et al. 2008) under equal-weighted parsimony with the "traditional search" option (100 replications of Wagner trees followed by TBR-arrangements, and then TBR again to the shortest trees found). WinClada (Nixon 2002) was used for preparation of trees. Two different searches were performed, one with the complete dataset and other with only 17 taxa, excluding *T. parishi*, *T. bruchianus*, *T. zottai*, and *T. circumfluus* due to their high number of missing entries.

TABLE 1. Matrix of 21 taxa and 27 characters. Names of characters and states in Appendix 1, "-" represents inapplicable states and "?", unknown states. Species in bold were deleted in the reduced dataset analysis.

Character number:	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Ephoron sp.	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	2	-	0	2	-	0	-	0	0	0	1
Asthenopus sp.	1	0	0	0	0	1	2	0	0	0	3	2	0	0	0	0	2	-	1	2	0	0	-	0	0	0	2
Campsurus segnis	2	1	0	0	1	2	1	0	0	2	0	2	1	2	1	1	2	-	2	2	0	2	0	0	0	1	1
C.essequibo	2	1	0	0	1	1	2	0	0	2	0	2	1	2	1	1	2	-	2	2	0	2	0	0	0	1	1
C.albifilum	2	1	0	0	1	1	2	0	0	2	3	2	1	0	1	1	2	-	2	2	0	0	-	0	0	1	1
C.violaceus	2	1	0	0	1	1	2	0	0	2	3	2	1	1	1	1	2	-	1	2	0	0	-	0	0	1	1
T.igaranus	2	1	1	1	1	2	1	0	1	1	2	1	1	3	1	1	1	-	1	1	3	2	0	1	1	1	0
T.bellus	2	1	1	1	1	2	1	0	1	1	2	1	1	3	1	1	1	-	1	1	3	1	0	1	1	1	0
T.arenales	2	1	1	1	1	2	1	0	1	1	2	1	1	3	1	1	1	-	1	1	3	2	0	1	1	1	0
T.bruchianus	2	1	1	1	2	2	0	1	0	1	1	?	?	?	?	?	?	-	?	?	?	?	?	?	?	1	0
T.sarae	2	1	1	1	2	2	0	1	0	1	1	1	1	3	1	1	0	0	1	0	1	3	2	1	0	1	0
T.obscuripennis	2	1	1	1	2	2	0	1	0	1	1	1	1	3	1	1	0	0	1	0	2	3	2	1	0	1	0
T.unguiculatus	2	1	1	1	2	2	0	1	0	1	1	1	1	3	1	1	0	1	1	0	1	3	3	1	0	1	0
T.limoncocha	2	1	1	1	2	2	0	1	0	1	1	1	1	3	1	1	0	0	1	0	1	3	1	1	0	1	0
T.harrisi	2	1	1	1	1	2	1	0	1	1	2	1	1	3	1	1	1	-	1	1	3	1	0	1	1	1	0
T.parishi	2	1	?	?	?	?	?	?	?	1	?	1	1	3	1	1	0	?	1	0	1	?	?	?	0	-	-
T.puella	2	1	1	1	2	2	0	1	0	1	1	1	1	3	1	1	0	0	1	0	2	3	2	1	0	1	0
T.circumfluus	2	1	1	1	1	2	1	0	1	1	2	?	?	?	?	?	?	-	?	?	?	?	?	?	?	1	0
T.primus	2	1	1	1	2	2	0	1	0	1	1	1	1	3	1	1	0	0	1	0	1	3	2	1	0	1	0
T.zottai	2	1	?	?	?	?	?	?	?	1	2	1	1	3	1	1	1	-	1	1	3	2	0	1	1	-	-
T.spatula	2	1	1	1	2	2	0	1	0	1	1	1	1	3	1	1	0	1	1	0	1	3	2	1	0	1	0

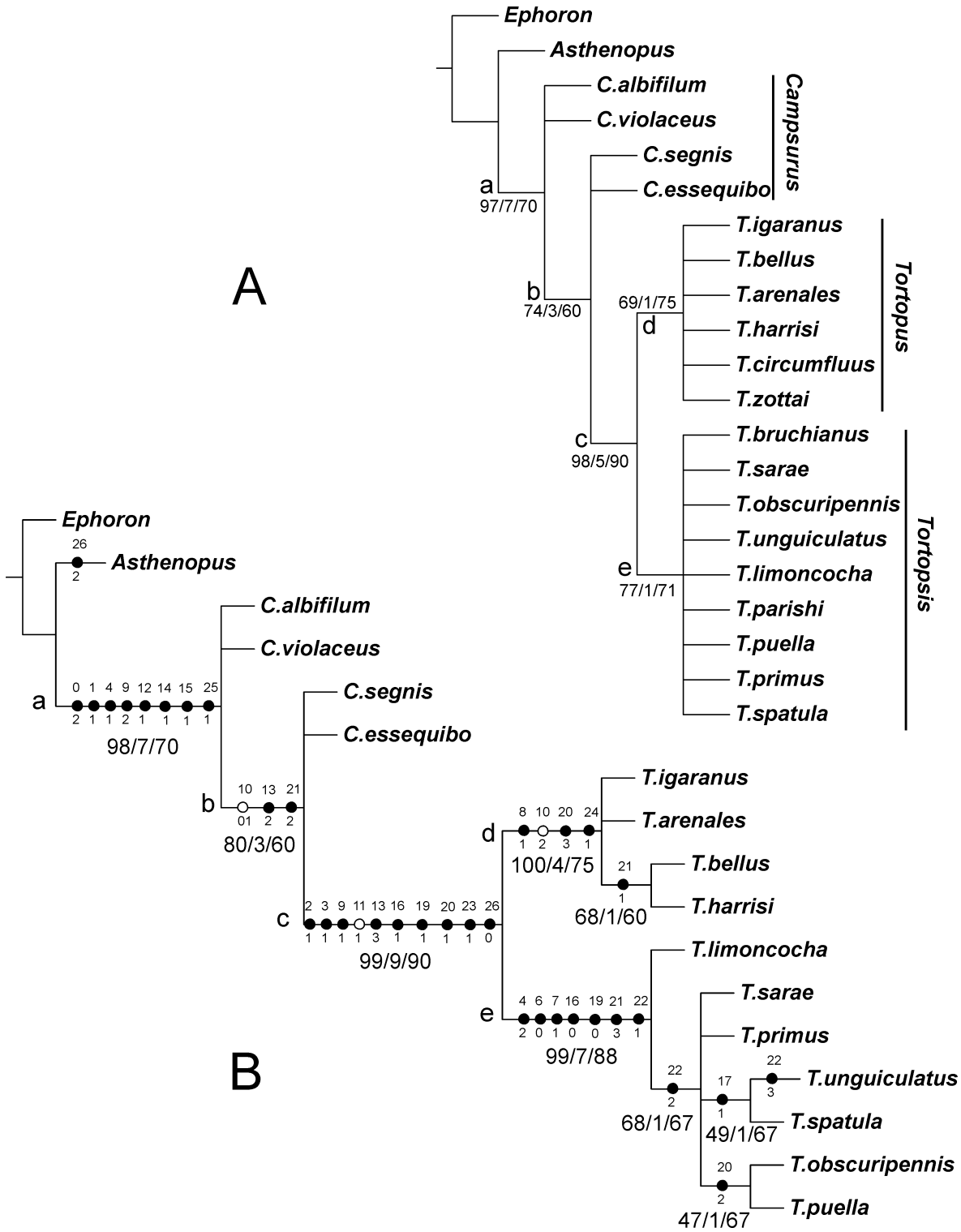


FIGURE 1. A, strict consensus of 234 shortest trees obtained with the complete data set (58 steps, Ci=81, Ri=93); B, strict consensus of 3 shortest trees obtained with the reduced data set (58 steps, Ci=81, Ri=92). Values near nodes indicate group support (frequency difference/ absolute Bremer Support/ relative BS). Black circles indicate unique apomorphies, white circles indicate parallelism or reversal, the small numbers above and below these marks are character and state numbers respectively.

Phylogeny results

Complete dataset (21 taxa x 27 characters): common parsimony (all characters equally weighted) found 234 shortest trees of 58 steps (Ci, Consistency Index=81; Ri, Retention index=93). Group support of all the nodes in the consensus trees are high, see Fig. 1A (values below nodes are frequency difference/absolute Bremer Support/relative BS).

Reduced dataset (17 taxa x 27 characters): three shortest trees were found, with a length of 58 steps, Ci=81 and Ri=92. The strict consensus of these trees (Fig. 1B) is shown with character changes plotted in the nodes. Group supports are high for all the nodes (Fig. 1B).

The synapomorphies for the nodes in the consensus are the same in both searches (shared nodes in complete and partial dataset). The monophyly of the subfamily Campsurinae is recovered (node a, Fig. 1A–B), supported by the following synapomorphies: 1) two intercalary cubital veins, one anterior and one posterior to tornus (char. 0: state 2); 2) vein CuA of fore wing markedly sigmoid (char. 1: state 1); 3) female fore wing veins on R sector reduced in number, from 0 to 2 veins between R_2 and IR (char. 4: state 1); 4) legs reduced and fin-like (character 9: state 2, posteriorly reversed in node c); 5) styliger plate reduced to a pair of pedestals (char. 12: 1); 6) pedestal muscles absent (char. 14: 1); 7) penial arms articulated to both ninth abdominal sternum and pedestals (char. 15: 1); and 8) eggs bowl-shaped (char. 25: 1).

The node b includes *C. segnis* and *C. essequibo* with *Tortopsis* and *Tortopus*, relation supported by the following synapomorphies: 1) mesosternum with furcasternal protuberances of each side contiguous at least on basal 1/3 (Fig. 52, char. 10: states 01); 2) pedestals with a lateral and blunt projection on outer margin (char. 13: 2); and 3) parastyli 2–3 times the length of pedestals (Fig. 2, char. 21: 2).

Tortopus + *Tortopsis* (node c) is also supported as a natural group, sharing: 1) female wing veins thickened (char. 2:1); 2) female hind wing with reticulate network of veins in anal sector (char. 3: 1); 3) distorted legs (char. 9: 1); 4) forceps bisegmented (char. 11: 1); 5) pedestals with a dorsal and pointed outer projection (char. 13: 3); 6) gonopore associated with a sclerotized margin (Fig. 2, char. 16: 1); 7) penes fused on basal 1/5 or less (Fig. 2, char. 19: 1); 8) penes cylindrical and straight (char. 20: 1); 9) forceps with a ventral knob on basal segment (char. 23: 1); and 10) eggs without polar caps (char. 26: 0).

All the shortest trees share the following apomorphies for *Tortopus* (node d): 1) female parastyli receptors with long furrows anterior to sockets (Figs. 68–69, char. 8: 1); 2) penes entirely flattened (Fig. 2, char. 20: 3); 3) male ninth abdominal sternum almost separated in two portions by a median notch (Fig. 2, char. 24: 1); and in some trees: 4) mesosternum with furcasternal protuberances contiguous only on basal corner (Fig. 4, char. 10: 2).

Tortopsis (node e) is characterized, in all the trees, by: 1) R sector of female fore wing without traces of additional veins between R_2 and IR (i.e. no distinct R_3 and intercalary, Fig. 44, char. 4: 2); 2) female parastyli receptors C or V-shaped (Figs. 73 and 76, char. 6: 0); 3) female parastyli receptors with sockets opening towards median line (Figs. 68–69, char. 7: 1); 4) male gonopore associated with a claw-like structure (Fig. 72, char. 16: 0); 5) penes separated from base (Fig. 55, char. 19 :0); 6) parastyli more than 5 times length of pedestals (Fig. 63, char. 21: 3); 7) parastyli in lateral view curved on apical 1/4 (Fig. 56, char. 22: 1).

Species relationships for *Tortopus* are only resolved for *T. bellus* + *T. harrisi*, grouped as sister taxa because their parastyli are shorter or subequal to pedestals (Fig. 12, char. 21: 1). In *Tortopsis*, all the species except *T. limoncocha* are grouped by parastyli smoothly curved from base (char. 22: 2). *Tortopsis unguiculatus* + *T. spatula* are grouped by apical claw-like structure of penes with wide base (Figs. 43 and 64, char. 17: 1); and *T. obscuripennis* + *T. puella* by penes cylindrical and straight, with wide flat apex (char. 20: 2).

Discussion

The apomorphies defining Campsurinae mostly coincide with the proposal of Kluge (2004) except for two additional synapomorphies recovered in the present analysis: female fore wing veins on R sector reduced in

number, and legs (except male fore legs) fin-like. This last feature, characteristic of *Campsurus* species, is later reversed to complete but distorted legs in *Tortopus* + *Tortopsis*. This reversal and the fact that *Campsurus* itself was not recovered as a monophyletic group, is probably a consequence of biased character selection and taxon sampling (aimed to resolve *Tortopus*-*Tortopsis*). Anyway, the results are indicating a probable heterogeneous nature of *Campsurus*.

The node c (*Tortopus* + *Tortopsis*) is supported by many of the synapomorphies indicated previously for *Tortopus* (eg, Traver 1950, McCafferty 1975). The list of synapomorphies for this node should be used to distinguish all the species of *Tortopus* and *Tortopsis* from the other in the family. *Tortopus* (as restricted here) and *Tortopsis* are defined by four and seven characters respectively, all newly proposed here.

The erection of the new genus *Tortopsis* for some of the species previously placed in *Tortopus* is justified by the large morphological difference between both groups of species. This morphological gap is evident in the nymphs, female and male adults, with an amount of evolutionary change comparable to that distinguishing the other genera in the family.

Species relationships inside *Tortopus* and *Tortopsis* are only partially resolved. Interestingly *Tortopus bellus*, a Central American species, was recovered as sister of *T. harrisi* (from the Paraguay River basin). In *Tortopsis*, the plesiomorphic *T. limoncocha* from Ecuador splits first, and the only two species included from Central and North America (*T. primus* and *T. puella*) are not recovered as sister taxa.

Key to the South American genera of Polymitarcyidae (modified from Domínguez et al. 2006)

Adults

1 Middle and hind legs reduced and flap-like, tibiae and tarsi absent. . . .*Campsurus* Middle and hind legs reduced but with all segments present 2

2(1) Fore wings with numerous cross veins connecting longitudinal and intercalary veins in the entire wing; hind wings with anal margin not reticulated; forceps stout without basal projections (parastyli) ..... *Asthenopus* Fore wings without numerous cross veins connecting longitudinal and intercalary veins basally to CuA (Figs. 8, 14, 44); hind wings with reticulated anal margin; slender forceps with basal projections (parastyli) and ventral knob (Figs. 2, 57) 3

3(2) Male ninth abdominal sternum longitudinally divided (mf in Fig. 2); parastyli short (ps in Fig. 2), less than 3 times the length of pedestals; penes bladelike and fused at least on basal 1/5 (Fig. 2); female fore wing with short but strongly marked R_3 and intercalary vein (Fig. 8), parastyli receptors on abdominal sternum VIII relatively small and submedian in position (Figs. 35, 70, 82, 84)..... *Tortopus* Male ninth abdominal sternum entire (Figs. 57, 73); parastyli long (ps in Figs. 57–58) more than 5 times the length of parastyli base; penes cylindrical at least basally and completely divided (Fig. 57); female fore wing with no intercalaries between R_{2+3} and IR veins (rarely with 1 or 2 weak veins, formed by fusion of crossveins) (Fig. 44), parastyli receptors on abdominal sternum VIII large and sublateral in position (Figs. 46–52, 75, 78) ..... *Tortopsis*

Nymphs

1 Dorsum of head mostly glabrous, without large tufts of tightly grouped short setae; occiput roundly convex; mandibular tusks short, broad, and robust with two or three large distal tubercles (Fig. 93); pronotum thin (Fig. 93)..... .....Asthenopodinae, *Asthenopus* Dorsum of head with patches of short setae, mainly anteriorly to lateral ocelli; occiput flat, subquadrate in dorsal view; mandibular tusks elongated and slender (Figs. 94–96); pronotum broader (Figs. 94, 96) ....Campsurinae.. 2

2(1) Mandibular tusks with prominent basal or sub-basal tubercle on median margin (rarely tubercle absent), from some to many apical crenulations, numerous setae on outer margin of mandibles (Fig. 94); abdominal gill I bifurcated..... .....*Campsurus* Mandibular tusks with 1 (Fig. 96) or 2 (Fig. 95) prominent tubercles on distal third of median margin, few long setae on outer margin of mandibles; abdominal gill I single 3

3(2) Mandibular tusks with 2 tubercles (submedian and subapical) on median margin (Fig. 95); distal projection of fore tibia-tarsus 2/5 the length of claw ..... *Tortopus* Mandibular tusks with a single subapical tubercle on median margin (Fig. 96); distal projection of fore tibia-tarsus 2/3 the length of claw ..... *Tortopsis*

Key to the species of *Tortopus*

Male adults

1 Parastylus length shorter than length of its base (Figs. 10, 19) 2
Parastylus length subequal to base to 2 times length of base (Figs. 2, 24, 36) 3
2(1) Abdominal terga and sterna shaded brownish gray ..... *Tortopus bellus*
Abdominal terga shaded gray, sterna much less marked ..... *Tortopus harrisi*
3(1) Parastylus relatively long and thin at base (ps in Figs. 2–3) ..... *Tortopus igaranus*
Parastylus relatively short and thick at the base (Figs. 24, 36) 4
4(3) Abdomen shaded with gray on dorsum, ventrally paler; penes relatively thin basally (Fig. 24) ..... *Tortopus zottai*
Abdomen shaded strongly with brownish gray, dorsally and ventrally; penes with a wider base (Fig. 36) ..... *Tortopus arenales*

Female adults

1 Large species, fore wing length 15.8–17.5 mm, only known from Texas (USA) ..... *Tortopus circumfluus*
Small to medium size species, fore wing length 8.5–16.0 mm, known from Central to South America 2
2(1) Shading of body restricted exclusively to the dorsal portion 3
Shading of body well marked in dorsal and ventral portions 4
3(2) A pale species, shading of body very light, wing veins whitish translucent; head shaded gray in a pair of oblique bands from lateral ocelli to hind margin (Figs. 5, 85) ..... *Tortopus igaranus*
A darker species (Fig. 86), body shaded more strongly with gray, wing veins purplish brown; head shaded gray between lateral ocelli and on occiput ..... *Tortopus harrisi*
4(2) Head and pronotum shaded as in Fig. 81; sockets on sternum VIII relatively narrow, the medial margin much longer than the outer margin (Fig. 35, 82) ..... *Tortopus arenales*
Head and pronotum shaded as in Fig. 83; sockets on sternum VIII wider, the medial margin not markedly longer than the outer margin (Fig. 13, 84) ..... *Tortopus bellus*

Key to the species of *Tortopsis*

Male adults

1 Penes flattened and somewhat widened distally (Fig. 2 in Molineri 2008) 2
Penes cylindrical, long and slender (Figs. 41, 57, 64) 3
2(1) Penes slightly widening from base to apex ..... *Tortopsis puella*
Penes abruptly widened in distal half ..... *Tortopsis obscuripennis*
3(1) Parastyli with a longitudinal ventral furrow (Figs. 62–65, 77); apical penial spine rounded and flattened (Figs. 66, 77). ..... *Tortopsis spatula*
Parastyli entire; apical spine hooked 4
4(3) Parastyli relatively straight in lateral view, only curved on apical 1/4 (Fig. 58) ..... *Tortopsis limoncocha*
Parastyli curved from its base (Fig. 42) 5
5(4) Parastyli strongly curved, the main axis of the apical third forms an angle of 90° with the corresponding axis of the basal third (Fig. 42) ..... *Tortopsis unguiculatus*
Parastyli curved smoothly from its base 6
6(5) Known distribution restricted to southern Bolivia and Northwestern Argentina ..... *Tortopsis sarae*
Known distribution restricted to North America ..... *Tortopsis primus*[1]

Female adults[2]

1 Wings dark, all veins shaded strongly with gray or black; fore wing length 19.5–20.5 mm; color pattern on head and pronotum as in Fig. 89 ..... *Tortopsis obscuripennis*
Wings lighter, yellowish to brownish, some veins may be dark, mainly in costal region, fore wing length variable.. 2
2(1) Parastyli receptors on abdominal sternum VIII elongated and with slightly sinuous anterior margin (Figs. 49–52), anterior margin reaching the anterior margin of the sternum; head with a whitish zone behind median ocellus 3

1. Morphological characters are not included because male adults of *T. primus* were not available for study.
2. *T. unguiculatus* was not included in the key because female adults were not available. *T. zottai* is only known from males.

Parastyli receptors on abdominal sternum VIII generally not elongated (except *T. spatula*), margin not sinuous (Figs. 46–48); head shaded black behind median ocellus 4

3 (2) Head shaded gray to black between lateral ocelli and with few small markings also in occiput (Fig. 90); abdomen with thin blackish medial line on terga III–IX; on sternum VIII, anterior and posterior margins of sockets run more or less parallel to each other (Figs. 50–52) ..... *Tortopsis puella*

Head shaded gray in a V-shaped line between lateral ocelli and another medial thin line running anteriorly toward median ocellus, occiput without traceable marks (but material studied was very faded); abdomen with thin blackish medial line on terga I–VIII; on sternum VIII, anterior and posterior margins of sockets are divergent toward medial line (Fig. 49) ..... *Tortopsis primus*

4(2) Head shaded with black between ocelli, occiput without marks or with very light gray and small markings near hind margin (Figs. 87, 91) 5

Head shaded with black between ocelli and with gray markings on occiput (Figs. 53, 60, 88, 92) 6

5(4) Eggs yellowish, known distribution: NW Argentina and S Bolivia ..... *Tortopsis sarae*

Eggs orangeish, known distribution: Central Argentina ..... *Tortopsis bruchianus*

6(4) Color pattern on head and pronotum as in Fig. 88; parastyli receptors with C-shaped sockets (Figs. 55–56, 75) .... *Tortopsis limoncocha*

Color pattern on head and pronotum as in Fig. 92; parastyli receptors with V-shaped sockets (Figs. 61–62, 78) .... *Tortopsis spatula*

Descriptions

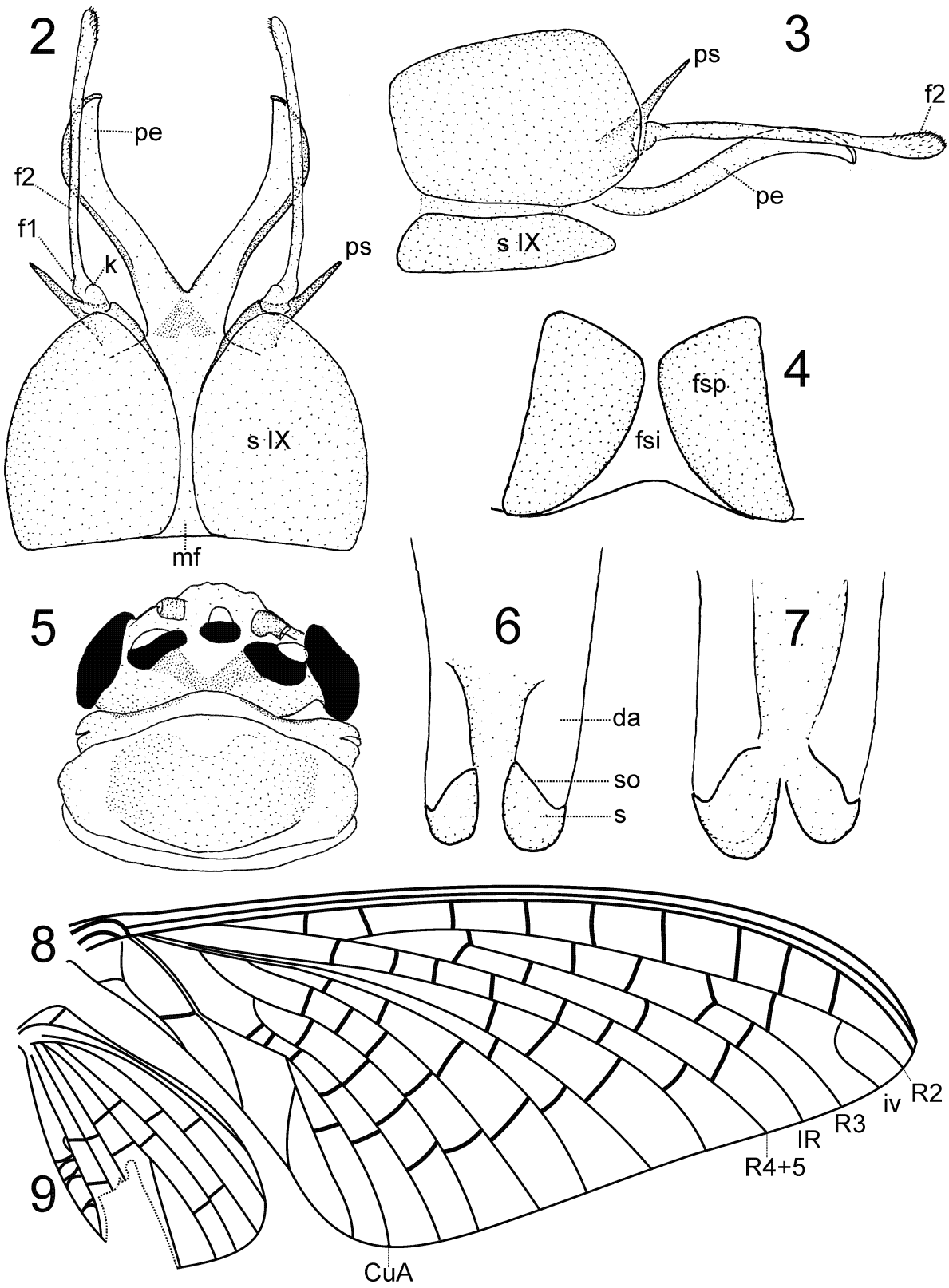
Tortopus Needham & Murphy

Tortopus Needham & Murphy (in part), 1924: 23; Ulmer (in part), 1933: 197; Traver (in part), 1950: 596.
Type-species: *Tortopus igaranus* Needham & Murphy, original designation.
Species composition: *T. igaranus*, *T. circumfluus*, *T. harrisi*, *T. zottai*, *T. bellus*, *T. arenales* sp. nov.

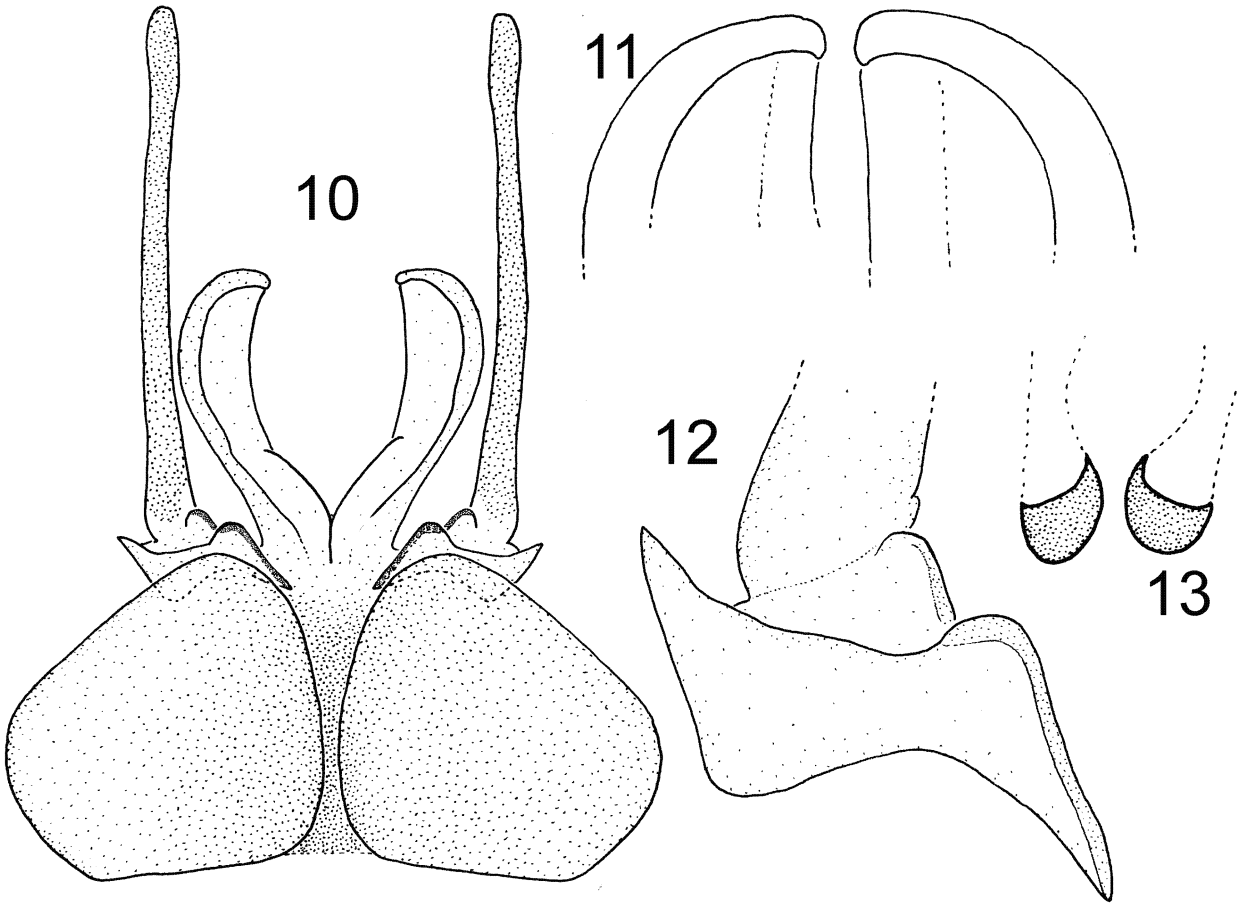
Adult: fore legs of male normal, remaining legs of male and all legs of female distorted and non-functional. Mesosternum: furcasternal protuberances approximating each other anteriorly (Fig. 4) so furcasternal longitudinal impression narrow basally and progressively wider posteriorly. Female pronotum with thin anterior portion (or ring), about 1/6 of the total length of pronotum in dorsal view. Wings sexually dimorphic, all veins of female thickened; posterior margin of hind wings of female with a reticulated pattern of veinlets. Female fore wing with veins R_3 and short intercalary before it present (Fig. 8). Abdomen. Female abdominal sternum VIII with relatively small and deep sockets (forceps receptors), with its openings directed anteriorly, and with well marked longitudinal furrows on sternum associated to them (Figs. 70–71). Male genitalia: abdominal sternum IX divided by a mediolongitudinal membranous furrow (Fig. 2); parastyli short, straight and pointed, less than 3 times the length of their bases; penes bladelike with their basal 1/5–1/4 fused (Fig. 2); lateral margin of penes narrowly sclerotized, apex not forming a hooked spine. Penial arms formed by a single transverse bar which is articulated to the posterior corners of tergum IX. Forceps two-segmented, basal segment short and small, with a ventral knob (Figs. 2); distal segment long, slender and clublike.

Nymph (only the nymph of *T. harrisi* is known, for a complete characterization see Molineri et al. 2010): head with fronto-clypeal region expanded, straight and not surpassing ventrally the mandibular tusks (Fig. 95); mandibular tusks long with two large tubercles (submedian and subapical) on inner margin; maxilla with a basal finger like gill. Large filtering setae present on mouthparts and fore legs. Apex of tibia-tarsus in fore legs not strongly expanded (dorsal projection 2/5 of total length of claw). Abdomen with vestigial unilamellate gill on segment I.

Eggs. Hemispherical, bowl-shaped (Figs. 67–69, 72). Length, 325–400 µm; width, 260–345 µm. No polar caps or attachment structures. Chorion with microsculptures consisting of slightly elevated pentagonal and hexagonal cells, or shallow subcircular grooves.



FIGURES 2–9. *Tortopus igaranus*. 2, male genitalia, ventral view (f1 and f2 = forceps segment 1 and 2, k = knob, mf = median furrow, pe = penes, ps = parastilus, sIX = ninth abdominal sternum); 3, same, lateral view; 4, mesofurcasternal plates (female paratype, fsi = furcasternal impression, fsp = furcasternal plates); 5, head (female paratype); 6, sockets on abdominal sternum VIII (female paratype, da = depressed area, s = socket, so = sockets´openning); 7, same (holotype); 8, fore wing (female paratype, R_2, R_3 and R_{4+5} = main veins of radial sector, IR = radial intercalary, iv = intercalary vein); 9, hind wing (female paratype).



FIGURES 10–13. *Tortopus bellus*: 10, male genitalia, v.v.; 11, details of apex of penes; 12, detail of pedestal, v.v.; 13, sockets on female abdominal sternum VIII.

Discussion and diagnosis. The adults of *Tortopus* can be separated from those of its sister genus *Tortopsis* by: 1) mesofurcasternal plates approximating each other only basally, with inner margins diverging posteriorly from their basal 1/3 or less (Fig. 4); 2) male abdominal sternum IX longitudinally divided by a median furrow (Fig. 2); 3) parastyli short, less than 3 times the length of their bases (pedestals); 4) penes bladelike and basally fused, at least on basal 1/5; 5) female fore wing with veins R_3 and short intercalary present (Fig. 8) (veins IRSa and RSa_2 in Kluge 2004); 6) sockets on female abdominal sternum VIII relatively small and submedian in position (Fig. 70), openings towards fore margin of sternum. The characters useful to separate *Tortopus* and *Tortopsis* from the other genera of the family are listed in the phylogenetic section (apomorphies of node c). The coupling apparatus of *Tortopus* s.s. apparently involves male forceps (not parastyli, poorly developed) and female sockets. Male forceps are not large enough to embrace female abdomen, but they seem to fit in the submedian sockets. Parastyli are so poorly developed that they could not reach female sockets during copula. In contrast, the coupling apparatus of *Tortopsis* (described in McCafferty & Bloodgood, 1989, for a species now moved to *Tortopsis*, see below) involves the strongly developed male parastyli and female sockets.

Tortopus igaranus Needham & Murphy

Tortopus igaranus Needham & Murphy, 1924:24 (female) in part

Type material (CUIC). Types in alcohol: holotype (female abdomen) and 4 female paratypes from Peru, río Putumayo between Puerto Alfonso and the mouth of the Igará-Paraná, 14-VIII-1920. One female specimen

from Perú, río Igará-Paraná, 15-17-VII-1920 (1 pair of wings dissected, CUIC slide No. 629.3); and 1 female (body without wings, very damaged) from Peru, Puerto Bermudez (no more data). Type slides: the two holotype slides (No. 629.1) were not studied, CUIC reported them as completely broken and with missing parts. Paratype slides: No. 629.3 correspond to the female from Igará-Paraná mentioned above, but the slide (1 wing pair) presents the following data (presumably a mistake): blue carton "PARATYPE/Cornell U./ No.629.3", white carton "Cornell University/N0 654/SUB. 14 SL.♀/Tortopus/~~Campsurus~~/igaranus/Rio Putumayo/DATE 14 Aug.´20 Peru".

The following material is removed from the type series since they represent female adults of a different species: six females originally designated as paratypes (Needham & Murphy 1924), were removed from the vial containing the holotype (Peru, río Putumayo between Puerto Alfonso and the mouth of the Igará-Paraná, 14-VIII-1920). The slides No. 629.2, 629.4 and 629.5 are not conspecific with the holotype, the bodies in alcohol that correspond to the slides 629.2 and 629.4 are among the 6 females mentioned above (the slide 629.5 does not have an associated specimen in alcohol). Additional material (IML). Five male and 4 female imagos from Colombia: Depto. Amazonas, Leticia, Isla Beatriz, 93 m, 8-II-1999, S 4º 4' 23" W 69º 59' 12", light trap 18–20 h, M. C. Zúñiga, E. Domínguez & C. Molineri cols.

Holotype (only female abdominal segments VII–X). Eggs orangeish. Abdominal tergum VII damaged, incomplete; terga VIII–X shaded slightly with gray, lighter in X. Abdominal sterna without gray shading, parastyli receptors on sternum VIII relatively small and near the medial line, with paired shallow longitudinal furrows directed anteriorly from each socket (Fig. 7). Cerci translucent yellowish white, vestigial terminal filament translucent whitish.

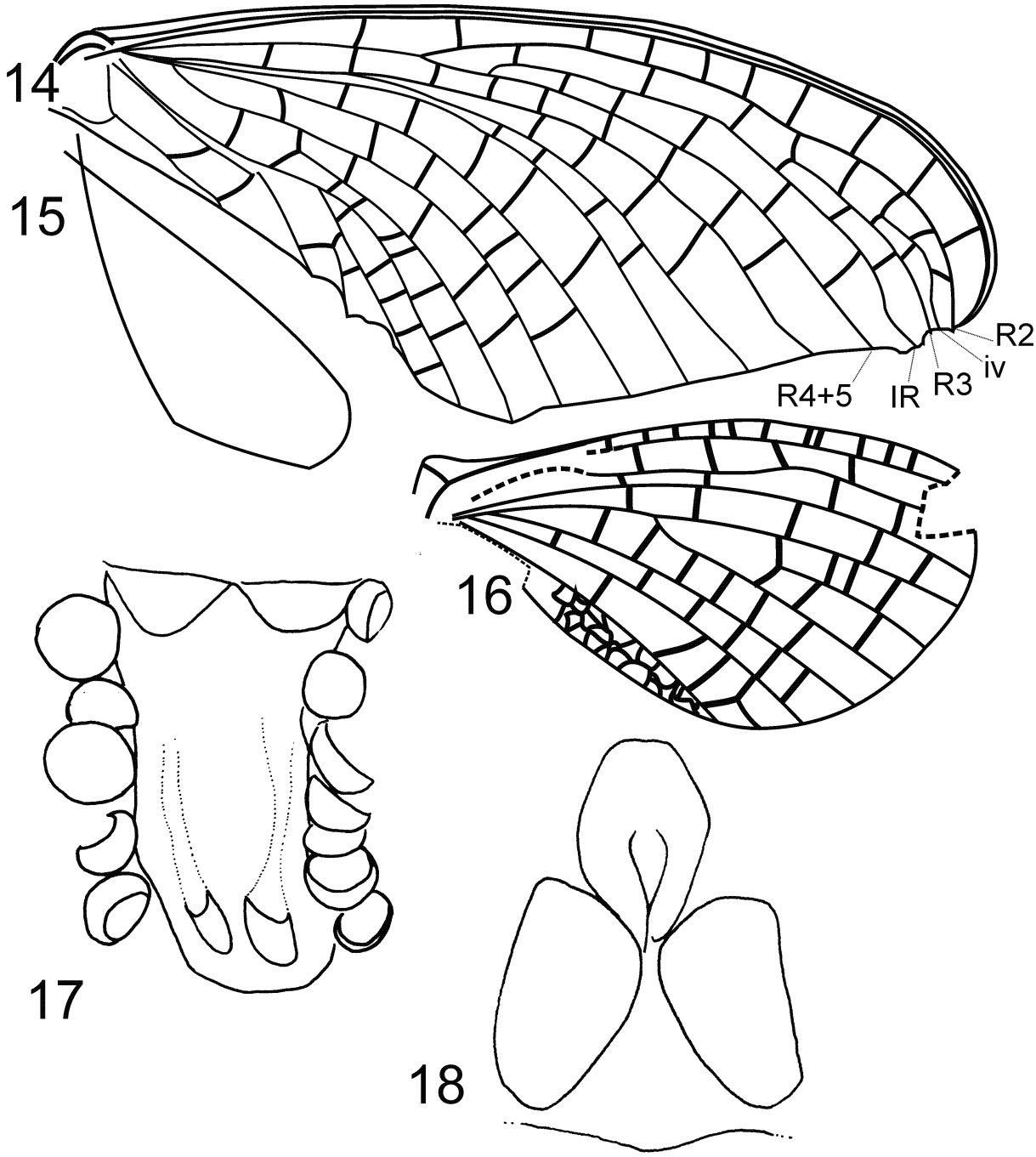
Paratype female adults. One of the four specimens from Putumayo river is much damaged presenting only the thorax and the wings (fore wings, 12.5 mm; hind wings, 5.0). The other 3 are in better condition (one of them with a pair of wings dissected, without associated slide), body length: 7.0 (shrunken specimen)-8.5 mm; fore wings, 9.8–10.0 mm; hind wings, 3.5–3.9 mm. The paratype specimen from Igaraná-Paraná (and associated slide) is in a rather good condition, measures: body, 6.5 mm (shrunken), fore wing 10.2 mm, hind wing, 3.9 mm. General coloration yellowish white, eggs orangeish. Head with a whitish triangular mark behind median ocellus, occiput with a pair of grayish oblique bands extending from each lateral ocellus to the medial line near hind margin (Fig. 5). Antennae: scape and pedicel yellowish tinted with gray, flagellum hyaline. Thorax. Pronotum markedly convex dorsally, with well developed anterior hump; shaded with gray except laterally, medial line whitish, anterior margin shaded with gray sublaterally. Mesonotum whitish yellow, except medioposterior zone whitish, anterior phragma orangeish. Metanotum whitish medially, rest yellowish. Thoracic sterna pale, furcasternal protuberances with divergent medial margins (Fig. 4). Legs whitish except coxae yellowish. Wings. Membrane hyaline to whitish translucent, longitudinal veins yellowish brown, cross veins whitish; R_3 and short intercalary vein before it present in fore wings (Fig. 8); reticulate pattern of cross veins in anal region of hind wings slightly marked (Fig. 9). Abdomen. Terga translucent whitish slightly and widely shaded with gray, darker on terga VIII–IX, tergum X whitish. Abdominal sterna pale, parastyli receptors (Fig. 6) on sternum VIII as holotype.

Length of voucher female imagos (collected with the males described below): body, 9.0–9.2 mm; fore wings, 8.5–10.0 mm; hind wings, 3.5–3.6 mm; cerci, 2.2–2.7 mm.

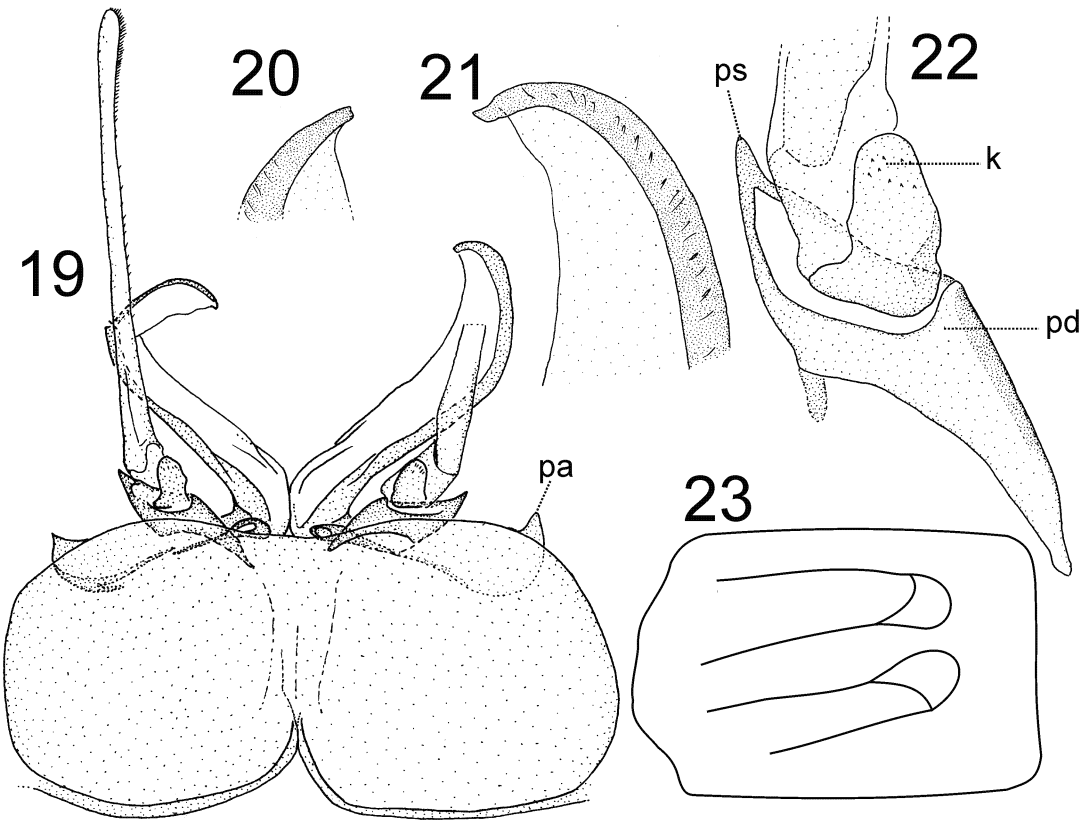
Eggs (Figs. 67–69). Subcircular outline. Length, 325 µm; width, 300 µm. No attachment device present. The convex area of the egg is sculptured with pentagonal and hexagonal cells (Fig. 68). The concave area shows a regular arrangement of shallow circular grooves (Fig. 69). The entire zone forming the margin between the above mentioned areas is smooth (Fig. 67).

Male imago. Length (mm): body, 7.5–9.8; fore wing, 8.0–8.9; hind wing, 3.4–3.9 mm; fore leg (from base of coxae to apex of claw), 3.7–4.0; cerci, 20.0–22.0. General coloration whitish yellow. Head whitish shaded gray on pair of oblique bands on occiput, each band extending from lateral ocellus posteriorly towards medial line. Antennae: scape and pedicel whitish shaded light gray, flagellum hyaline. Thorax. Pronotum dorsally convex, anterior ring hyaline translucent, projecting anteriorly ("anterior hump"), a blackish marks is present laterally on fore margin; posterior ring of pronotum whitish translucent shaded with gray medially; propleura and presternum hyaline to whitish translucent. Mesonotum whitish yellow with darker margins and carinae,

shaded slightly with gray along medioparapsidal sutures and inner margins of posterior scutal protuberances. Metanotum whitish translucent shaded gray anteromedially. Meso- and metaplaurae and sterna pale. Legs yellowish white, shaded with light gray on fore leg, more markedly on fore tibiae and tarsi, except intertarsal joinings. Wings. Membrane hyaline except apical third of C and Sc area whitish translucent; veins whitish translucent shaded with gray on veins Sc and RA. Abdomen whitish translucent shaded gray dorsally, very slightly on anterior segments but darkening posteriorly; terga III–VII with a pair of submedian bands, each band turns laterally towards hind margin; terga VIII–X shaded more widely, stronger on hind margin of tergum X; medial line of all terga pale. Abdominal sterna pale, with blackish spot in the middle of sternum IX. Genitalia whitish except parastyli and outer margin of penes yellowish. Caudal filaments whitish translucent except basal segment yellowish.



FIGURES 14–18. *Tortopus circumfluus*, female holotype. 14, fore wing; 15, hind wing (scheme); 16, hind wing, enlarged; 17, abdominal sternum VIII; 18, mesofurcasternal plates.

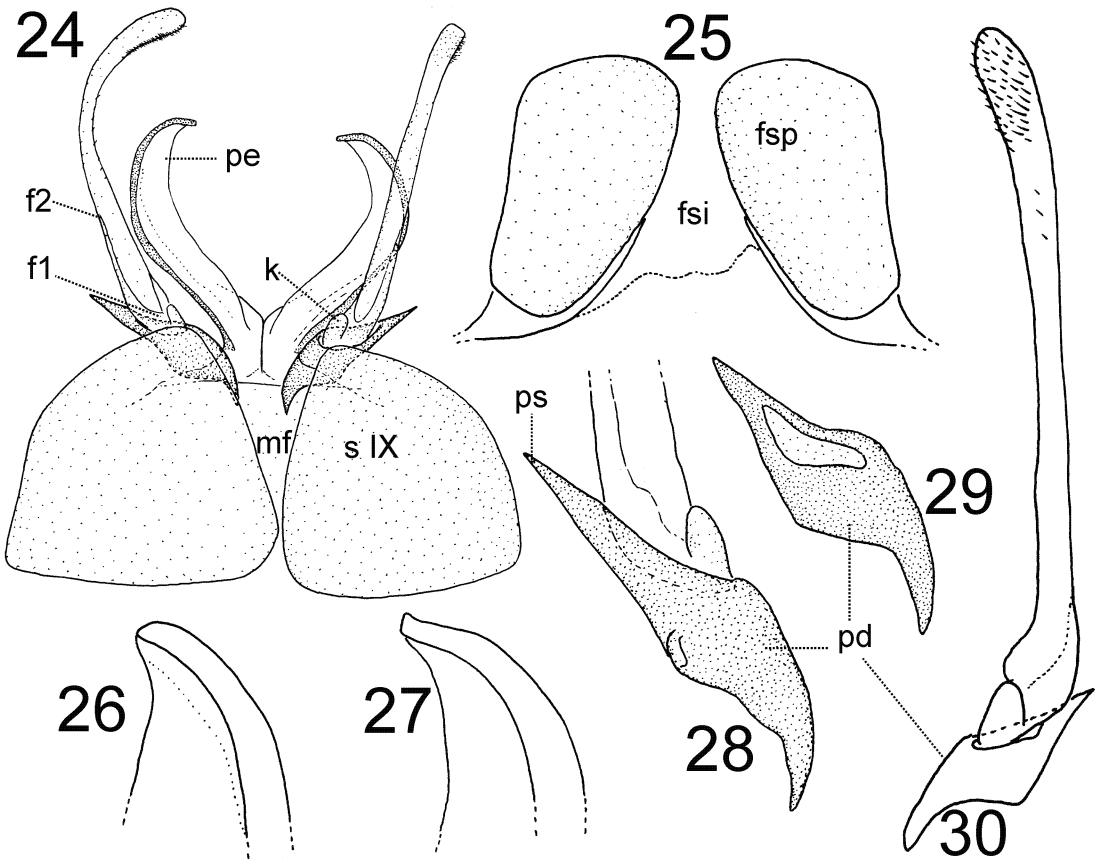


FIGURES 19–23. *Tortopus harrisi*, male holotype: 19, genitalia, v.v. (pa = penial arm); 20–21, details of apex of penes; 22, detail of pedestal and base of forceps, v.v. (k = knob, pd = pedestal, ps = parastylus); 23, female sternum VIII.

Discussion and diagnosis. From the study of the type series, two groups of females representing two different genera (*Tortopus* and *Tortopsis*) were distinguished. Fortunately, the holotype abdomen in alcohol was preserved enough to show important characters for species identification (holotype slides were reported as broken and with lost parts). The holotype and conespecific paratypes of *T. igaranus* were compared to newly collected material from sites near to the type localities. Descriptions given above are based on this morphotype. The abdomens of the above described paratypes coincide completely with the holotype in morphology and coloration, including the shape of the parastyli receptors. Veins R_3 and the short intercalary before it on fore wings are hard to distinguish in the relatively damaged wings of the paratypes, they are present in one slide (CUIC No. 629.3) and on one of the specimens in alcohol.

The holotype and the 4 conspecific paratypes of *T. igaranus* present the following characters: head coloration formed mainly by a pair of oblique bands running from lateral ocelli to medial posterior line; mesonotum without a gray marking before mesoscutellum; furcasternal protuberances diverging from its anterior portion; fore wing with R_3 and short intercalary vein before it; cross veins in fore and hind wings whitish; parastyli receptors on sterna VIII small and submedian.

The six females from río Putumayo here excluded from the type series represents a different species in the genus *Tortopsis*. These specimens can be distinguished from the holotype and paratypes referred above by the following characters: head coloration more extended in occiput; pronotum in dorsal view rectangular, with well separated anterior and posterior rings; mesonotum with a gray V-shaped marking before mesoscutellum; furcasternal protuberances with parallel sides on anterior half, diverging only on the posterior portion; veins R_3 and short intercalary before it absent in fore wing; cross veins in fore and hind wings as dark as longitudinal veins; parastyli receptors on sterna VIII C-shaped and relatively large, more lateral in position. These specimens could be the female of *Tortopsis unguiculatus* (Ulmer) or a new species, but their overall bad condition necessitates leaving them unnamed.



FIGURES 24–30. *Tortopus zottai*, male paratype. 24, genitalia, v.v. (f1 and f2 = forceps segment 1 and 2, k = knob, mf = median furrow, pe = penes, sIX = ninth abdominal sternum); 25, mesofurcasternal plates (fsi = furcasternal impression, fsp = furcasternal plates); 26–27, details of apex of penes; 28, detail of pedestal and base of forceps, v.v.; 29, pedestal; 30, pedestal and forceps (pd = pedestal, ps = parastilus).

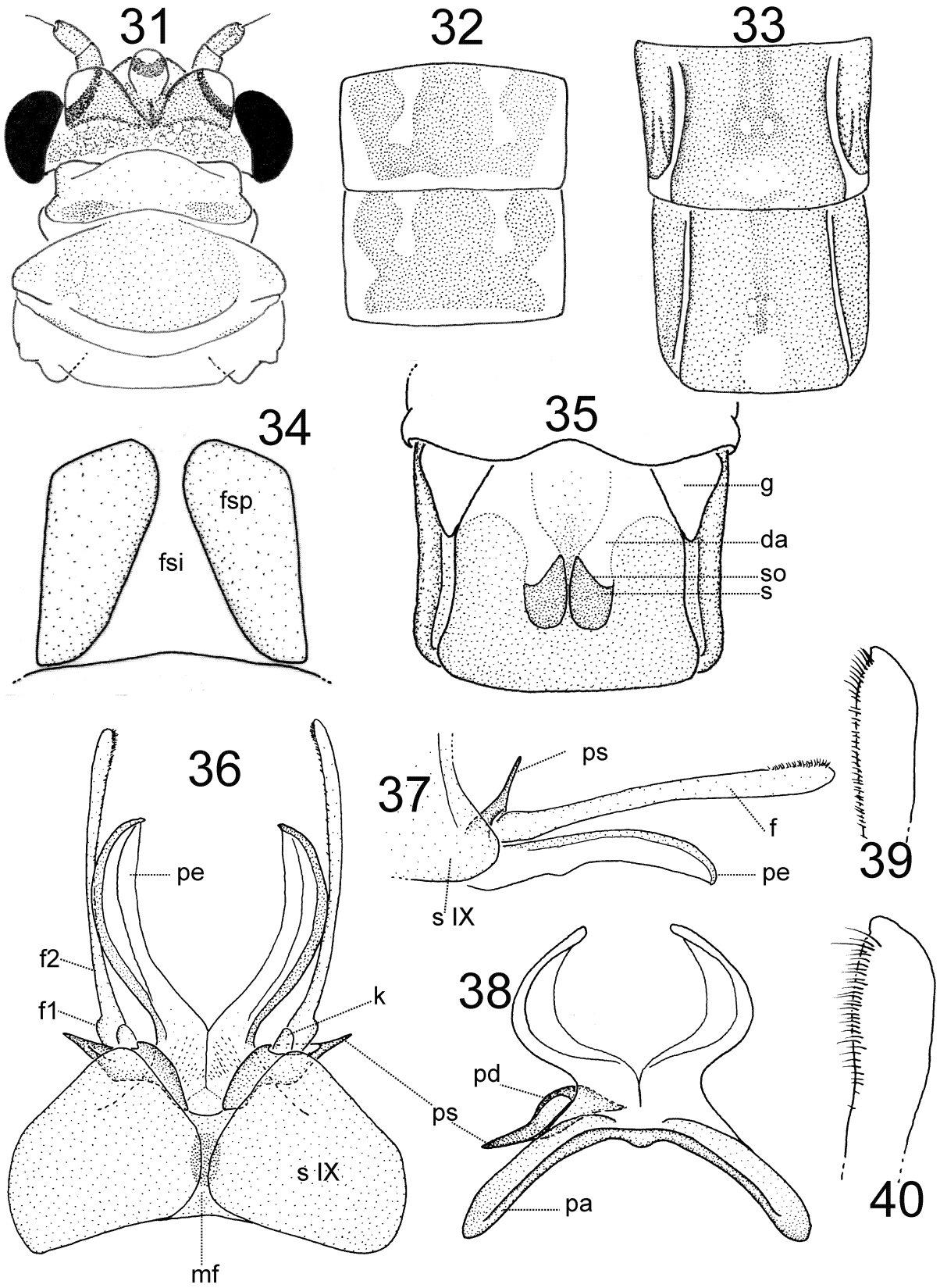
Tortopus igaranus can be distinguished from all other species in the genus by the following combination of characters: 1) fore wing length 8.0–8.9 mm (female 8.5–12.5 mm); 2) parastyli relatively long (1.5 times length of pedestal) and thin from its base (Figs. 2–3); 3) ventral knob relatively small (Fig. 2); 4) penes not strongly expanded (Fig. 2); 5) female with sockets on s. VIII with oblique opening as in Figs. 6–7; and 6) a very pale species, head shaded gray in a pair of oblique bands from lateral ocelli to hind margin.

Tortopus bellus **Lugo-Ortiz & McCafferty**

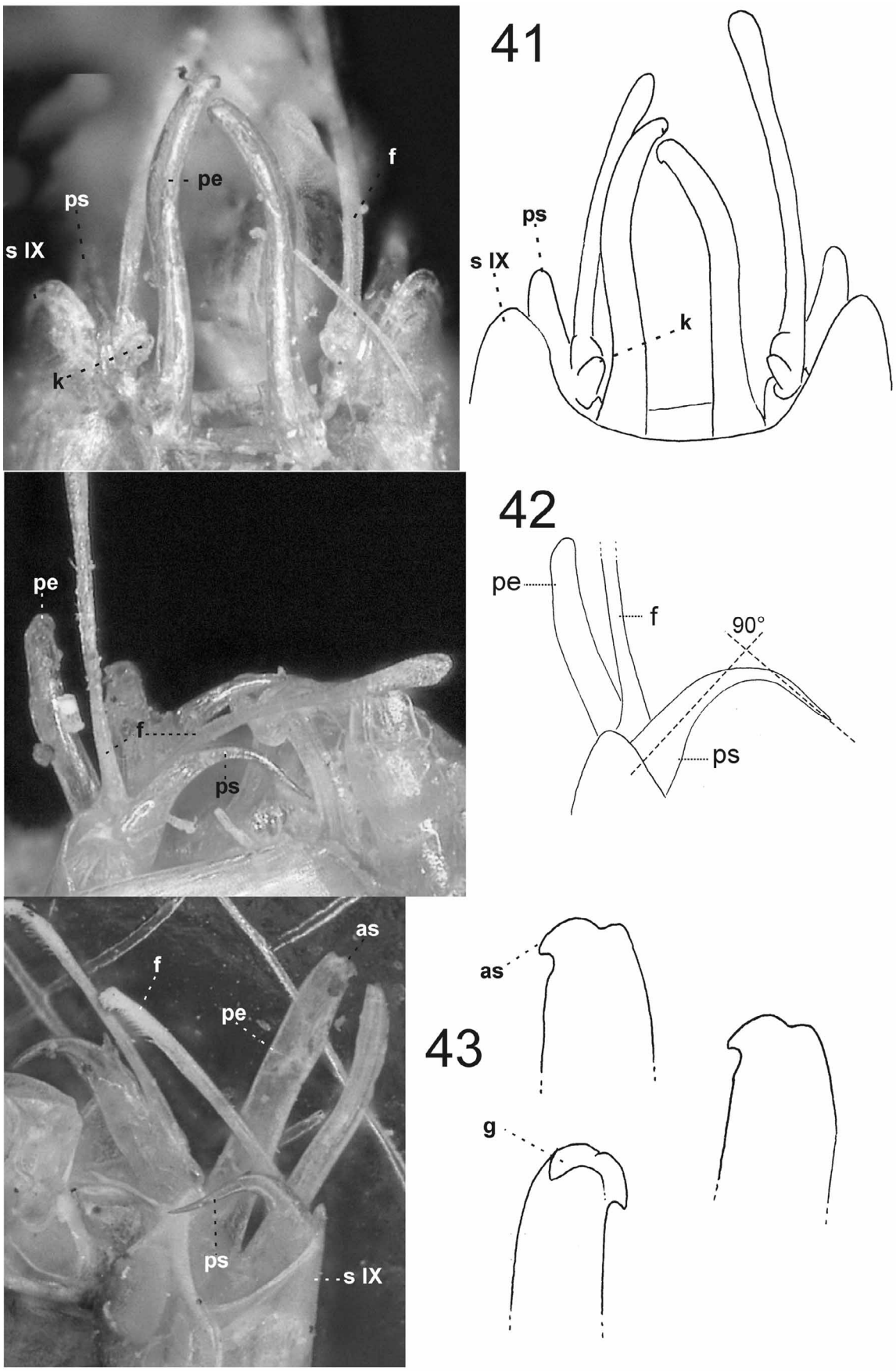
Tortopus bellus Lugo-Ortiz & McCafferty 1996: 24.

Material (FAMU): 1 male (genitalia on slide 1116) and 1 female imagos from Costa Rica: Heredia, Est. Biol. La Selva, río Puerto Viejo, 19-VI-1986, Holzenthal, Heyn & Armitage cols. Attempts to borrow the holotype male from Purdue Entomological Collection were not successful. Type locality: Costa Rica, Heredia (no more locality data).

Male imago. Length (mm): body, 10.5 (8.3 in original description); fore wing, 12.9 (10.5 in original description); hind wing, 6.2. General coloration yellowish brown. Head yellowish brown shaded black on dorsum almost entirely, shaded heavier between ocelli. Antennae yellowish shaded gray on scape, black on pedicel, flagellum hyaline. Thorax orangeish brown shaded black mainly on pronotum. Pleura and sterna slightly paler shaded black on mesofurcasternal membrane and metasternum. Fore legs yellowish shaded with black except at articulations of segments and claws, pale; legs II–III whitish yellow shaded gray on femora

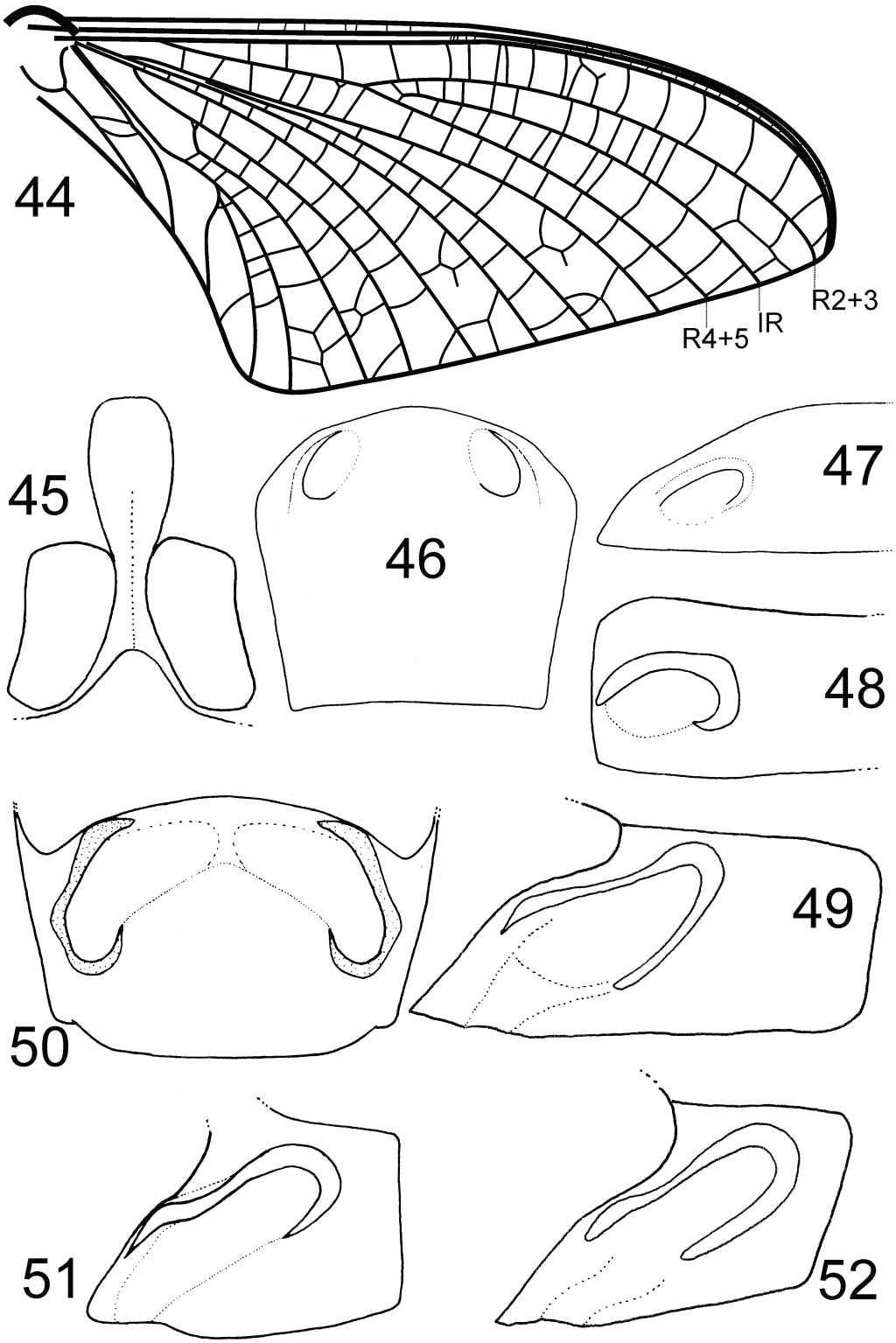


FIGURES 31–40. *Tortopus arenales*. 31, male head, d.v.; 32, male abdominal terga VI–VII; 33, male abdominal sterna VII–VIII; 34, male mesofurcasternal plates; 35, female abdominal sternum VIII; 36, male genitalia, v.v.; 37, same, l.v.; 38, penes after treatment with potash; 39–40, detail of apex of forceps.

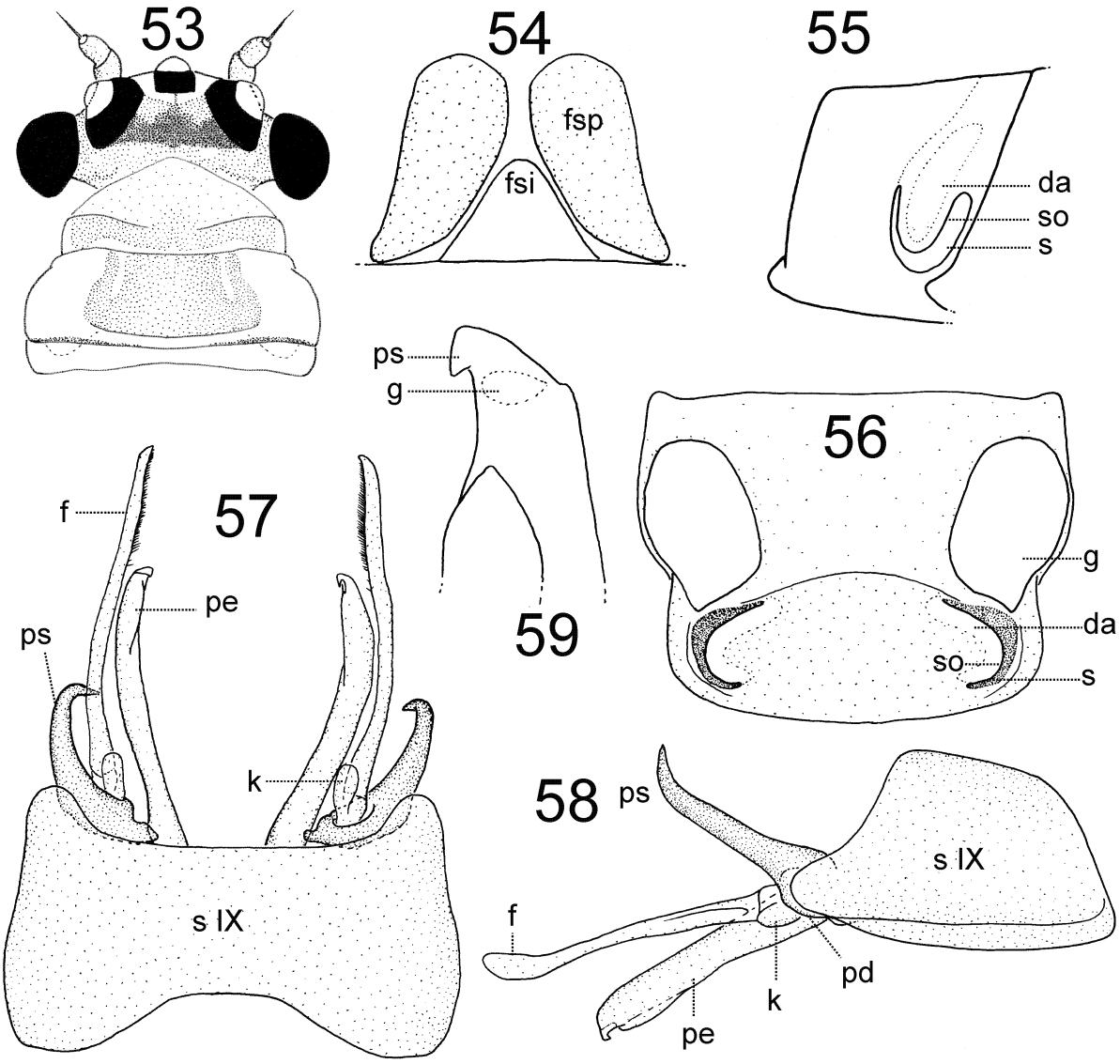


FIGURES 41–43. *Tortopsis unguiculatus*, type male genitalia, photographs and interpretations (line drawings). 41, ventral view; 42, lateral view; 43, laterodorsal view (details of apex of penes).

and tibiae. Wings membrane hyaline translucent, veins brownish yellow, lighter toward apex. Abdomen yellowish completely shaded brownish gray except some pale markings, segment X slightly paler than the rest. Genitalia (Figs. 10–12): sternum IX shaded with black on median 1/3, stronger on median furrow; pedestals and short parastyli (Fig. 12) yellowish translucent; forceps whitish yellow shaded almost completely with black; penes translucent yellowish white, apex rounded (Fig. 11).



FIGURES 44–52. *Tortopsis*, female imago. 44, *T. obscuripennis*, fore wing. *T. sarae*: 45, mesofurcasternum; 46, abdominal sternum VIII,v.v.; 47, same, l.v. *T. obscuripennis*: 48, abdominal sternum VIII, l.v. *T. primus*: 49, abdominal sternum VIII, l.v. *T. puella*: 50, abdominal sternum VIII,v.v.; 51–52, same, l.v.



FIGURES 53–59. *Tortopsis limoncocha*. 53, male head, v.v.; 54, male mesofurcasternal plate; 55, female abdominal sternum VIII, l.v.; 56, same, v.v.; 57, male genitalia, v.v.; 58, same, l.v.; 59, detail of apex of penes.

Female imago. Length (mm): body (shrunken abdomen), 10.5; fore wing, 16.0; hind wing, 6.9; cerci, 4.5. As in male, exceptions follow. Antennae with scape and pedicel brownish black. Thorax shaded more markedly with brownish gray. Legs yellowish white shaded brownish, turning lighter towards apex. Wings as male except usual sexual dimorphism (thicker veins). Abdomen yellowish strongly shaded brownish gray. Sternum VIII shaded strongly with black, lighter anteriorly; sockets blackish, relatively short and with more or less transverse opening (Fig. 13), anterior depressed area paler. Cerci whitish.

Discussion and diagnosis. A short description of the male is given to complete the original description by Lugo-Ortiz & McCafferty (1996) with some new characters for the group. The female adult is described for the first time. *Tortopus bellus* can be distinguished from other species in the genus by: 1) fore wing length 10.5–12.9 mm (female 16.0 mm); 2) parastyli very short and pointed (Fig. 10, 12); 3) ventral knob relatively small (Fig. 12); 4) penes relatively wide (Fig. 10); 5) female with sockets on s. VIII relatively wide and with transverse opening (Fig. 13); and 6) a relatively dark species, dorsum of head almost entirely shaded black.
Male genitalia of *Tortopus bellus* is very similar to *Tortopus harrisi*, but in *T. bellus* the knob at the base of forceps is reduced, pedestals have a widely rounded posteromedial corner (opposite to parastylus), forceps are completely shaded black and penes are much wider. Further differences between both species include: a darker coloration in *T. bellus* with abdominal terga and sterna shaded strongly with brownish gray (sterna

unmarked in *T. harrisi*), and wing venation without short marginal intercalaries in MA and R regions (*T. harrisi* holotype presents 3 of these veins).

Tortopus circumfluus Ulmer

Asthenopus sp. Eaton 1871: 59, pl. I, fig. 3 (female)
Campsurus sp. Eaton 1883: 41, pl. V, fig. 8b (female)
Tortopus circumfluus Ulmer 1942: 110 (female)

Material (RBINS): holotype and paratype female imagos from Texas, no more data. Some more detail is mentioned by Eaton (1883) and Ulmer (1942): USA: Texas, Victoria?, Bosque County, Belfrage col.

Female imago (pinned). Length (mm): body (shrunken), 9.8–10.1; fore wing, 15.8–17.5; hind wing, 6.9; cerci, 5.0–5.2. General coloration whitish yellow. Furcasternal plates widely diverging posteriorly (Fig. 18). Wings (Figs. 14–16) membrane whitish translucent, fore wing veins C, Sc and R_1 purplish brown, other longitudinal and cross veins yellowish light-brown; R_3 and short intercalary vein before it present on fore wings (Fig. 14). Hind wings with yellowish white veins except Sc grayish brown. Abdomen: sternum VIII with parastyli receptors located submedially (Fig. 17), with relatively deep sockets and marked longitudinal furrows. Cerci whitish.

Eggs. Suboval, no attachment structures visible at 100X. Length, 340 µm; width, 260 µm.

Discussion and diagnosis. Only female adults from Texas are currently known. Ulmer´s figure (Ulmer 1942, p. 127, fig. 17a) of the wings shows veins R_3 and the intercalary before it very well developed and long, but Eaton´s (1871, pl. I, fig. 3) figure does not show these veins at all (only a 1-cell marginal intercalary attached to R_{2+3}). The length of R_3 in Ulmer figure 17a are correct following the examination of the types. It seems that Eaton and Ulmer worked on different specimens, but Ulmer figures should be taken as valid for this species. Since the collection of the types (and only known specimens) prior to 1871, no conspecific specimens have been recorded again from Texas or other USA localities (J. G. Peters pers. comm.). A probable mislabeling of specimens prior to Ulmer´s revision should be taken as a possibility. McCafferty (1994, p. 3) confirmed the presence of *T. circumfluus* in Texas (citing Lugo-Ortiz & McCafferty 1994), but no new specimens were collected to support the statement. Lugo-Ortiz & McCafferty (1994) only give the original record of the type material, so McCafferty´s (1994, p. 3) confirmation seems erroneous. A short redescription based on the re-examination of the types is provided to account for new characters in the group. The synonymy between *T. circumfluus* and *T. bellus* is suspected but this will be confirmed only when male adults or fresh females of the former species could be collected.

Tortopus circumfluus, known only from female adults, can be distinguished from all other species of the genus by the following combination of characters: 1) fore wing length 15.8–17.5 mm; 2) abdominal sternum VIII with relatively deep sockets and marked longitudinal furrows (Fig. 17). The coloration is not longer recognizable in the old and dry specimens.

Tortopus harrisi Traver

T. harrisi Traver 1950: 604; Domínguez 1985: 69.

Type material (CUIC): holotype male imago, 2 slides No. 3031, one slide with a pair of wings, the other with the genitalia, labeled: “Tortopus /harrisi -/Holotype/♂ im..Wings/corumba, Mat. Grosso,/Brazil/14/23-XII-19/ R G Harris” and “Tortopus /harrisi/Holotype/♂ im.- Genitalia/Corumba, Mat. Grosso,/Brazil/14/23-XII-19/ spec pinned/R G Harris”.

Other material (IML): 15 (pinned) female imagos from Paraguay, Depto. San Pedro, Carumbé, 28/I to 10/ III -1965, R. Golbach col. Three of these specimens were re-hydrated in water prior to study, and then preserved in alcohol.

Female imago. Length (mm): body, 10.0–13.0; fore wing, 10.5–15.0; hind wing, 4.5–6.2; cerci shrunken. General coloration yellowish light brown, eggs yellowish orange. Head shaded with black between lateral ocelli and with a lighter grayish pattern on occiput. Antennae shaded slightly with gray. Thorax. Pronotum shaded with black on anterior and posterior margins, large zone on median area shaded gray. Meso- and metanotum shaded black on carinae and posteromedian triangular marks. Legs yellowish. Wings. Membrane hyaline, veins purplish light brown, darker on C, Sc and R_1 veins; R_3 and short intercalary vein before it present on fore wings. Abdomen shaded gray dorsally, ventrally pale; terga with thin medial black line; a relatively wide zone forming a medial band is shaded gray on terga I–VII, terga VIII–IX shaded almost completely except two pairs of long pale dashes; pale sublateral areas present at least on terga II–VI. Sternum VIII with small submedian sockets and long anterior furrows (Fig. 23).

Nymph. Described in Molineri et al. (2010).

Eggs. Suboval, no attachment structures. Length, 360–380 µm; width, 270–310 µm. The chorion is almost completely sculptured with a hexagonal pattern.

Discussion and diagnosis. *Tortopus harrisi* is known from the male holotype and some females here attributed to this species. This species can be distinguished from all other species of the genus by: 1) male fore wing length 10.5 mm (Traver 1950 reported 9.0 mm for the same specimen), female fore wing 10.5–15.0 mm; 2) parastyli very short and pointed (Fig. 19, 22); 3) ventral knob relatively large (Fig. 22); and 4) penes relatively narrow basally, not expanded (Fig. 19), sclerotized margin narrowly ending (Figs. 20–21). The female imagos described here are only tentatively associated to this species, based on general size and coloration. These females are from Carumbé (San Pedro, Paraguay), a locality on the Paraguay River relatively close to the type locality Corumbá (Mato Grosso, Brazil), some kilometres above the same river.

Tortopus zottai **(Navás)**

Campsurus zottai Navás 1920: 11.
Tortopus zottai; Domínguez 1987: 11.

Type material (MACN): lectotype, paralectotype and 17 specimens, all male imagos from Argentina: Buenos Aires, XII-1916, A. Zotta col.

Discussion and diagnosis. this species known only from males was redescribed by Domínguez (1987). It constitutes the most Southern record of the genus. Illustrations of furcasternal protuberances (Fig. 25) and genitalia (Figs. 24, 26–30) are given. Male imagos can be separated from all other species of the genus by: 1) fore wing length 12.0–12.5 mm; 2) parastyli at least 1.5 times length of its base, slightly becoming thinner towards the apex (Figs. 28–30); and 3) fused basal portion of penes relatively thin, distal portions not expanded (Fig. 24), becoming thinner toward apex (Figs. 26–27).

Tortopus arenales **sp. nov.**

Material: holotype male imago from Ecuador: Prov. Esmeralda, Canton Eloy Alfaro, Parroquia Telembí, Estero Arenales, 80 m, 15-IV-2002, S 0º 40' 6" W 78º 59' 25", E. Domínguez col. Paratypes: 13 male and 21 female imagos same data as holotype; 10 male and 26 female imagos same data except Estero Cayapas, 70 m, 15-IV-2002, S 0º 40' 19" W 78º 59' 29", E. Domínguez col.; 11 male and 8 female imagos same data except Estero Calle Mansa, 50 m, 17-IV-2002, S 0º 42' 10" W 78º 58' 01", E. Domínguez col.; and 17 female imagos same data except Estero Charco Vicente, 40 m, 14-IV-2002, S 0º 41' 36" W 78º 54' 33", E. Domínguez col. Holotype, 3 male and 3 female imagos paratypes at MECN; 2 male and 2 female imagos in CUIC and FAMU; remaining material deposited in IML.

Male imago. Length (mm): body, 10.0–11.5; fore wing, 10.0–11.7; hind wing, 4.9–5.2; foreleg, 4.7–5.0; cerci, 26.0–30.0. General coloration yellowish white shaded with brown. Head shaded strongly with brownish gray on a band between ocelli, shading slighter posteriorly forming a profuse anastomosed pattern on occiput

(Fig. 31); head not shaded ventrally and before to median ocellus. Antennae: scape and pedicel completely shaded with gray except at apical margin, flagellum hyaline. Thorax. Pronotum (Fig. 31) translucent brownish white shaded widely with brownish gray, anterior ring shaded stronger on submedian zones, paler posteriorly; posterior ring shaded strongly medially with a thin dark medial line and two paler sublateral spots; propleura and presternum translucent brownish white. Mesonotum yellowish white shaded brownish gray along medioparapsidal sutures forming a pair of bands that become darker and converge posteriorly; mesopleura and mesosternum shaded very slightly with gray on pleura, but strongly on basisternum; furcasternal protuberances diverging posteriorly from anterior margin (Fig. 34). Metanotum yellowish white shaded brownish gray widely in anterior zone, stronger shading restricted more medially towards posterior margin; metapleura and sternum brownish white shaded strongly with gray on a pair of submedian anterior marks. Legs. Fore legs shaded completely and strongly with brownish gray except on the very pale claws; middle and hind legs yellowish white slightly shaded gray. Wings. Membrane hyaline shaded brownish gray on C and Sc areas, longitudinal veins shaded brownish, cross veins pale. Abdomen whitish translucent shaded strongly with brownish gray, except on lateral areas. Tergum I shaded submedially, with a translucent medial band; terga II–VII with thin pale median and paramedian dashes, also with a pale oblique dash near lateral margins (Fig. 32); terga VIII–X shaded more widely and strongly except on submedian and lateral pale marks; all terga except the first with a thin dark median line. Abdominal sterna (Fig. 33) shaded strongly on median region except on pale medial line and paired submedial oval marks, shading darker around the medial line; indentations left by nymphal gill muscles (subcircular lateral areas on sterna II–VII) yellowish white shaded gray except on pale medial margin. Genitalia (Figs. 36–40): sternum IX shaded strongly with gray on mediolongitudinal furrow but getting much lighter laterally; pedestals whitish turning yellowish towards apex of parastyli, parastyli relatively short and straight (Fig. 36–38); small first forceps segment whitish, second segment strongly shaded gray; penes whitish, outer margin yellowish, shaded slightly gray on each penial arm. Caudal filaments whitish translucent shaded brownish gray except at joinings.

Female imago. Length (mm): body, 9.6–13.0; fore wing, 11.2–14.5; hind wing, 4.5–6.2; cerci, 3.1–4.0. General coloration as male, eggs yellowish white. Metasternal black marks thinner and longer than in male. Wings darker than in male, membrane slightly tinged with yellow, longitudinal and cross veins shaded with brownish, more strongly on C, Sc and R_1 veins; R_3 and short intercalary vein before it present on fore wings. Brownish shading on body as in male except slightly paler on abdominal sterna; intersegmental membrane between sterna VII–VIII paler than the rest, sternum VIII with parastyli receptors located submedially (Figs. 35, 70–71) and strongly shaded gray. Cerci whitish.

Eggs (Fig. 72). Suboval, no attachment structures. Length, 400 µm; width, 330–345 µm. The relatively thick covering of the egg is relatively smooth.

Etymology: from the type locality, Estero Arenales.

Discussion and diagnosis. *Tortopus arenales* sp. nov. can be separated from all other species of the genus by the following combination of characters: 1) fore wing length 10.0–11.7 mm (male), 11.2–14.5 mm (female); 2) parastyli with relatively wide base, rest very thin and acute, as long as pedestal (Fig. 36–37); 3) ventral knob well developed (Fig. 36); 4) penes relatively wide at base (fused portion), not strongly expanded distally (Fig. 36); 5) female sockets with oblique opening (Fig. 35, 70–71); and 6) a relatively dark species, shading on occiput forming a profuse anastomosed pattern (Fig. 31).

Tortopsis **gen. nov.**

Tortopus Needham & Murphy (in part), 1924: 23; Ulmer (in part), 1933: 197; Traver (in part), 1950: 596; McCafferty, 1975: 489; Scott et al. 1959; Molineri 2008

Type-species: *Campsurus unguiculatus* Ulmer, original designation.

Species composition: *T. bruchianus*, *T. limoncocha* sp. nov., *T. obscuripennis*, *T. parishi*, *T. primus*, *T. puella*, *T. sarae*, *T. spatula* sp. nov.

Adult: fore legs of male normal, remaining legs of male and all legs of female distorted and non-functional. Mesosternum: furcasternal plates approximating each other on basal half (Fig. 54) so furcasternal longitudinal

impression narrow almost entirely, becoming wider only near posterior margin. Female pronotum with anterior ring well developed, at least 1/3 of total length of pronotum. Wings sexually dimorphic, all veins of female thickened; posterior margin of hind wings of female with a reticulated pattern of veinlets. Female fore wing without R_3 and short intercalary vein before it (similar to Fig. 44), in some large females one or both forewings may show 1 or 2 weak veins in this area, but their aspect is different (thinner, weaker) from the other longitudinal veins, as they are formed by the coalescence of few crossveins. Abdomen. Female abdominal sternum VIII with relatively large sublateral parastyli receptors, sockets opening towards the median line of the sternum (Figs. 46, 51). Male genitalia: abdominal sternum IX entire (Fig. 57); large parastyli present, curved dorsally, more than 5 times the length of their bases (pedestals); penes cylindrical, long and slender, completely divided (Fig. 57); apex of penes with a hooked (or rarely blunt) sclerotized spine (Fig. 59). Penial arms formed by a single transverse bar which is articulated to the posterior corners of tergum IX. Forceps two-segmented, basal segment short and small, with a ventral knob (Figs. 57); distal segment long, slender and clublike.

Nymph (for a complete characterization see Molineri 2008): head with prominent frontal ridge (Fig. 96); fronto-clypeal region expanded and concave, extending ventrally beyond mandibular tusks; mandibular tusks long with a large subapical denticle on inner margin (Fig. 96); maxilla with a basal finger like gill. Large filtering setae present on mouthparts and fore legs. Legs modified for burrowing with robust segments and flat tibiae. Fore tibia-tarsus with a prominent distal projection (dorsal projection 2/3 the length of the claw). Abdomen with vestigial unilamellate gill on segment I, gills on segment II–VII normal (large and bilamellate).

Eggs. Hemispherical, bowl-shaped (Figs. 79–80). Length, 355–450 µm; width, 290–375 µm. No polar caps or attachment structures; only one species (*T. spatula* sp. nov.) with a long filament coiled along the main axis of the egg (Figs. 79–80). Chorion with microsculptures consisting of slightly elevated pentagonal and hexagonal cells, or shallow subcircular grooves.

Discussion and diagnosis. The adults of *Tortopsis* gen. nov. can be separated from its sister taxon *Tortopus* by: 1) mesofurcasternal plates approximating each other basally and medially, with inner margins diverging only on distal half (Figs. 45, 54); 2) male abdominal sternum entire (Figs. 57, 73); 3) parastyli very long, more than 5 times the length of pedestals (Figs. 57–58); 4) penes cylindrical at least basally and completely divided (Fig. 57); 5) female fore wing without R_3 and short intercalary before it (Fig. 44), rarely expressed as 1 or 2 weak short veins; 6) parastyli receptors on abdominal sternum VIII relatively large and sublateral in position (Figs. 46–52, 75, 78), openings towards medial line. As mentioned previously, the characters distiguishing *Tortopus* and *Tortopsis* from the other genera of the family are listed in the phylogenetic section (apomorphies of node c). The coupling system in *Tortopsis,* as described in McCafferty & Bloodgood (1989), involves very well developed male parastyli and female sockets.

Tortopsis unguiculatus (Ulmer) New combination

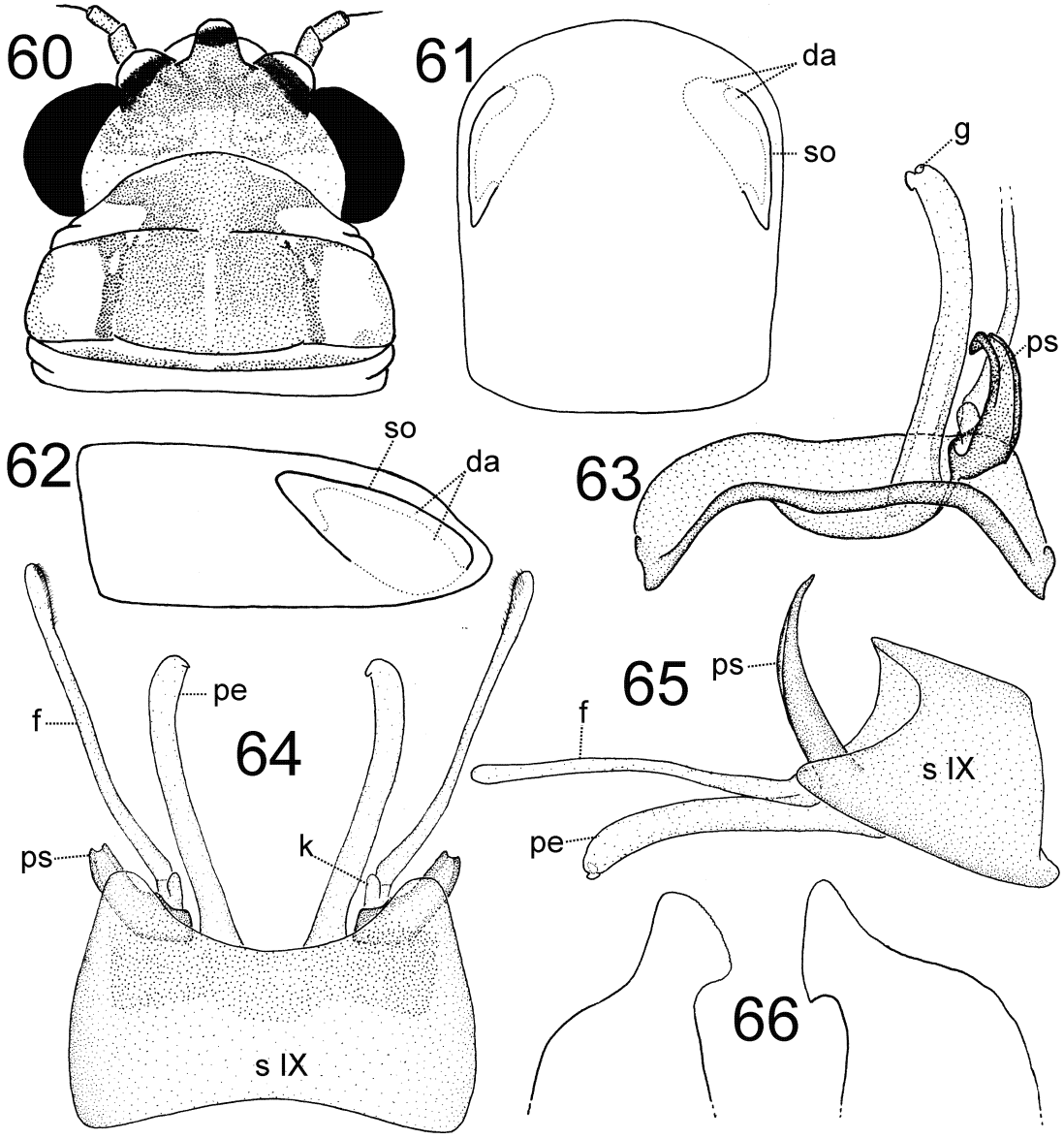
Campsurus unguiculatus Ulmer 1920: 4.
Tortopus unguiculatus; Ulmer 1942: 109; Traver 1950: 600.

Material (ZMH): 3 male labeled “Type”, “Columbien/Behn vend. 3.XII.1900.”, “G. Ulmer determ./1916–1923”.

Male imago. General coloration faint in the old pinned types. Genitalia: long and cylindrical penes completely separated from their bases (Fig. 41); sclerotized spine on inner apical margin with wide rounded base and slightly hooked apex (Fig. 43); parastyli long and acute, markedly curved dorsally, the main axis of the basal third, form a 90° angle with the axis of the distal third (Fig. 42); parastyli conical and entire, not furrowed longitudinally (Fig. 41).

Discussion and diagnosis. Ulmer (1920) described this species from 3 male imagos from Colombia, and later (Ulmer, 1942) provided a description of a female imago from Colombia and cited some male imagos from Reventazón (Costa Rica). Additional records exist for this species in Mexico, Nicaragua (Zelaya) and

Costa Rica (Maés 1988) and Guatemala and Honduras (Lugo-Ortiz & McCafferty 1996), but this material should be revised with the new data offered here to confirm its specific identity. *Tortopsis unguiculatus* can be distinguished from all other species of the genus by: 1) fore wing length 9.0–11.0 mm (male), 11.0–12.0 mm (female); 2) wings hyaline translucent, veins whitish translucent; 3) parastyli long and very strongly curved (Fig. 42); 4) penes cylindrical, apical spine with wide base and a small hook (Fig. 43).



FIGURES 60–66. *Tortopsis spatula*: 60, female head; 61, female abdominal sternum VIII, v.v.; 62, same, l.v.; 63, male genitalia after potash (left forceps and penes omitted); 64, male genitalia, v.v; 65, same, l.v.; 66, details of penes.

Tortopsis bruchianus (Navás) New combination

Campsurus bruchianus Navás 1926: 110.
Tortopus bruchianus; Domínguez 1987: 9.

Material (MACN): lectotype and 2 paralectotypes female adults from Argentina, Córdoba, Alta Gracia, La Granja, 20/I/1924, Bruch col. One paralectotype is pinned, the other females are in alcohol.

Discussion and diagnosis. This species is known only from female imagos, redescribed and illustrated in Domínguez (1987). *Tortopsis bruchianus* can be recognized by: 1) fore wing length 17.5 (18.5–19.0 in Domínguez 1987); 2) wings whitish translucent except longitudinal veins near costal margin shaded purplish brownish on proximal half; 3) female parastylus receptors C-shaped (similar to Fig. 46); 4) head shaded black between ocelli, occiput apparently without dark markings (not well visible); 5) the sublateral pale marks on posterior ring of female pronotum are present but not very visible. *T. bruchianus* is very similar to *T. sarae*, presently they can only be separated by egg color with *T. bruchianus* having orange eggs whereas the eggs of *T. sarae* are yellowish in color.

Tortopsis obscuripennis (Domínguez) New combination

Tortopus obscuripennis Domínguez 1985: 71; Molineri 2008: 10.

Material (IML): holotype and 18 paratypes female imagos from Argentina: Salta, Aguas Blancas, Estancia El Arrayazal, 9-XII-1981, Domínguez col. Other material from Argentina and Bolivia listed in Molineri (2008).

Female imago. Head black between ocelli, with gray anastomosed marks on occiput (some times very slightly marked). Pronotum with anterior ring widely shaded black, and posterior ring shaded grayish black on central area, lateral to this shading there is an isolated narrow gray mark, and also shaded near anterolateral corner. Wings with very dark veins; vein R_3 and short intercalary before it absent in fore wings but some females present a weak vein in zig-zag formed by coalescence of cross veins, with a length of 2 cells. Abdominal terga with thin black medial line, surrounded by a paler grayish band, and more laterally with wide submedian dark bands. Sternum VIII with relatively small C-shaped sockets, with indistinct margin (not sclerotized or pigmented), depression subcircular (Fig. 48).

Egg. Suboval, no attachment structures. Length, 390–410 µm; width, 340–350. The chorionic cover is sculptured with a hexagonal pattern.

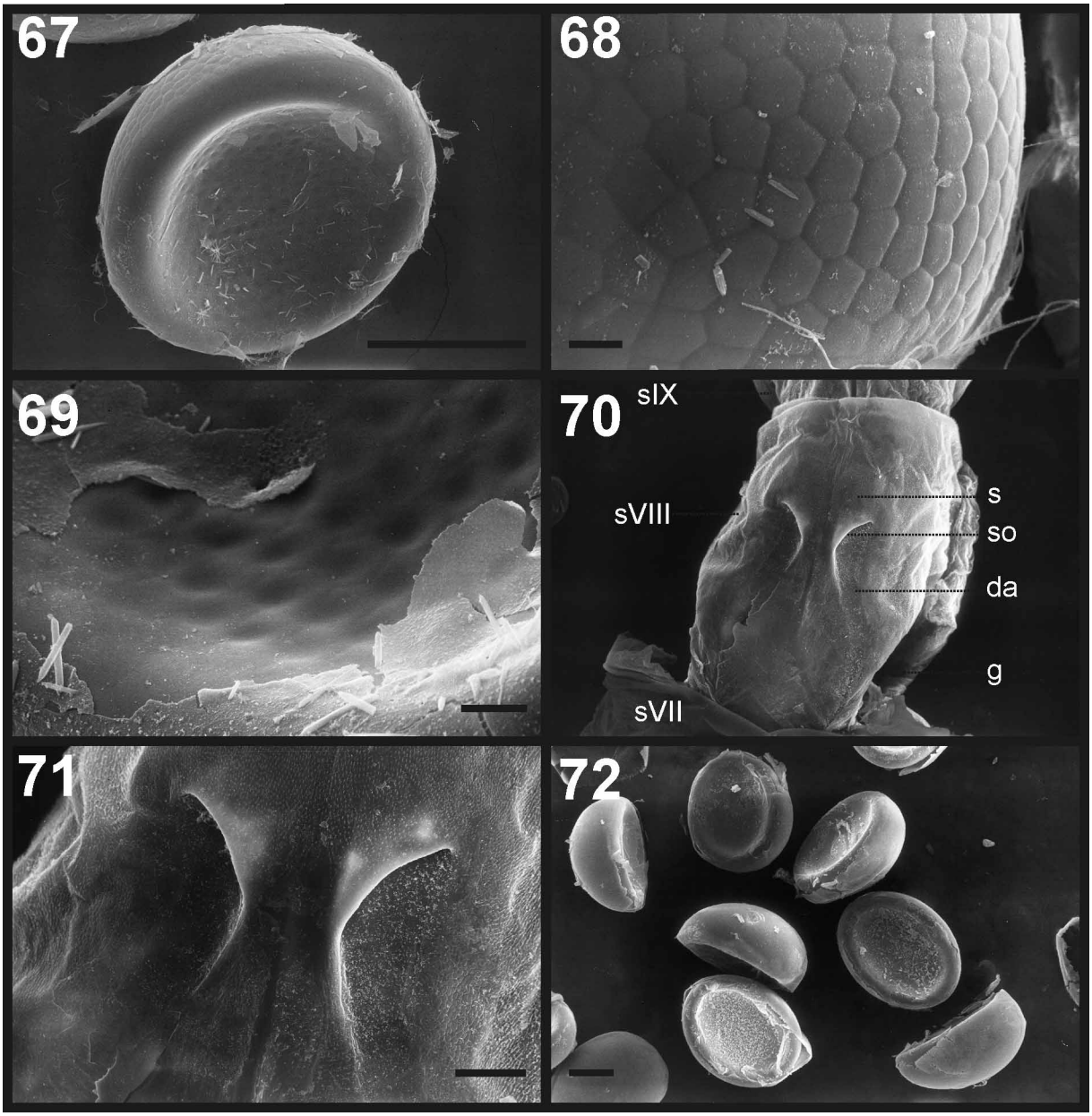
Discussion and diagnosis. This species, originally described from female adults (Domínguez 1985) is currently known from all the stages (Molineri 2008) and has been recorded from Argentina and Bolivia. *Tortopus obscuripennis* can be separated from all other species of the genus by: 1) fore wing length 15.0 mm (male), 19.5–20.5 mm (female); 2) relatively dark wings (membrane translucent), all veins shaded gray; 3) parastyli long and moderately curved; 4) penes abruptly widening in distal half; 5) female parastylus receptors C–shaped (Fig. 48); 6) head shaded black among ocelli, occiput with a finely reticulated grayish pattern; 7) female pronotum with anterior ring widely shaded black, and posterior ring shaded grayish black on central area, lateral to this shading there is an isolated narrow gray mark, and also shaded near anterolateral corner.

Tortopsis parishi (Banks) New combination

Campsurus parishi Banks 1918: 10.
Tortopus parishi; Ulmer 1942: 110.

Material: the only specimen known (male holotype) is deposited at Harvard. In spite of the attempts to borrow the material, neither the specimen nor photographs were available for study.

Discussion and diagnosis. This species is known from one male imago from Ecuador (Durar). The original description and figures are inadequate to species characterization but clearly indicate that this species belongs to *Tortopsis*, as is recovered in the phylogenetic tree (Fig. 1A). The main feature used to assign the species to *Tortopsis* is the form of the penes, widely separated from each other from their bases. Fore wing length is reported to be 10–12 mm (Banks 1918).



FIGURES 67–72. SEM photographs. *Tortopus igaranus*: 67, egg, general view; 68, egg, detail of convex side; 69, egg, detail of concave side. *Tortopus arenales*: 70, female abdominal sternum VIII; 71, same, detail of sockets; 72, eggs.

***Tortopsis primus* (McDunnough) New combination**

Campsurus manitobensis Ide, 1941 (syn.)
Campsurus primus McDunnough, 1924 (orig.)
Tortopus manitobensis (Ide), 1941 (syn.)

Material (FAMU): 2 female adults from USA, Iowa: Cherokee Co., Cherokee, 28-VIII-1953, H. H. Ross col.; and 3 female adults from Illinois, Urbana, 16-VIII-1956, at light, J. Kingsolver col.

Female adult. Length (mm): body, 15.0–16.0; fore wing, 15.0–16.0; hind wing, 7.0; cerci, 5.5. General coloration whitish yellow, pigments very faded (one of the females show some light gray markings described below). Head: with a mediolongitudinal gray line from median ocellus to a transversal V-shaped line between lateral ocelli, remainder completely faded. Thorax: pronotum yellowish with anterior ring shaded gray, and

posterior ring shaded with light gray but pattern not distinguishable. Wings: membrane yellowish white, veins yellowish except those near costa shaded gray. Abdomen: shaded gray dorsally, terga with wide median band darker than the rest, except on tergum I–II paler medially, and thin medial blackish line on terga I–VIII. Sternum VIII with large sockets, the sclerotized margin of the socket reaches the anterior margin of the sternum; anterior and posterior margins of socket diverging each other toward medial line; anterior margin slightly sinuous; the depression delimited by the socket is elongated.

Egg. Suboval, no attachment structures. Length, 390–410 µm; width, 310–330 µm.

Discussion and diagnosis. This species is known from adults of both sexes but no formal description of female was found. Here a short description of the female adult is provided based on the scarce material available. This species is widely distributed in Mexico, USA and Canada (Randolph & McCafferty 2002). *Tortopsis primus* can be separated from all other species of the genus by: 1) fore wing length 12 mm (male), 15.0–16.0 mm (female); 2) wings slightly tinted yellowish white, veins yellowish; 3) parastyli long and moderately curved; 4) penes cylindrical, slender; 5) female parastylus receptors large and with divergent anterior and posterior margins of socket; 6) color pattern very faded, apparently a very pale species.

Tortopsis puella **(Pictet) New combination**

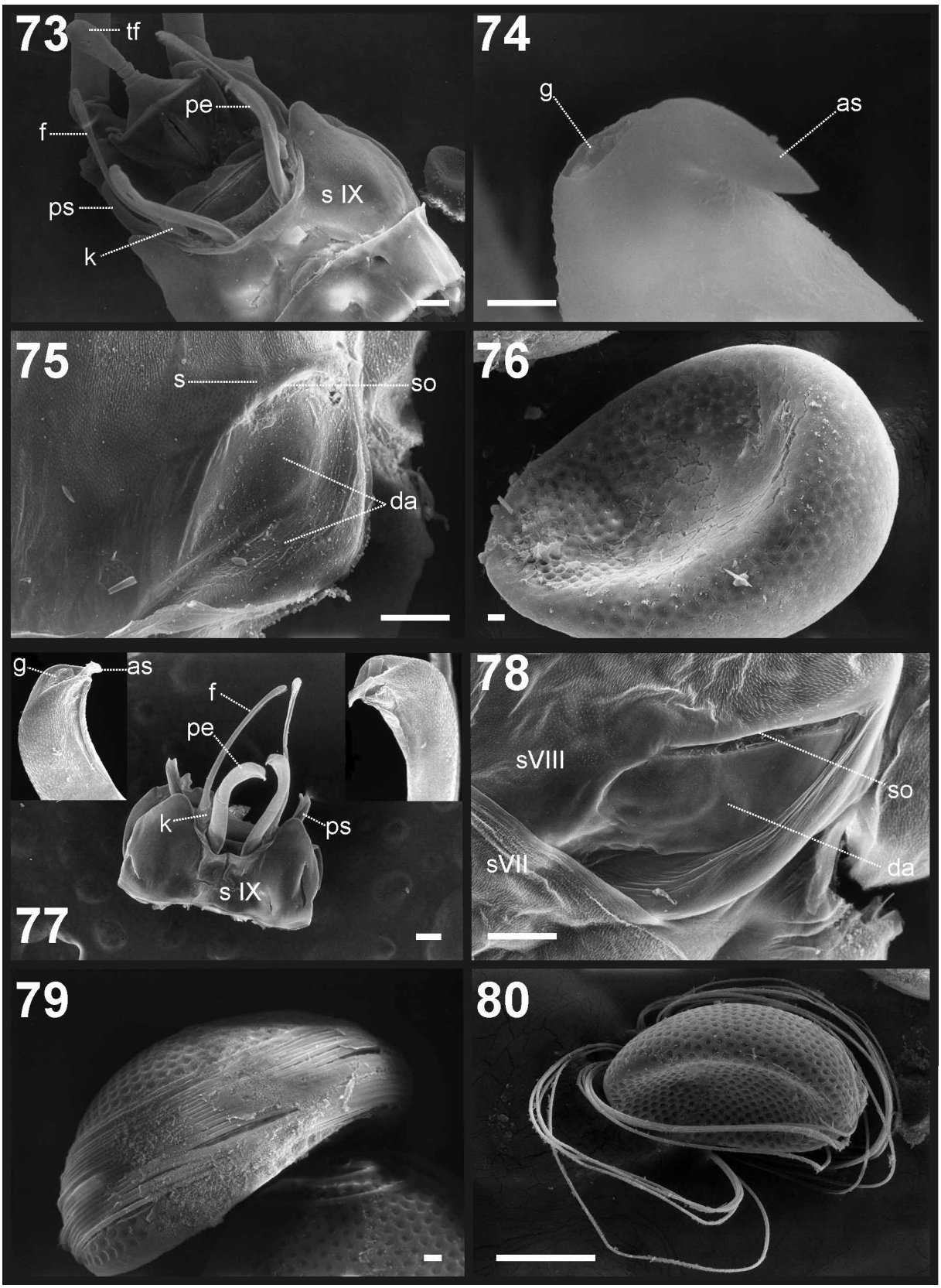
Campsurus puella (Pictet), 1843 (comb.)
Campsurus incertus Traver, in Needham et al. 1935 (syn.)
Palingenia puella Pictet, 1843 (orig.)
Tortopus incertus (Traver), in Needham et al. 1935 (syn.)

Material (IML): 3 male imagos from USA: Florida, Liberty Co., Apalachicola R. at Hwy. 20, Bristol, 5-IX-1972, P.H. Carlson; 7 female imagos same data except date 10-X-1973; 4 male and 6 female imagos same data but no date nor collector.

Female adult. Length (mm): body, 9.0–13.0; fore wing, 12.0–16.0; hind wing, 5.0–6.2; cerci, 5.0–6.0. Head: whitish around median ocellus, blackish between lateral ocelli, occiput with gray anastomosed marks mainly on lateral thirds. Thorax: pronotum with anterior ring widely shaded black, and posterior ring shaded grayish black on central area, lateral to this shading there is an isolated narrow gray mark, and also shaded near posterolateral corner. Wings: membrane whitish hyaline, veins whitish, except those near costa shaded gray; some females show a weak and short (1 cell) vein between R_{2+3} and IR, formed by the coalescence of 2 cross veins. Abdomen: terga with wide median band darker than the rest, except on tergum I whitish medially, and thin medial blackish line on terga III–IX. Sternum VIII with large sockets, the sclerotized anterior margin of the socket is somewhat sinuous (Figs. 50–52) and reaches the anterior margin of the sternum; anterior and posterior margins of socket are more or less parallel; the depression delimited by the socket is elongated.

Egg. Suboval, no attachment structures. Length, 450–490 µm; width, 370–390 µm. The chorion is sculptured with small grooves.

Discussion and diagnosis. This species is known from adults of both sexes and nymphs from SE and SW USA. A short description of the female adult is presented, enumerating those characters useful in separating the female adults of this species from those of other species of the genus. Male adults and nymphs were sufficiently treated elsewhere (Needham et al. 1935, Scott et al. 1959, McCafferty 1975, Molineri 2008). The adult stage of *Tortopsis puella* can be separated by: 1) fore wing length 14.0 mm (male), 12.0–16.0 mm (female); 2) wing veins dark, mainly on basal half and costal margin; 3) parastyli moderately curved; 4) penes cylindrical; 5) female parastylus receptors large, elongated, with sinuous medial margin (Figs. 50–52); 6) female head not shaded black behind median ocellus; 7) female pronotum color pattern similar to other species, but with a gray band near posterolateral corner.



FIGURES 73–80. SEM photographs. *Tortopsis limoncocha*: 73, male genitalia, v.v.; 74, apex of penes, detail; 75, female abdominal sternum VIII, detail of left socket; 76, egg. *Tortopsis spatula*: 77, male genitalia, v.v. and detail of apex of penes; 78, female abdominal sternum VIII, detail of left socket; 79, egg; 80, egg, thread partially uncoiled.

FIGURES 81–86. *Tortopus*, female adults. *T. arenales*: 81, head and pronotum; 82, abdominal sternum VIII. *T. bellus*: 83, head and pronotum; 84, abdominal sternum VIII. *T. igaranus*: 85, head and pronotum. *T. harrisi*: 86, head and thorax.

Tortopsis sarae (Domínguez) New combination

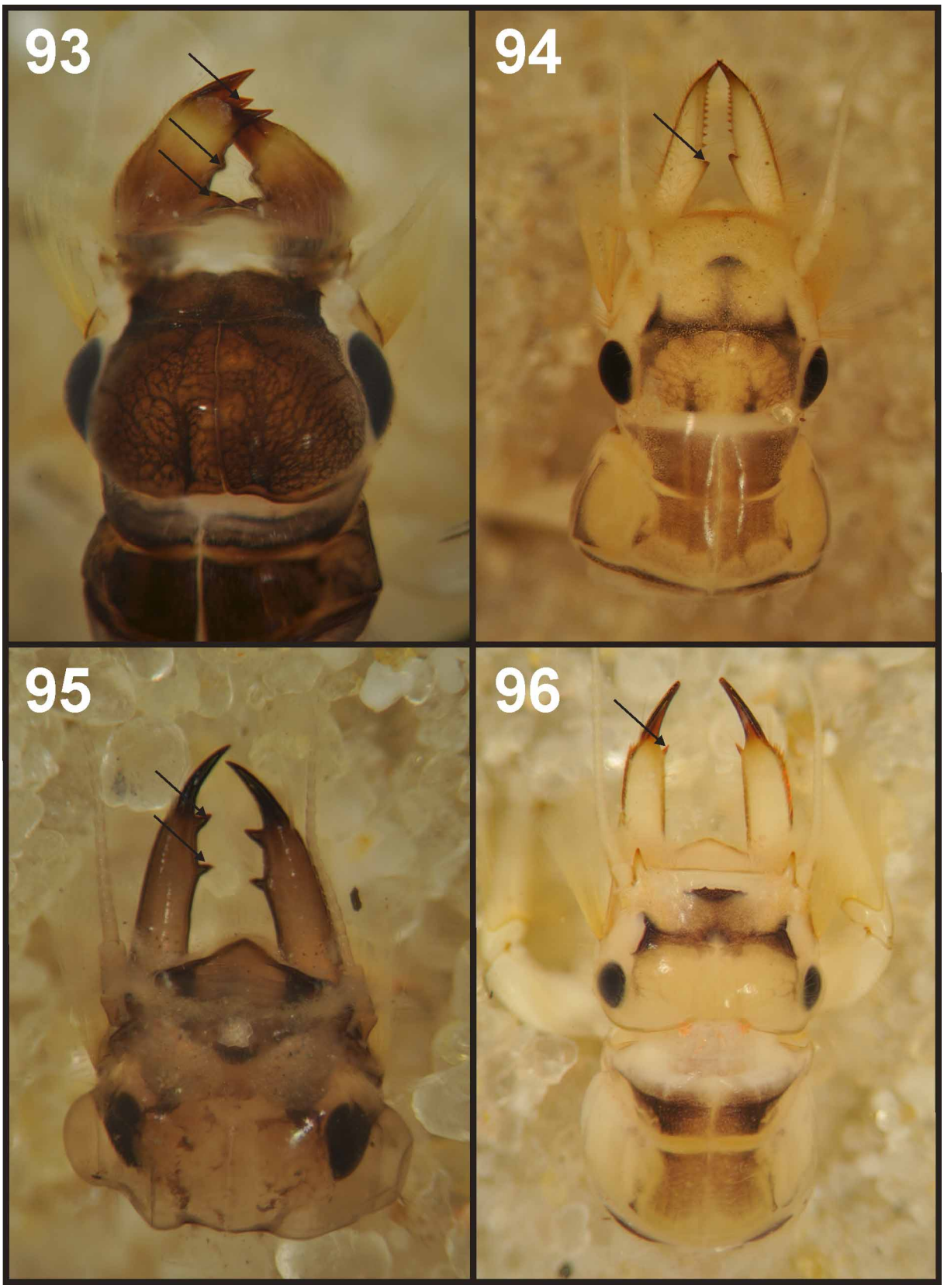
Tortopus sarae Domínguez 1985: 71; Molineri 2008: 13.

Material (IML): holotype and 16 paratypes female imagos from Argentina: Jujuy, 10 km N Ledesma, río Zora, 14-XII-1983, E. Domínguez col. Other material reported in Molineri (2008). New localities: 10 male and 10 female imagos from Argentina: Tucumán, Acheral, río Aranillas, 366 m, S 27º 6' 59.9" - W 65º 27' 43.9", 29-XII-2007, C. Molineri & J. Giordano cols.; 1 reared male adult and 15 nymphs from Argentina: Tucumán, ca. Manuela Pedraza, río Balderrama, 335 m, S 27º 12' 0.6" - W 65º 21' 30.3", 14-XI-2009, C. Molineri col.

FIGURES 87–92. *Tortopsis*, female adults, head and pronotum. 87, *T. bruchianus*; 88, *T. limoncocha*; 89, *T. obscuripennis*; 90, *T. puella*; 91, *T. sarae*; 92, *T. spatula*.

Female imago. Head shaded black between ocelli, occiput without marks. Pronotum with sublateral gray lines not completely separated from the rest of the pigmented area. Furcasternal plates basally contiguous (Fig. 45). Wings: veins C, Sc y R_1 (and membrane in between) shaded with brownish gray, rest of wing whitish. Vein R_3 and short intercalary before it absent in fore wings but some females present a weak vein in zig-zag formed by coalescence of cross veins, with a length of 3 cells or less. Abdominal terga widely pigmented except on sublateral dashes on terga II–VII, black thin median line present on terga I–VIII, tergum IX with a thin pale median line. Sternum VIII with C-shaped sockets (Figs. 46–47).

Egg. Suboval, no attachment structures. Length, 355–375 µm; width, 290–305 µm. The chorionic cover is smooth.



FIGURES 93–96. Polymitarcyidae, nymphal head: 93, *Asthenopus* sp.; 94, *Campsurus* near *violaceus*; 95, *Tortopus harrisi*; 96, *Tortopsis obscuripennis.*

Discussion and diagnosis. *Tortopsis sarae* is currently known from all the stages (Domínguez 1985, Molineri 2008). A short description of the female imago is given to complete its characterization. This species

can be recognized by: 1) fore wing length 13.0–13.5 (male), 17.5–18.0 (female); 2) wings whitish translucent except C and Sc areas brownish; 3) parastyli moderately curved; 4) penes cylindrical; 5) female parastylus receptor C-shaped (Figs. 46–47); 6) head shaded black behind median ocellus, occiput very pale, at most with a small grayish netting near hind margin; 7) female pronotum shaded as in *Tortopsis obscuripennis*.

***Tortopsis limoncocha* sp. nov.**

Material: holotype male imago from Ecuador: Limon Cocha, río Jivino, 250 m, 6-VI-1984, E. Domínguez col.; allotype female imago, and 36 male and 2 female imagos paratypes same data as holotype; 1 male paratype from Ecuador: Coca, 4-IV-1984, E. Domínguez col. All the material in IML except holotype and 3 male paratypes at MECN, 1 male paratype at CUIC and 1 male paratype at FAMU.

Male imago. Length (mm): body, 11.0–11.8; fore wings, 10.5–12.5; hind wing, 4.8–6.0, fore leg, 4.8–5.5; cerci, 28.0–30.0. General coloration yellowish white. Head whitish shaded gray strongly between ocelli, shaded lighter on occiput except pale median area (Fig. 53). Antennae: scape and pedicel whitish shaded gray, flagellum hyaline. Thorax. Anterior ring of pronotum hyaline shaded widely with gray posteriorly, a whitish tranversal line separate it from the posterior ring; posterior ring hyaline becoming whitish laterally, widely shaded gray; hind margin shaded black on a transversal thin line (Fig. 53); propleura and sternum yellowish white. Mesonotum yellowish white shaded gray except on posteromedian membranous area, shaded stronger on carinae and V-shaped mark between posterior scutal protuberances; mesopleura and sternum yellowish white shaded slightly gray on basisternum (in some males, not shaded) and margin of sclerites; furcasternal protuberances with medial margins parallel anteriorly (Fig. 54). Metanotum yellowish white shaded gray medially, pleura and sternum paler, shaded gray medially on sternum. Legs yellowish white shaded gray on fore leg, stronger on tibiae and tarsomeres 1–4, claws pale. Wings membrane hyaline, longitudinal veins whitish translucent shaded gray, stronger on veins Sc and R_1, cross veins pale. Abdomen whitish translucent with a thin medial black line in all terga except I and X; tergum I shaded gray laterally, terga II–VII shaded gray almost completely except on submedial elongated pale marks; terga VIII–X shaded more strongly except submedial and sublateral pale marks on terga VIII–IX. Abdominal sterna shaded gray uniformly (some males not shaded at all) except medial line and paramedian posterior spots, pale; sterna shaded strongly on indentations of nymphal gill muscles; sternum VIII with sublateral blackish longitudinal lines. Genitalia (Figs. 57–59, 73–74): sternum IX completely shaded gray; parastyli yellowish, long and curved at the apex (Fig. 58, 73); forceps and penes whitish translucent shaded light gray on penes, penes divided from the base with strongly sclerotized and distal hook (Fig. 59, 74). Caudal filaments whitish translucent.

Female imago. Length (mm): body, 13.0–15.0; fore wings, 14.0–16.0; hind wing, 6.0–6.5; cerci, 5.0. Similar to male except wing membrane slightly yellowish and longitudinal and cross veins shaded stronger with gray; vein R_3 and short intercalary before it absent. Pronotum without well marked sublateral gray lines, mesosternum with relatively narrow basisternum. Abdominal terga with a pattern similar to males except on terga VIII–IX shaded more widely; the wide median band as dark as the rest. Sternum VIII with lateral C-shaped parastyli receptors (Figs. 55–56, 75), shaded gray on inner margins, depression somewhat elongated.

Eggs. Suboval, one of the sides slightly more pronounced than others, no attachment structures. Length, 385–400 µm; width, 330 µm. Chorion slightly sculptured with hexagonal plates almost entirely, and with shallow grooves on the concave area near the more pronounced pole (Fig. 76).

Etymology: from the type locality, Limon Cocha.

Discussion and diagnosis. *Tortopsis limoncha* sp. nov. can be distinguished by: 1) fore wing length 10.5–12.5 mm (male), 14.0–16.0 mm (female); 2) wings whitish translucent, darker on costal margin and veins; 3) parastyli relatively straight, curved apically (Fig. 58); 4) penes cylindrical (Fig. 57); 5) parastylus receptors C-shaped (Figs. 55–56, 75); 6) head shaded black behind median ocellus, shaded gray on occiput except pale median area; 7) pronotum shaded rather similar to *Tortopsis obscuripennis* and *Tortopsis sarae* but the sublateral isolated gray marks on posterior ring of female pronotum are thinner.

***Tortopsis spatula* sp. nov.**

Material: holotype male imago from Colombia: Depto. Amazonas, Leticia, caño km 11 hacia Tarapacá, S 4º 7' 30" W 69º 57' 25", 93 m, light trap 18–20 h, 28-I-1999, Z, D & M cols. Paratypes: 3 male and 1 female imago same data as holotype; 1 female imago from Leticia, caño km 15 hacia Tarapacá, 93 m, light trap 18–20 h, 10-II-1999, S 4º 5' 41" W 69º 59' 1", Z, D & M cols.; 26 male and 7 female imagos from Colombia: Depto. Amazonas, Parque Nacional Amacayacu, río Amacayacu, 93 m, light trap 18–20 h, 3-II-1999, S 3º 48' 28" W 70º 15' 21", Z, D & M cols.; 1 male from Colombia: Depto. Amazonas, Puerto Nariño, Loreto Yacu, S 3º 44' 26" W 70º 27' 19", light trap 18–20 h, 5-II-1999, Z, D & M cols. Holotype, allotype and 5 paratypes male imagos at MUSENUV; 2 male paratypes at CIUC and 2 male paratypes at FAMU, remaining paratypes at IML.

Male imago. Length (mm): body, 9.0–12.0; fore wing, 9.5–11.2; hind wing, 4.1–5.3; foreleg, 4.2–5.8; cerci, 26.0–33.0. General coloration yellowish white shaded heavily with brownish gray (much lighter specimens were also collected, but the description below is based on those with the better marked color pattern). Head yellowish white shaded widely with gray on dorsum, except around median ocellus, shaded stronger between lateral ocelli (similar to Fig. 60). Antennae: scape and pedicel yellowish white completely shaded with gray, flagellum hyaline. Thorax. Pronotum with anterior ring relatively long, strongly shaded with gray dorsally; posterior ring shaded gray except on sublateral areas. Mesonotum whitish yellow shaded widely with gray along medioparapsidal sutures and medial line, and shaded with black on a V-shaped mark between posterior scutal protuberances. Metanotum whitish yellow shaded gray except laterally. Thoracic pleura and sterna whitish yellow, darker on carinae; metasternum shaded with gray in the middle. Legs yellowish white shaded with grayish on fore femur, tibia and first tarsal segment, rest of leg shaded much lighter; middle and hind legs yellowish shaded gray except tarsi whitish. Wings. Membrane hyaline, longitudinal and cross veins translucent shaded slightly with brownish. Abdomen. Tergum I shaded widely with brownish gray except medial band, terga II–VIII shaded more extensively but with a pair of submedian pale marks increasing in size towards rear segments, also with a pale oblique dash laterally; terga IX–X shaded more strongly, IX with pale marks submedially near fore margin and laterally, the lateral pale marks are surrounded with black. Abdominal sterna shaded widely with brownish gray except on pair of submedian spots and along medial and sublateral thin bands. Genitalia (Fig. 63–66, 77): sternum IX shaded very strongly in posterior margin; large parastyli orangeish, curved dorsally and with a longitudinal ventral furrow along its entire length (Fig. 63–65, 77); forceps and penes translucent yellowish white, shaded slightly gray on second forceps segment; spine at apex of penes blunt, semicircular (Fig. 66, 77). Caudal filament whitish translucent.

Female imago. Length (mm): body, 11.0–14.0; fore wing, 12.4–15.2; hind wing, 5.2–6.5; cerci, 4.5–5.5. General coloration as in male but more strongly marked, eggs yellowish white. Head black between ocelli, with gray anastomosed marks on occiput (Fig. 60). Pronotum with wide sublateral gray band, not well distinguished from the remaining gray marks (Fig. 60). Wings membrane hyaline slightly tinged with yellow, veins more strongly shaded with brownish. Abdomen shaded uniformly with gray on terga, except on sublateral pale dashes. Sternum VIII with V-shaped parastyli receptors on sternum VIII (Figs. 61–62, 78), margin of socket weakly sclerotized, depression elongated.

Egg (Figs. 79–80). Suboval, with a long thread coiled around the convex area of the egg. Length, 330–375 µm; width, 270–300 µm. The entire surface is covered by well marked subcircular grooves.

Observations. The specimens from Amacayacu are very pale, the color pattern is the same but much less marked dorsally, and almost completely absent ventrally.

Etymology. From the latin "spatula", meaning spoon, an allusion to the flat and thin shape of penean apical spine.

Discussion and diagnosis. *Tortopsis spatula* sp. nov., known from imagos of both sexes, can be distinguished from all other species of the genus by: 1) fore wing length 9.5–11.2 mm (male), 12.4–15.2 mm (female); 2) pale wings, veins translucent hyaline; 3) parastyli moderately curved, with a longitudinal ventral furrow (Fig. 63–65, 77); 4) apical spine of penes rounded and flattened (Figs. 66, 77); 5) female parastyli receptors with V-shaped sockets (Figs. 61–62, 78); 6) head shaded black behind median ocellus, occiput with

gray anastomosed marks (Fig. 60); 7) female pronotum as described in *Tortopsis obscuripennis* but the sublateral gray mark is broad and not completely isolated from the main central shading (Fig. 60). The form of the penean spine suggests a close relationship with *T. unguiculatus*, as recovered in shortest phylogenetic trees with the reduced data set (Fig. 1B).

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Appendix 1. List of characters and states

{0 Fore wings, number of intercalary cubital veins (Kluge 2004): state 0= four or more, small and sigmoid; state 1= two located just on or posteriorly to tornus of wing; state 2= two, one anterior and one posterior to tornus.

{1 Fore wings, vein CuA (Kluge 2004): state 0= smoothly curved or sigmoid only on basal 1/4; state 1= markedly sigmoid.

{2 Female wing veins (Traver, 1950): state 0= normal (as thick as in male); state 1= thickened.

{3 Female hind wing anal sector: state 0= normal (some cross veins may be present) state 1= anastomosed (Fig. 16);

{4 Female fore wing veins on R sector: state 0= R_2, IR, R_3, and at least two intercalaries present; state 1= R_2, IR, a somewhat reduced R_3, and a short intercalary present (Fig. 8); state 2= without longitudinal or intercalary veins between IR and R_1 (some fused crossveins may be present, forming 1 or 2 short attached marginal intercalaries)(Fig. 44);

{5 Female parastyli receptors on abdominal sternum VIII: state 0= absent; state 1= single; state 2= paired.

{6 Female parastyli receptors (form): state 0= C or V shaped (Figs. 73, 76); state 1= U-shaped (Figs. 68–69); state 2= bottle-like.

{7 Female parastyli receptors, sockets´ opening towards: state 0= anterior margin (Figs. 73, 76); state 1= median line (Figs. 68–69).

{8 Female parastyli receptors with long furrows anterior to sockets: state 0= no (Figs. 73, 76); state 1= yes (Figs. 68–69).

{9 Legs of imagos of both sexes (except male forelegs): state 0= weak; state 1= distorted; state 2= flap or fin-like.

{10 Mesosternum, furcasternal protuberances: state 0= contiguous; state 1= contiguous on basal 1/3 (Fig. 52); state 2= contiguous only on basal corner (Fig. 4); state 3= separated.

{11 Male genitalia, number of forceps segments (without pedestals): state 0: three segments; state 1= two segments; state 2= one segment.

{12 Male genitalia, styliger formed by: state 0= median plate and pedestals; state 1= only pedestals.

{13 Male genitalia, pedestals: state 0= normal (subquadrate, without distal projections); state 1= inner projected; state 2= outer projected, projection lateral and blunt; 3= outer projected, projection dorsal and pointed.

{14 Male genitalia, pedestal muscles (Kluge 2004): state 0= present; state 1= absent.

{15 Male genitalia, articulation of penial arms (Kluge 2004): state 0= ninth abdominal tergum; state 1= ninth abdominal sternum and pedestals.

{16 Male genitalia, gonopore: state 0= associated with a claw-like structure (Fig. 72); state 1= associated with a sclerotized margin (Fig. 2); state 2= other form or not associated with any sclerotized structure.

{17 Male genitalia, penes (apical claw-like structure): state 0= slightly becoming thinner (Fig. 72); state 1= with wide base, then abruptly thin or blunt (Figs. 43, 64).

{18 Male genitalia, penes (general structure): state 0= flat and apically divided structure; state 1= same, added cylindrical subdistal *finger* (main portion of the penes of Asthenopodinae-Campsurinae); state 2= same but finger more complex, with two or three additional lobes.

{19 Male genitalia, fusion of penes: state 0= separated (Fig. 55); state 1= fused on basal 1/5 or less (Fig. 2); state 2= fused on basal 1/2 or more.

{20 Male genitalia, penes (form): state 0= short and cylindrical, curved ventrally; state 1= cylindrical (Fig. 55), straight; state 2= cylindrical and straight, with wide flat apex; state 3= entirely flattened (Fig. 2).

{21 Male genitalia, parastyli length: state 0= parastyli absent; state 1= shorter or subequal to pedestal (Fig. 12); state 2= >2 but <3 times length of pedestals (Fig. 2); state 3= >5 times length of pedestals (Fig. 63).

{22 Male genitalia, parastyli curvature in lateral view: state 0= straight (Figs. 2, 12); state 1= curved on apical 1/4 (Fig. 56); state 2= smoothly curved from base (Fig. 63); state 3= strongly curved (Fig. 42).

{23 Male genitalia, knob at forceps base (Fig. 22): state 0= absent; state 1= present.

{24 Male genitalia, ninth abdominal sternum: state 0= entire, a median line may be present (Fig. 55); state 1= almost separated in two portions by a median notch (Fig. 2).

{25 Egg, form: state 0= entire (ovate to subquadrate); state 1= bowl-shaped.

{26 Egg, number of polar caps: state 0= none; state 1= one cap; state 2= two caps.