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Tasmanitachoides belongs to Trechini (Coleoptera : Carabidae): discovery of the larva, its phylogenetic implications and revised key to Trechitae genera

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Abstract. This study is aimed at solving the long-standing ambiguity about the phylogenetic placement of the Australian ground-beetle genus *Tasmanitachoides*. A recently published phylogeny of the supertribe Trechitae using morphological characters of larvae is re-examined in light of new discoveries. The results of the phylogenetic analysis of 65 informative characters for 36 taxa reject the previously maintained opinion of affinities between *Tasmanitachoides* and Tachyini. Instead it is hypothesised that the genus is a member of the monophyletic tribe Trechini and most likely belongs to the Trechodina radiation, represented in the analysis by the genera *Perileptus* and *Thalassophilus*. Older-instar larvae of *Tasmanitachoides*, *Kenodactylus* and *Mioptachys*, as well as the first-instar larva of *Pachydesus*, are described. An updated identification key to all analysed Trechitae genera is provided.

Additional keywords: Australia, immature stages, *Kenodactylus*, *Mioptachys*, *Pachydesus*, Trechodina.

Introduction

The carabid supertribe Trechitae is a well supported monophyletic group of ground beetles comprising ~5500 species worldwide. Most of the species are 2–10 mm in body length in both adult (Fig. 1*A*, *C*) and larval stages (Fig. 1*D*) and all are believed to be active predators. The supertribe includes a few tribes, some of which are ranked at the subtribal level by some authors, and the number and concepts of which vary markedly depending on the authority. Most commonly, the following tribes are recognised, each of them having ten or more genera and distributed in more than one zoogeographical region: Trechini, Zolini, Pogonini, Bembidiini, Tachyini and Anillini; the latter possibly including the bizarre monotypic *Horologion* Valentine, 1932 from North America (Erwin 1982). Grebennikov and Maddison (2005) published recently a detailed discussion on the supertribe's composition and distribution.

The relationships of *Tasmanitachoides* Erwin, 1972, a genus that includes 16 species living in sandy or gravel shores of small and medium-sized rivers in mainland Australia and Tasmania (Baehr 2001), are intriguing. The genus was erected to accommodate the species of the '*hobarti*' group of the poorly defined genus *Tachys* Dejean, 1821. Erwin (1972: 18) originally mentioned that adults of *Tasmanitachoides* 'show similarities to the trechines, but. . . . .these characters indicate an old lineage surviving in an old but stable habitat, and maintaining certain characteristics of an early 'trechine–bembidiine stock'. Up to now, the genus has been treated as an aberrant tachyine, partly because the first few known species were assigned to the genus *Tachys* (see Darlington 1962), and partly because the adults have the apical maxillary palpomere markedly shortened like members of the tribe Tachyini (Erwin 1972). On the other hand, adults of *Tasmanitachoides* markedly resemble those of the tribe Trechini, particularly those of the genus *Perileptus* Shaum, 1860, which, incidentally, have the apical maxillary palpomeres markedly shortened as well. Each time the genus *Tasmanitachoides* has been discussed, comments have been made on the peculiar 'trechine' appearance of the beetles (Baehr 1990, 2001) and the similarities with *Perileptus* have been considered to be the result of convergence and possible plesiomorphic adaptation to life on gravelly river banks (Baehr 2003).

David R. Maddison (personal communication) has informed me that his preliminary DNA analysis showed that *Tasmanitachoides* is a member of the Trechini rather than the Tachyini or Bembidiini. Recently, a putative larva of *Tasmanitachoides* was found in southern Queensland, Australia, and provides the opportunity to test the DNA-based hypothesis using larval characters. This study gives a description of the larva of *Tasmanitachoides* and incorporates data from some new and poorly known Trechitae taxa (*Kenodactylus* Broun, 1909, *Pachydesus* Motschulsky, 1864, *Jeannelius* Kurnakov, 1959) that were not included in Grebennikov and Maddison's (2005) morphological dataset. The main aim of the present study is to re-analyse Trechitae phylogeny based on the larval morphological characters in an attempt

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to resolve a long-standing controversy about the phylogenetic affinities of *Tasmanitachoides*.

Material and methods

The morphological matrix used for this work derives from that of Grebennikov and Maddison (2005) with additions and corrections (see Appendix 1). An identification key to all Trechitae genera is also based on the one given in the same publication with addition of the newly described taxa (Appendix 2). In some analysed taxa, larvae of all three instars were not available and, therefore, which characters are present in all or only some larval instars had to be assessed; this was done by observing patterns of morphological modifications among instars in larvae of the majority of analysed species and then hypothesising that the same pattern would hold true throughout all analysed taxa. The complete matrix in Hennig86/Nona format is available from the author and is supplied as Accessory Material alongside this paper on the *Invertebrate Systematics* website. The matrix was edited using Winclada 1.00.08 (Nixon 2002**)**. The most parsimonious trees were searched for in Hennig86 (Farris 1988) using two commands: 'mhennig*' (constructing of several trees and then applying branch-swapping), followed by 'bb*' (additional branch-swapping of the shortest trees). Bootstrapping was calculated using Nona 2.0 (Goloboff 1999) with at least 1000 random replications.

Assumptions on character transformations were treated in two ways: (1) all multistate characters, including number of claws, are unordered and fully reversible; and (2) multistate characters 29, 52, 53, 55, 56, 57, 66 and 69 are ordered and fully reversible. Treating character 29 (reduction of number of claws from two to one) as reversible is an implausible assumption from a biological point of view; this was done to test whether such an improbable hypothesis will be required by character optimization on the most parsimonious tree (MPT). Characters 21, 43, 44 and 54 were excluded from the analyses as parsimoniously uninformative. Most parsimonious reconstructions of character evolution were analysed using Winclada 1.00.08 (Nixon 2002).

Methods of handling larvae as well as terms related to larval morphology and chaetotaxy are the same as in Grebennikov and Maddison (2005).

Taxonomy

Tasmanitachoides rufescens Baehr, 1990

(Figs 1*A*, *B*, 2)

Material examined

1 L?3, Australia, Queensland, Burnett River, Gray's waterhole, 10.v.2003, G. Monteith and V. Grebennikov leg. (Canadian National Collection of

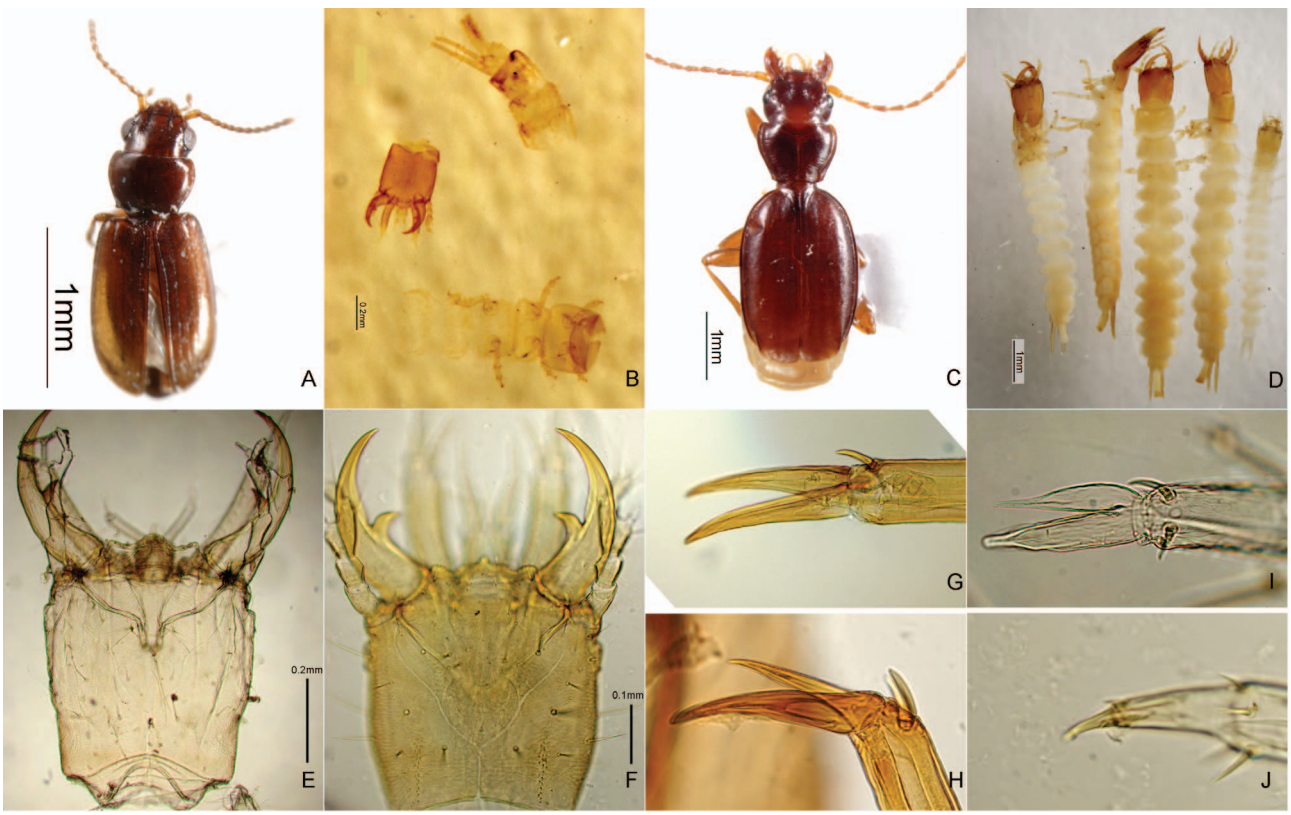

Fig. 1. Trechitae (*A–F*, *H–J*) and Patrobitae (*G*) beetles (Coleoptera : Carabidae). (*A*) *Tasmanitachoides rufescens*, adult, habitus, dorsal; (*B*) *T. refescens*, disarticulated larva; (*C*) *Kenodactylus audouini*, adult, habitus, dorsal; (*D*) *K. audouini*, one second- (on the right) and four third-instar larvae, habiti; (*E*) *K. audouini*, third-instar larva, head, dorsal; (*F*) *Pachydesus bohemani*, first-instar larva, head, dorsal; (*G*) *Diplous aterrimus* Dejean, 1828, larva, two equal claws; (*H*) *Amblistogenium minimum* Luff, 1972, larva, larger anterior and smaller posterior claws freely joining each other; (*I*) *K. audouini*, larva, larger anterior and smaller posterior claws fused at base; (*J*) *Mioptachys flavicauda*, larva, single claw.

Insects, Arachnids and Nematodes, Ottawa: CNC). This larva, together with other invertebrates, was floated from the river bank sand in a bucket of water, then scooped by a net, brought a day later to the Entomology laboratory of the Queensland Museum and extracted from the debris using Berlese funnel. An attempt to rear *Tasmanitachoides* larvae from many adults kept in captivity for some 20 days was not successful.

Diagnosis

Among the few two-clawed Trechitae older-instar larvae known, those of *Tasmanitachoides* may be distinguished by the combination of antennomere 2 having no setae and serrate terebra on mandibles (Fig. 2*A*). Moreover, the following character states of the older-instar *Tasmanitachoides* larva are unique within both supertribes Trechitae and Patrobitae: apical labial palpomere divided in two pseudosegments (versus entire or

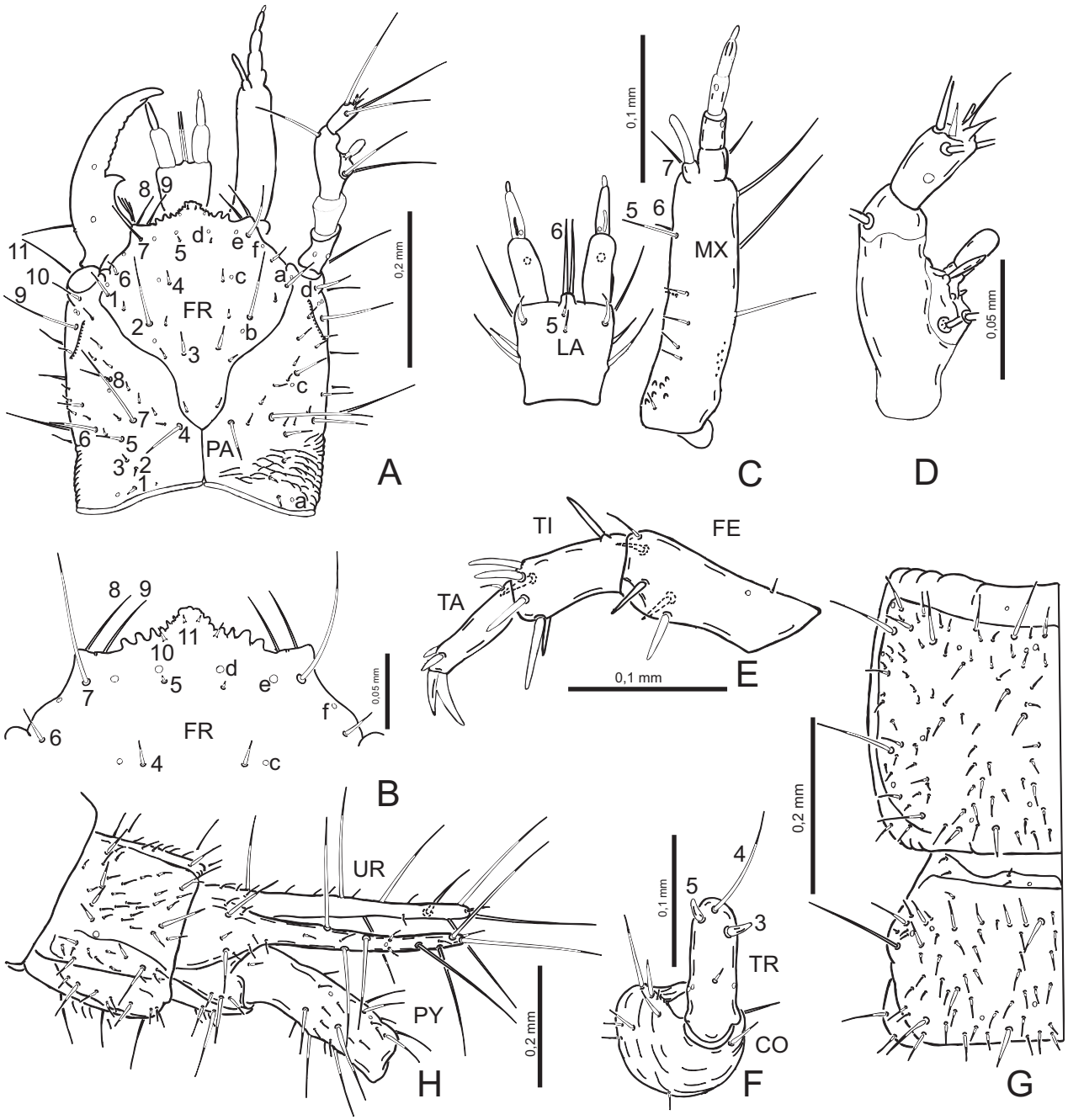

Fig. 2. Third-instar larva of *Tasmanitachoides rufescens*, details. (*A*) Head (right mandible, left antenna, and left maxilla are omitted), dorsal view; (*B*) nasale, dorsal view; (*C*) labium and right maxilla, dorsal view; (*D*) two distal right antennomeres, dorsal view; (*E*) pro- and mesonotum, left half, dorsal view; (*F*) claws, tarsus, tibia and femur of left hind leg, posterior view; (*G*) trochanter and coxa, ventral and lateral views respectively; (*H*) abdominal segments VIII, IX (with urogomphi) and X (with pygidium), left lateral view. Chaetotaxy system follows Bousquet and Goulet (1984).

divided in three pseudosegments); seta MX7 on basal maxillary galeomere as long as apical maxillary galeomere; and setae TR3 and TR5 on trochanter transformed into stout spines.

Description

Characters present in all instars

Spindle-like setae on body absent; no stemmata; number of setae/pores CI1 in anterior angles of epipharynx not recognisable on the single available larva; frontal suture sinuate; pore FRa on frontale present; pore PAb on parietale absent; ratio distances FR2–FR3 to FR1–FR2 ~1; ratio distances FR3–FR4 to FR4–FR5 ~1.5; seta FR6 on frontale located at lateral margins; basal antennomere with five pores; antennomere 2 of normal size; antennal fossa separated from pleurosoma by weak membrane; lateral surface of penultimate antennomere above base of sensorium sclerotised; penicillus present; terebra with ~6–7 rounded teeth along mesal edge; retinaculum of normal size; seta MD2 on mandible much shorter than retinaculum; apical labial and maxillary palpomere each subdivided into two pseudosegments; lacinia absent; base of stipes with ~5–6 teeth on dorsal surface; pore MXc located in distal quarter of stipes; apical galeomere ~4 times as long as basal; setae MX7 long, about as long as apical galeomere; seta MX6 half as long as MX5; setae MX11 and MX12 shorter than quarter of width of maxillary palpomere 3; seta LA6 on ligula conical; seta LA4 on labium present, seta LA5 on labium present, located on ligula close to seta LA6; legs with two claws; posterior claw about two-thirds length of anterior; both claws free, not joined together at their bases, thus they can change their position relative to each other; anterior claw without hyaline structure on dorsal surface; short and conical single claw seta attached at base of claw; setae TA3–6 absent; seta TA1 on tarsus located in basal third; setae TI1 and TI2 not longer than other apical setae on tibia; setae TR3 and TR5 markedly widened and transformed into stout spines; pores PRc, PRe, PRg, PRi on prothoracic tergum absent and pore PRh present; pores MEd, MEe on meso- and metathoracic terga absent; pore TEb on abdominal terga 1–8 absent; seta UR3 on urogomphi located near UR2 (Fig. 2*H*).

Characters restricted to first-instar larvae

Unknown.

Characters restricted to older-instar larvae

Head width 0.335 mm ($n = 1$). Epicranial suture present; ocular groove present; secondary setae on frontale absent; antennomere 2 without setae; stipes with gMX consisting of five setae: one seta at base and four at middle; galea as long as two proximal maxillary palpomeres; tarsus, tibia and femur without secondary setae; abdominal ventrites I–IX without secondary pores on each side near seta ST1; urogomphi with seven long setae; lateral sides of tergum IX without long secondary seta; seta URα long.

Remarks

The larva upon which the description is based was collected in association with ~15 adults of *Tasmanitachoides rufescens* Baehr, 1990, five adults of *Perileptus* sp., and five adults of *Elaphropus* sp. The larva obviously belongs to neither *Perileptus* nor *Elaphropus*, both genera being adequately known in their larval stage (Grebennikov and Luff 1999; Grebennikov and Maddison 2000), leaving *Tasmanitachoides* as the most likely genus.

Kenodactylus audouini (Guérin-Méneville, 1830)

(Fig. 1*C–E*)

Material examined

2L3, 1L2, New Zealand, Campbell Island, high water margin, 14.i.1969, G. Kuschel leg. (CNC). These larvae were previously studied and described by Johns (1974).

Diagnosis

Older-instar larvae of *Kenodactylus* are unique within the supertribe by the combination of two tarsal claws and absence of setae URα on the urogomphi.

Description

Characters present on all instars

Spindle-like setae on body absent; three partly amalgamated stemmata in anterior row and apparently one only posteriorly; seta CI1 in anterior angles of epipharynx single; frontal suture sinuate; pore FRa on frontale present; pore PAb on parietale present; ratio distances FR2–FR3 to FR1–FR2 ~1; ratio distances FR3–FR4 to FR4–FR5 ~1.5; seta FR6 on frontale located markedly mediad from lateral margins; basal antennomere with five pores; antennomere 2 of normal size; antennal fossa separated from pleurosoma by weak membrane; lateral surface of penultimate antennomere above base of sensorium sclerotised; penicillus present; terebra without teeth along mesal edge teeth; retinaculum of normal size; seta MD2 on mandible much shorter than retinaculum; apical labial and maxillary palpomeres not divided into pseudosegments; lacinia absent; base of stipes without teeth on dorsal surface; pore MXc located in distal quarter of stipes; galeomeres subequal in length; setae MX7 short, not longer than diameter of basal galeomere; seta MX6 as long as MX5; setae MX11 and MX12 shorter than quarter of width of maxillary palpomere 3; seta LA6 on ligula conical; seta LA4 on labium present, seta LA5 on labium present, located on ligula close to seta LA6; legs with two claws; posterior claw about three-quarters length of anterior; both claws joined together at their bases thus unable to change their position relative to each other; anterior claw without hyaline structure on dorsal surface; short and conical single claw seta attached at base of claw; setae TA3–6 absent; seta TA1 on tarsus located in basal third; setae TI1 and TI2 not longer than other apical setae on tibia; setae TR3 and TR5 not widened and not transformed into stout spines; pores PRc, PRe, PRg, PRi on prothoracic tergum absent and pore PRh present; pores MEd, MEe on meso- and metathoracic terga absent; pore TEb on abdominal terga 1–8 absent; seta UR3 on urogomphi located near UR2.

Characters restricted to first-instar larvae

Unknown.

Characters restricted to older-instar larvae

Head width 0.620 mm (L2, $n = 1$) and 0.860–0.890 mm (L3, $n = 2$). Epicranial suture present; ocular groove present; secondary setae on frontale present; antennomere 2 with secondary seta; stipes with gMX consisting of 10–12 setae; galea as long as two proximal maxillary palpomeres combined; tibia and femur with secondary setae; abdominal ventrites I–IX without secondary pores on each side near seta ST1; urogomphi with seven long setae; lateral sides of tergum IX with long secondary seta; seta URα absent.

Remarks

No larval autapomorphies are known for *Kenodactylus*.

Pachydesus bohemani (Jeannel, 1926)

(Fig. 1*F*)

Material examined

1L1, *ex ovo*, obtained from adults collected in South Africa, Knysna, Karatara river, 6.viii.2002, V. Grebennikov leg. (CNC).

Diagnosis

I am unable to find structural character states in the sole first-instar larva of *Pachydesus* available that would easily characterise this genus in its larval stage; see identification key in Appendix 2.

Description

Characters present on all instars

Spindle-like setae on body absent; stemmata present, partly merged; anterior angles of epipharynx with one seta CI1; frontal suture sinuate; pore FRa on frontale present; pore PAb on parietale absent; ratio distances FR2–FR3 to FR1–FR2 less than 1; ratio distances FR3–FR4 to FR4–FR5 1.5–2; seta FR6 on frontale located at lateral margins, markedly long with its apex reaching and exceeding anterior edge of frontale; basal antennomere with five pores; antennomere 2 of normal size; antennal fossa separated from pleurosoma by weak membrane; lateral surface of penultimate antennomere above base of sensorium sclerotised; penicillus present; terebra without teeth; retinaculum of normal size; seta MD2 on mandible much shorter than retinaculum; apical labial and maxillary palpomeres not subdivided; lacinia absent; base of stipes without teeth; pore MXc located in distal quarter of stipes; apical galeomere ~1.5 times as long as basal; seta MX6 to MX5 of equal size; setae MX11 and MX 12 shorter than quarter of width of maxillary palpomere 3; seta LA6 on ligula conical; seta LA4 on labium present, seta LA5 on labium present, located on ligula close to seta LA6; legs with two claws; posterior claw less then half length of anterior; both claws joined together at their bases thus they cannot change their position relative to each other; anterior claw without hyaline structure on dorsal surface; short and conical single claw seta attached at base of claw; setae TA3–6 absent; seta TA1 on tarsus located in basal third; setae TI1 and TI2 not longer than other apical setae on tibia; pores PRc, PRe, PRg, PRi on prothoracic tergum absent and pore PRh present; pores MEd, MEe on meso- and metathoracic terga absent; pore TEb on abdominal terga 1–8 absent; seta UR3 on urogomphi located near UR2.

Characters restricted to first-instar larvae

Head width 0.410 mm ($n = 1$). Frontal arms weakly or not sinuate, more or less V-shaped; epicranial stem present; egg-bursters absent on frontale and parietale; group gMX on stipes with 13 setae; teeth on coxa absent; sensillum EM1 on prothorax as seta; sensillum ES1 on mesothorax as four pores; sensillum ES1 on metathorax absent; sensillum EM1 on mesothorax as pore; sensillum EM1 on metathorax as pore; sensillum EP1 on IX abdominal segment as four pores.

Characters restricted to older-instar larvae

Unknown.

Remarks

The following character states of older-instar *Pachydesus* larvae are unique within both supertribes Trechitae and Patrobitae and represent putative autapomorphies of this genus: seta FR6 on frontale markedly long, with its apex reaching and exceeding anterior edge of frontale (L1); parietal sclerite with a longitudinal row of ~25 microteeth on each side more or less parallel and mesad to row of setae PA1–3 (L1); epipleurites of abdominal segments I–VIII with setae EP1, EP2, and one additional seta (L1); and sensillae ES1 on mesothorax and EP1 on abdominal segment IX each represented by a group of four (not just one) pores.

Mioptachys flavicauda (Say, 1823)

(Fig. 1*J*)

Material examined

2L?3, Canada, Quebec, Oka, under bark of *Pinus strobus*, S. Laplante leg. (CNC).

Diagnosis

Older-instar larvae of *Mioptachys* can be immediately distinguished from all other known Trechitae larvae by their complete lack of epicranial suture.

Description

Characters present in all instars

Apical galeomere ~5 times as long as its maximal width. See Grebennikov and Maddison (2000) for first-instar character states of *Mioptachys*.

Characters restricted to older-instar larvae

Head width 0.341 and 0.343 mm ($n = 2$). Epicranial suture absent; ocular groove present; secondary setae on frontale absent; antennomere 2 without setae; stipes with gMX consisting of six setae: two setae at base, three at middle and one near seta MX5; galea as long as two proximal maxillary palpomeres; tibia, tarsus and femur without secondary setae; terga with very few secondary setae; abdominal ventrites I–IX with 2–3 secondary pores on each side near seta ST1; urogomphi with six long setae; lateral sides of tergum IX without long secondary seta; seta URα long.

Remarks

The two larvae were collected together with the adults of *Mioptachys flavicauda* under the bark of a tree. Since these larvae did not belong to the genus *Tachyta*, the only other subcortical trechine genus in the region, and since they closely resemble first-instar *Mioptachys* larvae (Grebennikov and Maddison 2000), there is little doubt that they belong to this genus, which has only one species in Canada.

The lack of epicranial suture in older-instar larvae is unique to *Mioptachys* within both supertribes Trechitae and Patrobitae.

Jeannelius birsteini Ljovuschkin, 1956

Diagnosis

Markedly produced nasale and with two large lateral apices (Makarov and Koval 2003, figs 3, 4) is the most characteristic larval feature of this genus to distinguish it from other similar-looking Trechitae larvae.

Remarks

Makarov and Koval (2003) recently provided a detailed and extensively illustrated description of older-instar larvae of this cave-dwelling beetle from the western Caucasus. This published

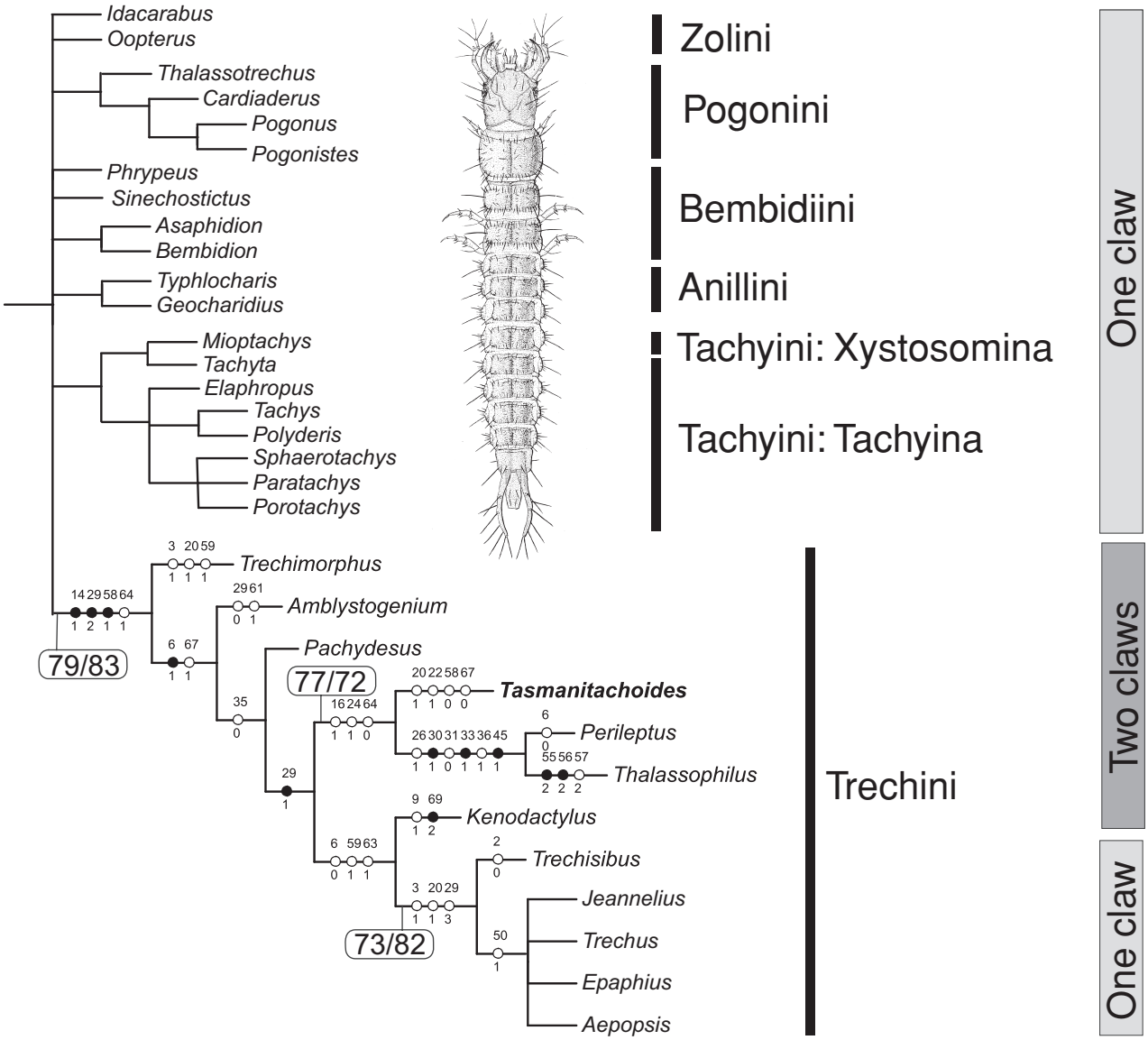

Fig. 3. Strict consensus showing phylogenetic placement of the monophyletic tribe Trechini within monophyletic Trechitae (Coleoptera : Carabidae) inferred from parsimony analysis of 69 larval morphological characters (four of them are uninformative and excluded) for 36 terminal taxa. The Trechini branch is one among 1677 shortest (= most parsimonious) trees (tree length 136, consistency index 55, retention index 81). Only unambiguously optimised evolutionary events are mapped on the Trechini internodes; closed black circles represent unique evolutionary events; white open circles represent convergences or subsequent reversals; character numbers are given above branches; apomorphic characters states are indicted below branches. Boxed slashed values at three branches represent bootstrap values for analysis 1 and 2 respectively. Habitus drawing of *Bembidion* larva represents general appearance of Trechitae larvae.

description was used to score all relevant character states without actually studying the specimens. Two changes, however, were made when scoring the characters of *Jeannelius* for the present analysis. Makarov and Koval (2003) stated that pore MEc on meso- and metathorax was lacking but that pore MEd was present. These two pores are easily confused and since all other Trechitae larvae known show the reverse condition, pore MEc was scored as present and pore MEd as absent (characters 42). They also indicated that the tarsal setae TA3, TA4, TA5 and TA6 were present in *Jeannelius* but markedly reduced in size and represented by conical sensillae. Because these setae are highly reduced in all known Trechitae larvae, they were previously scored as 'absent' and this state was considered an autapomorphy for the supertribe Trechitae (Grebennikov and Maddison 2005). Consequently, these setae were scored as 'absent' (character 34) for *Jeannelius*, even though the original description states otherwise.

Phylogenetic analysis and discussion

The first analysis with unordered multistate characters resulted in 1677 MPTs with a tree length of 136, a consistency index of 55 and a retention index of 81. The second analysis with some multistate characters ordered (see Material and methods) resulted in 2578 MPTs with a tree length of 140, a consistency index 54 and a retention index 80. Topologies of the strict consensus trees from both analyses are remarkably similar to that in Grebennikov and Maddison (2005, fig. 11), showing an unresolved basal polytomy of Trechitae, which is not surprising considering that the present work is based on the extended dataset of the former.

The obtained topologies strongly indicate that *Tasmanitachoides* is not a tachyine, but indeed a trechine. Strict consensus trees from both analyses retain Trechini (including *Tasmanitachoides*) as a well supported clade with the bootstrap value 79 and 83 respectively (Fig. 3). Unambiguous synapomorphies for this clade (Fig. 3) include: sclerotisation of the lateral surface of the penultimate antennomere above the base of the sensorium (Fig. 2*D*; character 14/1); posterior claw about half length of anterior one (character 29/2); secondary setae on frontale in older instars present (character 58/1); and secondary setae on femur in older instars present (character 64/1). All MPTs from the first analysis and 84% of MPTs from the second analysis place the genus *Tasmanitachoids* as the sister-group of *Perileptus* + *Thalassophilus* Wollastone, 1854. These three taxa form a reasonably well supported clade with the bootstrap values 77 and 72 in analysis 1 and 2 respectively (Fig. 3). Unambiguous synapomorphies (Fig. 3) include: terebra with small and numerous teeth (Fig. 2*A*; character 16/1); seta MX6 on stipes about half as long as MX5 (Fig. 2*C*; character 24/1); and secondary setae on femur in older instars absent (Fig. 2*E* character 64/0).

These results lead us to conclude that the genus *Tasmanitachoides* is not a tachyine, as originally thought, but a Trechini, as advocated by D. R. Maddison (personal communication), and shows close affinities to the subtribe Trechodina (represented in this analysis by the genera *Perileptus* and *Thalassophilus*).

Another remarkable feature of our topologies is that all one-clawed genera of Trechina (*Trechisibus* Motschulsky, 1863, *Jeannelius*, *Trechus* Clairville, 1806, *Epaphius* Stephens, 1827 and *Aepopsis* Jeannel, 1922) form a clade. A transformation series from two claws of equal length (as found in the outgroup, Fig. 1*G*), through increasing length reduction of the posterior claw (Fig. 1*H*, *I*), to a single claw (Fig. 1*J*), is clearly suggested. Moreover, in some ingroup taxa, both claws, when present, fuse at their base (as in *Kenodactylus*, Fig. 1*I*), preventing independent movement of each claw (compared with free claws of *Amblistogenium,* Fig. 1*H*). The obtained results support the previously proposed hypothesis that a reduction of the number of tarsal claws in Trechitae took place at least twice: in 'advanced' Trechini and in the weakly supported clade of Trechitae minus Trechini (Grebennikov and Maddison 2005).

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Appendix 1. The following 69 non-polymorphic character states for four newly included taxa should be added into the matrix Grebennikov and Maddison (2005)

Tasmanitachoides:	01?001000-000101000111010001101101001101111?????????????000000001000
Kenodactylus:	010000001000010000001002000110110100110111111?????????????110001101102
Pachydesus:	010001000000100000010020001201101001101111100010000121111????????????
Jeannelius:	011000000000010000011001000130110100110111111?????????????010001101100

Twelve newly added character states for the older-instar larvae of *Mioptachys* (characters 58–69) are: 000000010000.

Additionally, one correction to the 2005 matrix should be made: character 63 (presence or absence of secondary setae on tibia in older-instar larvae) should be scored as secondary setae present (1) for both *Trechus* and *Epaphius*.

- = inapplicable character.

Appendix 2. Identification key to larvae of the supertribe Trechitae (Coleoptera : Carabidae); modified from Grebennikov and Maddison (2005). Symbols (L1) and (L2-3) indicate that this character is applicable to first- or older-instar larvae respectively. Absence of these symbols indicates that the character is applicable to any instar

Key to separate first- and older-instar Trechitae larvae

1 Lateral side of stipes with two setae; urogomphi with five long setae on each side; hypopleural plates without setae ... first-instar larva (L1)

1*. Lateral side of stipes with three and more setae; urogomphi with six to seven (rarely more) long setae on each side; hypopleural plates with setae ..... second- or third-instar larva (L2–3)

Identification key to tribes and genera of the supertribe Trechitae

One claw.....8

1*. Two claws ..... 2 (Trechini, in part)

2 (1*). Claw seta less than 1/5 length of claw; longest claw without hyaline structure on dorsal surface; urogomphi with setae UR3 located near setae UR2; incisor area of mandible without serration .. 3

2*. Claw seta more than 1/2 length of claw; longest claw with hyaline structure on dorsal surface; urogomphi with setae UR3 located near setae UR4; incisor area of mandible with serration..... 7

3 (2). Pore PAb on parietale absent AND seta TA1 located in basal third of tarsus AND dorsal surface of maxillary base without microteeth. Equatorial and southern Africa..... .....*Pachydesus* (only first instar known)

3*. Features not as above. Austral regions of World, except Africa (only older instars known)..... 4

4 (3*). Antennomere 2 with one long seta at apex 5

4*. Antennomere 2 without setae 6

5 (4). Seta TA1 located at middle of tarsus; (L2–3) tibia without secondary setae; (L2–3) setae URα on urogomphi present..... .....*Trechimorphus*

5*. Seta TA1 located in basal third of tarsus; (L2–3) tibia with secondary setae; (L2–3) setae URα on urogomphi absent..... .....*Kenodactylus*

6 (4*). Terebra not serrate; (L2–3) femur with secondary setae; seta MX6 on stipes subequal in length to seta MX5 .....*Amblystogenium*

6*. Terebra serrate; (L2–3) femur without secondary setae; seta MX6 on stipes markedly shorter than seta MX5..... .....*Tasmanitachoides*

7 (2*). Pore PAb on parietale present; antennomere 3 with round sensorium; (L1) sensillum EM1 on meso- and metathorax present, pore-like; (L1) central ventral sclerotized plate on abdominal segments 1–8 without additional setae; (L1) sensillum EP1 on ninth abdominal segment presented as two or three pore-like sensilla..... *Perileptus*

7*. Pore PAb on parietale absent; antennomere 3 with elongated sensorium; (L1) sensillum EM1 on meso- and metathorax absent; (L1) central ventral sclerotized plate on abdominal segments 1–8 with one additional seta; (L1) sensillum EP1 on ninth abdominal segment absent..... ..... *Thalassophilus* (only first instar known)

8 (1). Mandible with two teeth in apical part besides retinaculum .....9 (Anillini)

8*. Mandible without apical teeth besides retinaculum (rarely with even and small serration along terebra)..... 10

9 (5). Antenna three-segmented ..... *Typhlocharis*

9*. Antenna four-segmented ..... *Geocharidius*

10 (8*). Head width ~0.29 mm; nasale as in Grebennikov and Maddison (2005, fig. 10); distance between setae FR3-FR4 ~2× longer than between FR4-FR5; stemmata absent; postocular groove present, cervical groove absent; terebra without teeth; seta LA6 present; seta TA1 in basal third of tarsus; pore PRh present; western North America..... .....*Phrypeus* (only first instar known)

10*. At least one of the characters is different 11

11 (7*). Apical maxillary and labial palpomeres clearly subdivided into two and three pseudosegments respectively; anterior angles of epipharynx with two short setae (seta CI1, after Makarov, 1996); (L2–3) antennomere 2 with one long seta at apex; (L2–3) frontale with two secondary setae basad of setae FR3; (L2–3) tibia and femur always with secondary setae..... .....12 (Trechini, in part)

11*. Apical maxillary and labial palpomeres complete, not subdivided into pseudosegments; anterior angles of epipharynx with one short seta (seta CI1, after Makarov, 1996); (L2–3) antennomere 2 without one long seta at apex or with more than one seta; (L2–3) frontale without two secondary setae basad of setae FR3 (L2–3); (L2–3) tibia and femur normally without secondary setae..... 14

12 (11). Pores MEa on meso- and metathorax and TEa on abdominal terga 1–8 absent ..... *Aepopsis*

12*. Pores MEa on meso- and metathorax and TEa on abdominal terga 1–8 present..... 13

13 (12*). (L2–3) Frontale without two secondary setae basad of FR3; (L2–3) nasale markedly produced and with two large lateral apices (Makarov and Koval 2003, figs 3, 4) .... *Jeannelius* (only older-instar known)

13*. (L2–3) Frontale with two secondary setae basad of FR3; (L2–3) nasale not markedly produced and without two large lateral apices..... *Trechus*, *Epaphius* and *Trechisibus*

14 (11*). Base of stipes on medial side with one or more teeth; seta LA5 on ligula always absent; (L2–3) urogomphi with six long setae on each side; (L1) epicranial stem sorter than diameter of proximal antennomere or absent .....15 (Tachyini)

14*. Base of stipes on medial side without teeth; seta LA5 on ligula present (except *Idacarabus*); (L2–3) urogomphi with seven (rarely more) long setae on each side; (L1) epicranial stem longer than diameter of proximal antennomere 23

15 (14). Cephalic capsule laterally rounded; (L1) egg-bursters on frontale consisting of two longitudinal rows of teeth along frontal sutures; (L1) frontale without spot of microspines; (L1) mandible on dorsal surface near pore MNb smooth, without microspines; (L2–3) postocular groove present; (L2–3) lateral sides of tergum 9 without long secondary seta at middle..... 16

15*. Cephalic capsule with parallel lateral sides; (L1) egg-bursters on frontale absent; (L1) frontale with spot of microspines proximally; (L1) mandible on dorsal surface near pore MNb with microspines; (L2–3) postocular groove absent; (L2–3) lateral sides of tergum 9 with long secondary seta at middle..... 17

16 (15). (L1) Parietale near seta PA6 with meshed microsculpture; distal seta of group gMX on stipes situated proximad of level of seta MX5; gMX on stipes consists of five setae; (L2–3) epicranial suture short but distinct..... *Tachyta*

16*. (L1) Parietale near seta PA6 smooth, without microsculpture; distal seta of group gMX on stipes situated distad of level of seta MX5; gMX on stipes consists of six setae; (L2–3) epicranial suture absent ..... *Mioptachys*

17 (15*). Mandible with serration on incisor area 18

17*. Mandible without serration on incisor area 20

(*continued next page*)

Appendix 2. (*continued*)

18 (17). Incisor area with ~10 small and equal teeth; (L1) frontale near pore FRb smooth, without microspines ..... *Sphaerotachys*

18*. Incisor area with three to five large teeth in proximal half and some small teeth distally; (L1) frontale near pore FRb with microspines 19

19 (18). Pore PAa on parietale located at level of seta PA1; (L1) parietale laterad of seta PA3 with microspines; (L2–3) frontale more elongated (ratio length/width 1.5)..... *Porotachys*

19*. Pore PAa on parietale located proximad of level of seta PA1; (L1) parietale laterad of seta PA3 smooth, without microspines; (L2–3) frontale less elongated (ratio length/width 1.3) . *Paratachys*

20 (17*). Pore PRh on protergum absent .....*Tachys*

20*. Pore PRh on protergum present 21

21 (20*). Pore PAb on parietale absent.....*Polyderis* (in part)

21*. Pore PAb on parietale present 22

22 (21*). (L1) Seta FR9 on frontale more than 2× longer than FR5; parietale laterad of seta PA3 with microspines.....*Elaphropus*

22*. Seta FR9 on frontale about as long as FR5; parietale laterad of seta PA3 smooth, without microspines ..... *Polyderis* (in part)

23 (14*). Spindle-like setae present (in L1 at least setae ES1 on pro- and mesothorax, EP1 and PY2 on abdominal segments 9 and 10 respectively; in L2–3 at least a few short irregular secondary setae); frontal arms nearly straight or only slightly curved (except *Thalassotrechus*); nasale often with two protruding parts..... 24 (Pogonini)

23*. Spindle-like setae absent; frontal arms curved; nasale only rarely with two protruding parts.....27

24 (23). Pore PRh on protergum absent; (L1) parietale with egg-bursters consisting of one large spine on each side near coronal stem; seta TA1 at middle of tarsus; (L1) lateral sides of cephalic capsule in basal third markedly rounded and without cervical groove; (L1) seta TE7 on all terga spindle-like ..... *Thalassotrechus*

24* Pore PRh on protergum present; (L1) parietale without egg-bursters; (L1) seta TA1 in proximal third of tarsus; (L1) seta TE7 on all terga normal, trichoid.....21

25 (24*). Length of setae MX11 and MX12 less than 1/4 diameter of maxillary palpomere 3; (L2–3) antennae with secondary setae on antennomere 2 only; (L2–3) meso-, metathoracic, and abdominal terga with numerous secondary setae in medial half ..... *Cardiaderus*

25*. Length of setae MX11 and MX12 more than half diameter of maxillary palpomere 3; (L2–3) antennae without secondary setae or they are on three basal antennomeres; (L2–3) meso-, metathoracic, and abdominal terga without numerous secondary setae in medial half 26

26 (25*). (L1) Dorsal surface of mandible between MN1 and MNb with 1–8 (usually 2–4) microspines; (L1) seta PY6 on pygidium spindle-like.....*Pogonus*

26*. (L1) Dorsal surface of mandible between MN1 and MNb smooth, without microspines; (L1) seta PY6 on pygidium trichoid .....*Pogonistes*

27 (23*).Sensillum PRh on prothorax absent; posterior row normally consisting of three stemmata; (L2–3) lateral side of tergum 9 with secondary seta at middle anteriorly of seta UR2..... ..... 28 (Bembidiini, in part: excluding *Phrypeus*)

27*. Sensillum PRh on prothorax present; posterior row with no or one stemma; (L2–3) lateral side of tergum 9 without secondary seta at middle anteriorly of seta UR2.....30 (Zolini)

28 (27). Setae FR4 and FR5 on frontale somewhat distantly located, distance between them not less than half of distance between FR3 and FR4; setae LA4 and LA5 on ligula flat; dorsal surface of claw with groove; (L2–3) tibia, tarsus and femur with secondary setae.....*Sinechostictus*

28*. Setae FR4 and FR5 on frontale drawn together, distance between them less than 1/3 that between FR3 and FR4; setae LA4 and LA5 on ligula conical, not flat; dorsal surface of claw smooth, without groove; (L2–3) tibia, tarsus and femur without secondary setae 29

29 (28*). Dorsal and lateral sclerites of body with frayed setae; setae MX11 and MX12 longer than half width of maxillary palpomere 3; setae LA6 on ligula divergent anteriorly with angle ~30 degrees between them; (L1) posterior angles of thoracic and abdominal terga with conical sensillae ..... *Asaphidion*

29*. Dorsal and lateral sclerites of body with simple setae only; setae MX11 and MX12 shorter than 1/4 or width of maxillary palpomere3; setae LA6 on ligula parallel to each other; (L1) posterior angles of thoracic and abdominal terga without conical sensillae ..... *Bembidion*

30 (27*). Ligula with setae LA5; posterior row of stemmata with single stemma; seta FR2 ~2× longer than FR7; lateral part of antennomere 3 apically near sensorium with two campaniform sensilla; seta AN6 about subequal in length to apical antennomere; (L2–3) stipes with gMX consisting of 30–33 setae; seta MX6 subequal in length to MX5; (L2–3) lateral side of stipes with 4 setae; (L2–3) lateral side of labium with 5–6 setae.....*Oopterus*

30*. Ligula without setae LA5; posterior row of stemmata absent; seta FR2 subequal to FR7; lateral part of antennomere 3 apically near sensorium with one campaniform sensillum; seta AN6 reduced to very short sensillum shorter that 1/20 length of apical antennomere; (L2–3) stipes with gMX consisting of eight setae; seta MX6 2X longer than MX5; (L2–3) lateral side of stipes with three setae; (L2–3) lateral side of labium with two to three setae..... *Idacarabus*