Systematic Entomology (2005), **30**, 38–59 DOI: 10.1111/j.1365-3113.2004.00259.x

Phylogenetic analysis of Trechitae (Coleoptera: Carabidae) based on larval morphology, with a description of first-instar *Phrypeus* and a key to genera

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Abstract. Sixty-nine characters of larval structure of twenty-eight genera of the supertribe Trechitae (Coleoptera: Carabidae) were analysed phylogenetically. The monophyly of Trechitae is strongly supported with five unique synapomorphies. The monophyly of Zolini + Bembidiini + Pogonini is supported with two synapomorphies. We propose that the tribe Trechini is a sister group to them and its monophyly is supported with two unique synapomorphies. The inferred branching pattern of Trechini genera is (*Perileptus* + *Thalassophilus*) + (*Amblystogenium* + (*Trechimorphus* + (*Trechus* + *Epaphius* + *Aepopsis* + *Trechisibus*))); *Perileptus* is a member of Trechodina rather than Trechina. The monophyly of Zolini is not supported. The monophyly of Pogonini is supported with two unique synapomorphies; its sister group relationships remain obscure; the branching pattern of pogonine genera is (((*Pogonus* + *Pogonistes*) + *Cardiaderus*) + *Thalassotrechus*). No evidence for monophyly of the tribe Bembidiini (*s. lato*; including subtribes Bembidiina, Tachyina, Xystosomina, and Anillina) was found. The relationships of *Phrypeus* are obscure; no evidence could be found linking it with Bembidiina. Without *Phrypeus*, Bembidiina might be a monophylum with a single synapomorphy. *Sinechostictus* branches basal of (*Bembidion* + *Asaphidion*) and therefore should be treated as a separate genus. Tachyina and Xystosomina form a monophylum based on two unique synapomorphies; a close relationship with a monophyletic Anillina is suggested. Reduction of the number of claws from two to one in Trechitae has taken place twice: within Trechina (*Trechus*, *Epaphius*, *Aepopsis* and *Trechisibus*) and in (Zolini + Bembidiini + Pogonini). The previously unknown larvae of the isolated genus *Phrypeus* are described and illustrated. A key to all twenty-eight analysed Trechitae genera based on characters of larvae and a list of larval autapomorphies for each genus are provided.

Introduction

The cosmopolitan supertribe Trechitae with about 5500 species is one of the largest and most complex within the family Carabidae. Although most members are normally collected in mesic conditions, they can be found in nearly all types of terrestrial habitat. Most of the species are active predators, between 2 and 10 mm long, and either winged or wingless.

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The supertribe Trechitae comprises four tribes. Among them the tribe Zolini (= Merizodini or Oopterini of some authors; see Deuve, 1997: 32) is the smallest and includes three subtribes with about forty species arranged in eleven valid genera: *Idacarabus* Lea, *Merizodus* Csiki, *Oopterus* Guérin-Méneville, *Percodermus* Sloane, *Pseudoopterus* Csiki, *Pterocyrtus* Sloane, *Sloaneana* Csiki, *Synteratus* Browne, *Zolus* Sharp, *Sinozolus* Deuve and *Chaltenia* Roig-Juñent & Cicchino. The first nine comprise the subtribe Zolina, whereas monotypic *Sinozolus* and *Chaltenia* make up the subtribes Sinozolina and Chalteniina, respectively (Roig-Juñent & Cicchino, 2001). The flying capacity of Zolini is poorly known. All members of Zolini are distributed exclusively in the south temperate zone (Patagonia, Falkland Islands, New Zealand, Australia (Victoria, Tasmania)). The only exception is the recently described, monotypic *Sinozolus* from China (Deuve, 1997); the first and only record of Zolini from the Northern Hemisphere. The group has attracted relatively little attention as adult beetles or larvae. Among the recent publications of Zolini are descriptions of two new subtribes each based on a new genus (Deuve, 1997; Roig-Juñent & Cicchino, 2001) as well as only two papers with descriptions of larvae of *Oopterus* and *Idacarabus* (Johns, 1974; Grebennikov, 1999).

The tribe Pogonini is the second smallest within Trechitae with about seventy-five species in eleven genera: *Bedeliolus* Semenov, *Cardiaderus* Dejean, *Diodercarus* Lutshnik, *Diplochaetus* Chaudoir, *Ochtozetus* Chaudoir, *Pogonistes* Chaudoir, *Pogonopsis* Bedel, *Pogonus* Dejean, *Syrdenus* Chaudoir, *Thalassotrechus* Van Dyke and *Olegius* Komarov. The tribe is cosmopolitan in distribution, with most species in the Palaearctic, particularly in the Mediterranean area. The majority of pogonine species live in saline habitats and are capable of flying. Recent works on pogonine adults include those by Komarov (1996) describing a new genus *Olegius* based on a single female from the southwest part of the Kara-Kum desert in Turkmenistan, and Bousquet & Laplante (1997) reviewing New World species. Larvae of four genera (*Cardiaderus*, *Pogonus*, *Pogonistes*, *Thalassotrechus*) were recently described by Grebennikov & Bousquet (1999).

The tribe Trechini has more than 2500 species (Ball & Bousquet, 2001) arranged in hundreds of genera (although the generic concept within Trechini is historically much narrower than in the majority of Carabidae; Kryzhanovskij, 1983), and this number continues to grow rapidly. Most trechine members are flightless, either troglobiontic or endogean, and normally have restricted distribution. The group is most diverse in temperate regions of both hemispheres. The tribe is broken into two subtribes: Trechodina and Trechina, which differ in the basic structure of the male genitalia (Casale & Laneyrie, 1982). Trechina is by far the more diverse (Casale & Laneyrie, 1982). Trechini has attracted much attention from entomologists. Jeannel (1926–30) revised the tribe worldwide; Uéno (numerous publications, for their list see Uéno, 1995) discovered diverse and previously unknown trechine faunas in caves and endogean habitats in Japan and South East Asia; Moore (1972) revised the Australian fauna; Belousov (1998) revised a complex of genera related to *Nannotrechus* Winkler from Caucasus. Papers with descriptions of larval Trechitae are numerous; among them Jeannel (1920) and Luff (1985) are the most informative for Trechina and Grebennikov (1996) and Grebennikov & Luff (1999) for Trechodina.

The tribe Bembidiini (including the tribe Tachyini of some authors) is the largest within Trechitae with about 3000 species represented in all zoogeographical regions of the world (Ball & Bousquet, 2001). Four subtribes constitute the tribe: Bembidiina, Tachyina (including Lymastina), Xystosomina and Anillina. Among them, cosmopolitan Bembidiina is the largest and consists of nine genera (Toledano, 2002) with most of the species found in the Northern Hemisphere associated mainly with riparian habitats: *Asaphidion* Gozis, *Zecillenus* Lindroth, *Bembidion* Latreille, *Ocys* Stephens, *Amerizus* Chaudoir, *Bembidarenas* Erwin, *Caecidium* Uéno, *Phrypeus* Casey, and *Orzolina* Machado. Recent evidence from larval morphology strongly indicated that *Sinechostictus* Motschulsky should also be treated as a separate genus (Grebennikov, 1997). The genus *Zecillenus* was revised by Lindroth (1980), whereas the genera *Asaphidion*, *Ocys*, and particularly *Bembidion* with well over 1000 species have never been completely revised. Relationships within the latter genus are particularly obscure; however, there are a number of works dealing with separate faunas or monophyletic units within *Bembidion* (e.g. Netolitzky, 1942–43; Lindroth, 1976; Erwin & Kavanaugh, 1981; Müller-Motzfeld, 1985, 1986a, b; Maddison, 1993; Toledano, 1998, 1999, 2000). The primarily arboreal subtribe Xystosomina has been recently erected by Erwin (1994) for seven genera in New World and Australia: *Philipis* Erwin, *Xystosomus* Schaum, *Geballusa* Erwin, *Gouleta* Erwin, *Batesiana* Erwin, *Mioptachys* Bates, and *Inpa* Erwin; since then the Australian genus *Philipis* was revised (Baehr, 1995). The subtribe Tachyina is worldwide in distribution and includes not less than a dozen genera; the most important recent contributions are those by Basilewsky (1968: Tachyini of Madagascar), Erwin (1974: revision of Pericompsus; 1975: revision of *Tachyta*), Baehr (1987: revision of Australian *Tachyura* and *Sphaerotachys*; 1990: revision of *Tasmanitachoides*). The subtribe Anillina with a few hundred species in about sixty genera is nearly cosmopolitan in distribution (with the notable exception of most of Asia) and includes the smallest Carabidae (e.g. *Agriloborus brevis* Jeannel is 0.7 mm long). The subtribe was revised twice by Jeannel (1937, 1963); since then about twenty new genera have been described (e.g. Cicchino & Roig-Juñent, 2001), mainly monotypic and often from a single series (e.g. Moore, 1980; Bruneau de Miré, 1986; Zaballos & Mateu, 1997; Zaballos, 1997; Mateu & Etonti, 2002) or even from a unique specimen (e.g. Sciaky & Zaballos, 1993; Sciaky, 1994). Recent works on Bembidiini larvae include those of Maddison (1993) and Grebennikov (1997) for *Bembidion* (*Bracteon*) Bedel and *Sinechostictus*, respectively (Bembidiina); Grebennikov & Maddison (2000) for seven genera of Tachyina and *Mioptachys* of Xystosomina; Arndt *et al.* (1999) and Grebennikov (2002) for the only two genera of Anillina known in larvae, *Typhlocharis* Dieck and *Geocharidius* Jeannel.

There is good support of the monophyly of the supertribe Trechitae based on adult morphology (Roig-Juñent & Cicchino, 2001: male protarsomeres are dentate and dilated on the inner side), larval morphology (Grebennikov & Maddison, 2000: 226) and 18S ribosomal DNA sequences (Maddison *et al.*, 1998, 1999). The exclusively Holarctic supertribe Patrobitae is considered to be a sister group of Trechitae based on adult morphology (Zamotajlov, 2002), 18S ribosomal DNA sequences (Maddison *et al.*, 1998,

1999) and larval morphology (Houston & Luff, 1975; Arndt, 1993, 1998; Zamotajlov, 1994, 2001; Bousquet & Grebennikov, 1999). Within the supertribe Trechitae, relationships are less clear. The phylogeny of the tribe Zolini was in obscurity until the recent work of Roig-Juñent & Cicchino (2001), who suggest that the tribe is monophyletic and a sister to Bembidiina. Grebennikov (1999) found no larval synapomorphies linking the two genera of Zolini, for which larvae are known, nor an indication of the relationships of these two genera to other trechites. Members of the tribe Pogonini have been proposed to be monophyletic based on adult characters (Bousquet & Laplante, 1997) and a sister to the rest of Trechitae (Roig-Juñent & Cicchino, 2001), whereas larval morphology supported the monophyly of the tribe but did not yield its sister group (Grebennikov & Bousquet, 1999). Adult morphology suggests that the tribe Trechini is monophyletic and a sister to Zolini + Bembidiini (Roig-Juñent & Cicchino, 2001); no phylogenetic studies were undertaken on larvae to challenge this opinion. The monophyly of Bembidiini had never been clearly addressed. The main and apparently only adult synapomorphy of the group is the markedly shortened apical maxillary palpomere (e.g. Maddison, 1993), a character known to occur within Trechitae outside of Bembidiini, for example, in the trechine genus *Perileptus* Schaum. Within Bembidiini, Erwin (1982) hypothesizes that Anillina is a polyphyletic group and Tachyina paraphyletic with respect to it. By contrast, Jeannel (1937, 1963) thought Anillina and the 'lymnastines' (*Lymastis* Motschulsky and *Micratopus* Casey) to be sisters, as are the remaining Tachyina (including Xystosomina) and Bembidiina. Evidence from larval morphology suggests that Xystosomina and Tachyina form a monophylum (Grebennikov & Maddison, 2000), whereas Anillina is monophyletic and sister to them (Grebennikov, 2002). Larvae of Bembidiina share no known synapomorphies with members of the rest of the Bembidiini (Grebennikov & Maddison, 2000; Grebennikov, 2002) and the sister group of the subtribe is unknown.

In the present study we undertook the first analysis of all known larval morphological data in order to address the phylogeny of Trechitae. The use of larval morphological characters for phylogenetic purposes in Coleoptera has been rather neglected compared with those of adults. The main difficulty, apparently, arose from the fact that the number of phylogenetically informative morphological characters in larvae was considered to be generally less than that in adults, perhaps due to our lack of knowledge of larvae, and to less developed larval sclerotization, as well as the lack in larvae of complex structures found only in adults (genitalia, wings). However, detailed investigations of larval chaetotaxy have shown it to be a source of abundant characters, useful for phylogenetic inference in several beetle families: Carabidae (Bousquet & Goulet, 1984); Staphylinidae (Ashe & Watrous, 1984; Thayer, 2000), Leiodidae (Wheeler, 1990; Kilian, 1998), Histeridae (Kovarik & Passoa, 1993), Hydraenidae (Delgado & Soler, 1996, 1997), Dytiscidae (Alarie & Balke, 1999), Ptiliidae (Grebennikov & Beutel, 2002).

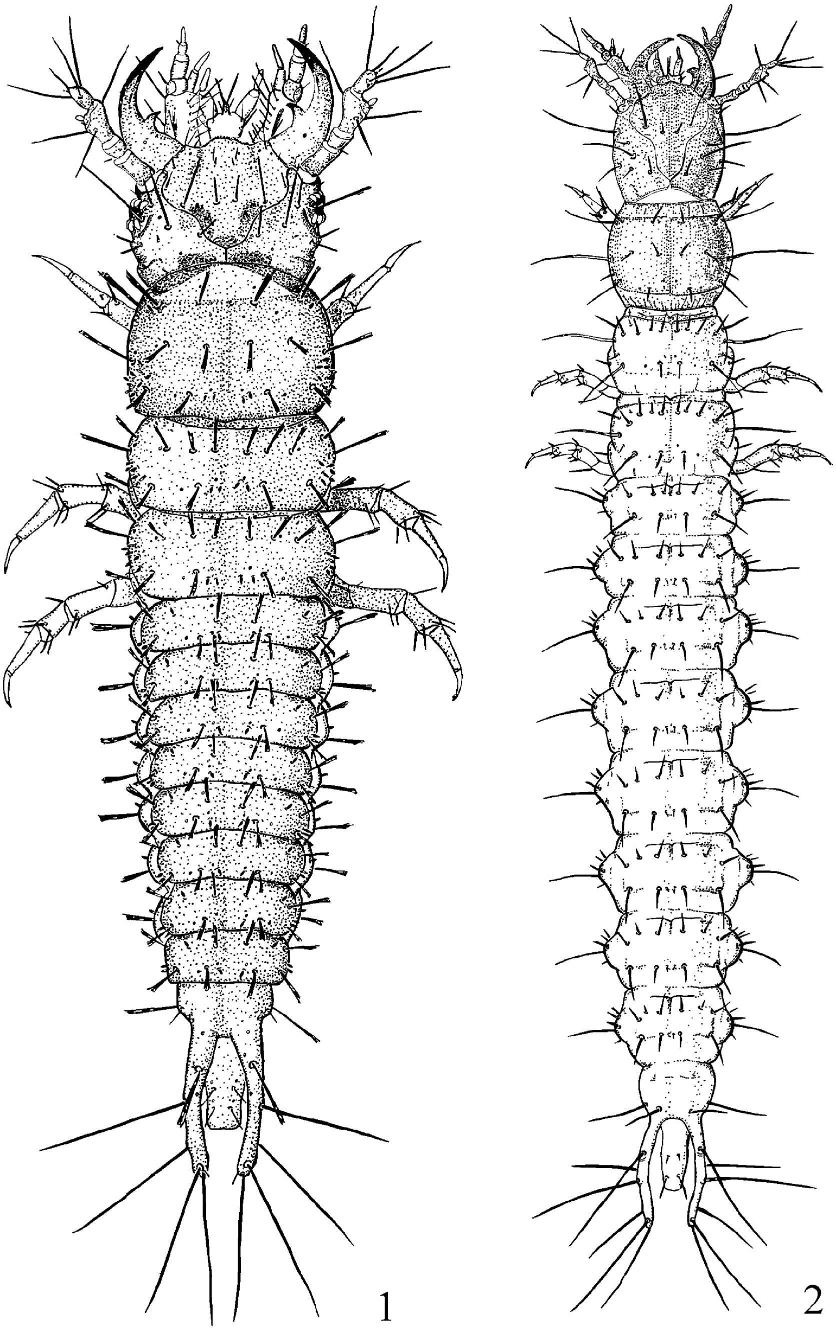
The main purpose of this paper is to provide a phylogenetic analysis of the supertribe Trechitae based on larval morphology. We will concentrate on a critical re-evaluation of the monophyly of the supertribe, all its four tribes and, when possible, subtribes based on this new set of characters. We describe and illustrate the previously unknown larvae of the bembidiine genus *Phrypeus*, list autapomorphies for each Trechitae terminal taxon analysed (Appendix 1), and provide an identification key to twenty-eight genera included in the analysis (Appendix 2).

Materials and methods

Trechitae larvae

The larvae used in this study originated mainly from rearing conducted by the authors in 1981–92 in Canada and the U.S.A. (DRM) and in 1995–97 in Russia, Ukraine, Uzbekistan and Turkmenistan (VVG). The remaining material was borrowed from the following public and private collections: ANCI, Australian National Collection of Insects, Canberra, Australia (B. P. Moore, A. Ślipiński); CAS, California Academy of Sciences, San Francisco, U.S.A. (R. Brett, D. Kavanaugh); CNC, Canadian National Collection of Insects (Y. Bousquet, A. Davies); EAC, Erik Arndt collection, Bernburg, Germany; JRC, J. Roberto Carrillo collection, Valdivia, Chile; MCZ, Museum of Comparative Zoology, Harvard, U.S.A. (P. D. Perkins); MLL, Martin L. Luff collection, Newcastle upon Tyne, U.K.; MPGU, Department of Zoology and Ecology, Moscow Pedagogical State University, Moscow, Russia (I. Kh. Sharova); NHML, The Natural History Museum, London, U.K. (S. Hine, M. J. D. Brendell); ZISP, Zoological Institute, St. Petersburg, Russia (G. S. Medvedev, B. M. Kataev).

The larvae were partly disarticulated (head cut off and body cut at the level of the fourth abdominal segment to facilitate maceration of internal tissues), cleaned in KOH and mounted on permanent microscope slides in Euparal medium and studied under compound microscopes with magnification up to 900×. Habitus drawings of a first-instar larva of *Asaphidion caraboides* (Fig. 1) and a third-instar larva of *Tachyta nana* (Fig. 2) are included to demonstrate the diversity of Trechitae larvae. Figures 3 and 4 illustrate the head of a third-instar larva (*Amblystogenium minimum*) with numerous secondary setae normally characteristic of second- and third-instar larvae of Carabidae. References to secondary setae (for example character 69: size of seta UR alpha) follow the system proposed by Bousquet (1985). Figures 5–10 show the chaetotaxy of the first-instar larva (*Phrypeus rickseckeri*), and the system proposed by Bousquet & Goulet (1984) for primary setae and pores has been followed. Seta CI1 in anterior angles of the epipharynx (Fig. 10) is indicated according to Makarov's (1996) designation. Appendix 3 includes the list of taxa studied, the current depository of the material and an indication of whether the larvae were reared *ex ovo* (+) or identified by association (cross in parentheses (+)). The terms of larval

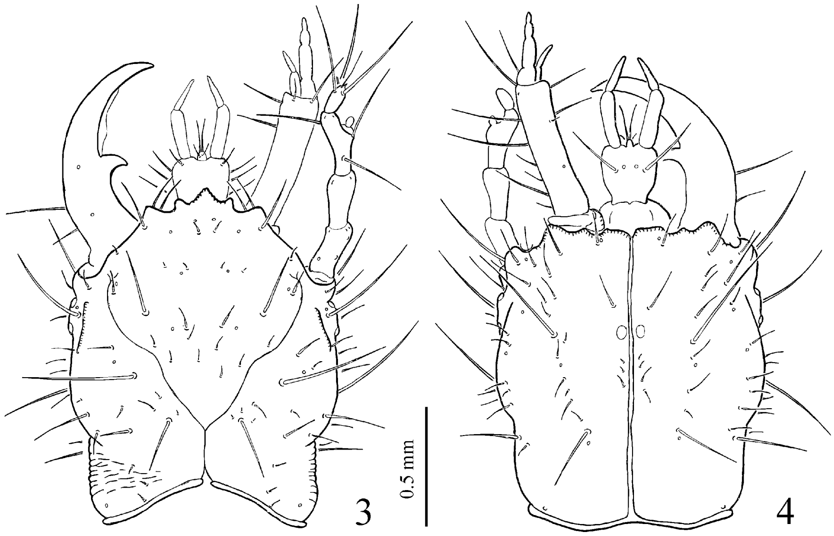


Figs 1, 2. Trechitae larvae, habitus, dorsal view. Fig. 1, *Asaphidion caraboides*, first instar; Fig. 2, *Tachyta nana*, third instar (from Grebennikov & Maddison, 2000).

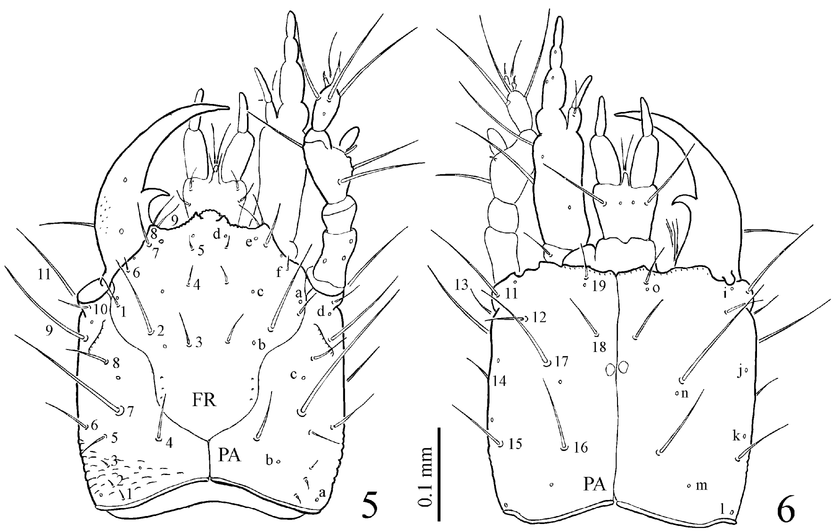
morphology are those of Lawrence (1991) and Bousquet & Goulet (1984). L1, L2 and L3 refer to the first-, second- and third-instar larvae, respectively.

Phylogenetic methods

A list of employed morphological characters of Trechitae larvae is given in Appendix 4. The disappearance of setae TA3–6 on the tarsus is coded as one character, because these four setae are either all present or all absent. The disappearance of the pores PRc (character 37), PRe (character 38), PRh (character 39), PRi (character 40) and PRj (character 41) on the pronotum is treated as five separate characters because at least some of these pores can disappear individually, leaving the remainder of them present. The matrix is given in Appendix 5; characters 1–45 are found in larvae of all instars; characters 46–57 are found only in first-instar larvae and



Figs 3, 4. Trechitae larvae, *Amblystogenium minimum*, head, third instar, dorsal (Fig. 3) and ventral (Fig. 4) views.



Figs 5, 6. Trechitae larvae, *Phrypeus rickseckeri*, head, first instar, dorsal (Fig. 5) and ventral (Fig. 6) views. Chaetotaxy system follows Bousquet & Goulet (1984).

characters 58–69 are found in older-instar larvae only. The supertribe Patrobitae was selected as an outgroup as the most justified sister group of Trechitae (for references see Introduction). Additionally, one member of the tribe Pterostichini, the group clearly outside of the Patrobitae + Trechitae monophylum, was added into the outgroup. Most parsimonious trees (MPTs) were sought with PAUP*4.0b10 (Swofford, 2002), using branch and bound searching. Decay indices were calculated by finding the MPTs without a clade using heuristic searches (with 100 random addition sequence replicate starting trees, and saving no more than twenty-five trees in each of the 100 replicates). Assumptions about character transformations were treated in three different ways: (1) multistate characters treated as unordered or ordered, as specified in Appendix 4, with character 29 (reduction of claws from two to one) treated as irreversible; (2) as (1) but with character 29 treated as ordered; (3) all multistate characters treated as unordered. The first of these includes the richest assumptions about likelihood of character transformation; the third the fewest assumptions. For each of these three options, character weighting was assumed to be (a) equal or (b) sensillar characters were given half the weight of nonsensillar characters. The rationale for this is an assumption that sensillar characters are more likely to be subject to convergence than nonsensillar. In total, six different analyses were run; their statistics are indicated in Table 1. Most parsimonious reconstructions of character evolution were analysed with MACCLADE (Maddison & Maddison, 2002).

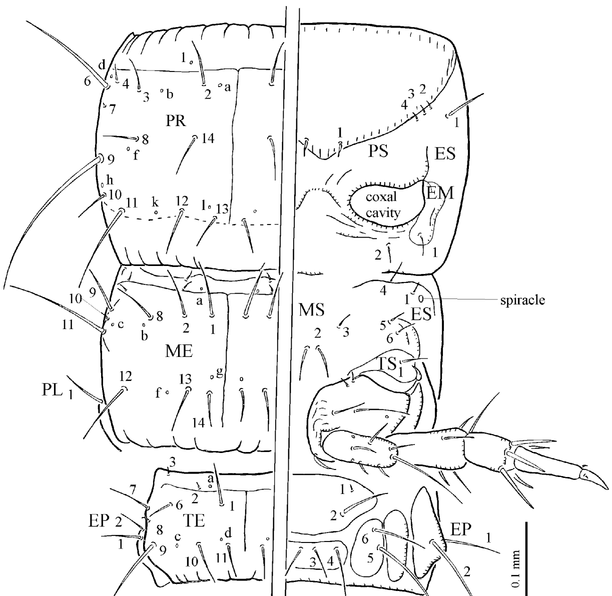


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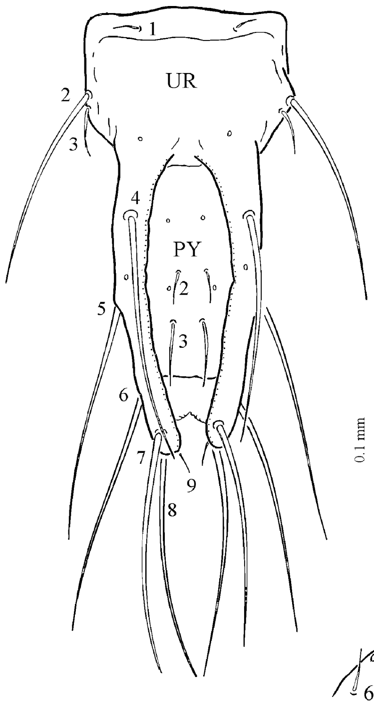
Fig. 7. Trechitae larvae, *Phrypeus rickseckeri*, prothorax, mesothorax and abdominal segment IV dorsal (left) and ventral (right) views. Chaetotaxy system follows Bousquet & Goulet (1984).

Description of larvae of *Phrypeus rickseckeri* (Hayward, 1897) (Figs 5–10)

Spindlelike setae on body absent; no stemmata (Figs 5, 6); anterior angles of epipharynx with single seta CI1 (Fig. 10); frontal suture sinuate (Fig. 5); pore FRa on frontale present, located distal of level PA2 (Fig. 5); pore PAb on parietale present (Fig. 5); ratio distances FR2–FR3 to FR1–FR2 less than 1.5; ratio distances FR3–FR4 to FR4–FR5 1.5–2 (Fig. 5); seta FR6 on frontale located at lateral margins (Fig. 5); basal antennomere with five pores (Fig. 5); antennomere 2 of normal size (Figs 5, 6); antennal fossa separated from pleurosoma by weak membrane (Fig. 5); lateral surface of penultimate antennomere above base of sensorium membranous (Fig. 5); penicillus present; terebra without teeth (Fig. 5); retinaculum of normal size (Fig. 5); seta MN2 on mandible much shorter than retinaculum; apical labial and maxillary palpomere complete, not subdivided (Fig. 6); lacinia absent; base of stipes without teeth; pore MXc located in distal fourth of stipes (Fig. 6); setae MX6 to MX5 of equal size; 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 (Fig. 5); legs with one claw; claw without hyaline structure on dorsal surface; short and conical single claw seta attached at base



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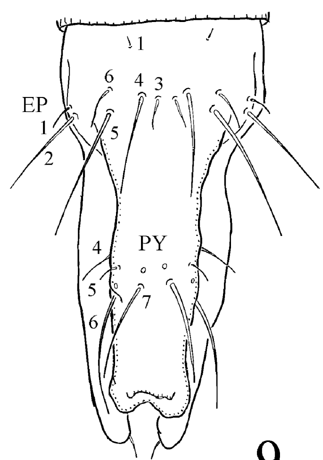

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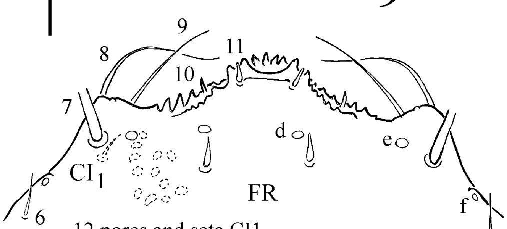

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Figs 8 and 10. Trechitae larvae, *Phrypeus rickseckeri*, first instar, detail. Figs 8, 9, abdominal segments IX and X dorsal (Fig. 8) and ventral (Fig. 9, long setae on urogomphi omitted) views. Fig. 10, anterior part of frontale ('nasale'), dorsal view. Chaetotaxy system follows Bousquet & Goulet (1984); setae CI1 on ventral surface of nasale close to anterior angles designated according to Makarov (1996).

Table 1. Tree length and the number of most parsimonious trees (MPTs) under different assumptions, as described in the text.

Assumptions		MPTs	
Character weights	Transformation assumptions	Tree length	Number of trees
Equal (1 : 1)	Irreversible, ordered, unordered	148	12 642
	Ordered, unordered	148	44 223
	Unordered	141	21 771
Unequal (2 : 1)	Irreversible, ordered, unordered	187	4704
	Ordered, unordered	187	672
	Unordered	178	620

of claw (Fig. 7); 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 (Fig. 7); pores MEd, MEe on meso- and metathoracic terga absent (Fig. 7); pore TEb on abdominal terga 1–8 absent (Fig. 7); seta UR3 on urogomphi located near UR2 (Fig. 8).

Characters restricted to first-instar larvae

Head width 0.29 mm ($n = 1$). Frontal arms weakly or not sinuate, closer to V (Fig. 5); epicranial stem present (Fig. 5); egg-bursters on frontale present as very faint teeth of microsculpture (Fig. 5); egg-bursters on parietale absent (Fig. 5); group gMX on stipes with more than six setae; teeth on coxa absent; sensillum EM1 on prothorax as seta (Fig. 7); sensillum ES1 on mesothorax as seta (Fig. 7); sensillum ES1 on metathorax absent (Fig. 7); sensillum EM1 on mesothorax as seta; sensillum EM1 on metathorax as seta; sensillum EP1 on IX abdominal segment as seta (Fig. 9).

Characters restricted to older-instar larvae

Unknown.

Material

2L1, *ex ovo*, raised by DRM from adults collected 10 June 1985, Canada, BC, Bull River at Kootenay River. H. Amerongen and D. Maddison leg., det. (DRM 85006).

Phylogenetic results and discussion

Six different analyses were run (see Materials and methods); the number of MPTs and the lengths of these trees are indicated in Table 1. A single tree, reflecting the strict consensus trees from the analysis with downweighted sensillar characters and presuming the most complex transformation assumptions, is shown in Fig. 11, annotated to show the results of other analyses. The most parsimonious reconstruction of character evolution on one of the MPTs is given in Fig. 12 with only unambiguously reconstructed character changes shown; examination of other MPTs suggests similar reconstructed patterns of character evolution.

Monophyly of Trechitae

Five unique larval synapomorphies strongly suggest that Trechitae is indeed a monophylum: claws with only one seta (character 32); tarsal setae TA3–6 absent (character 34); and prothoracic pores PRc, PRe and PRi absent (characters 37, 38 and 40, respectively). The last three characters represent the disappearance of three closely located sensilla on lateral parts of thoracic terga and might be genetically dependent on each other, thus providing slightly weaker support to the monophyly of Trechitae.

Zolini + Bembidiini + Pogonini

A group weakly supported as monophyletic by the presence of only one claw (character 29/3) and the attachment of claw setae to the base of the claw (character 31). These two synapomorphies are independently derived in some Trechini: Trechina.

Zolini

Larvae of the tribe Zolini were revised recently (Grebennikov, 1999) and it was stated that the monophyly of the tribe cannot be corroborated based on larval morphology. Our present study shows the same result: *Oopterus* and *Idacarabus* are part of the unresolved polytomy of Trechitae minus Trechini (Fig. 11).

Pogonini

Larvae of the tribe Pogonini were revised recently (Grebennikov & Bousquet, 1999) and since then no new taxa have been studied. The tribe appears clearly monophyletic based on two unique synapomorphies: the presence of spindlelike setae on the body (character 1) and the

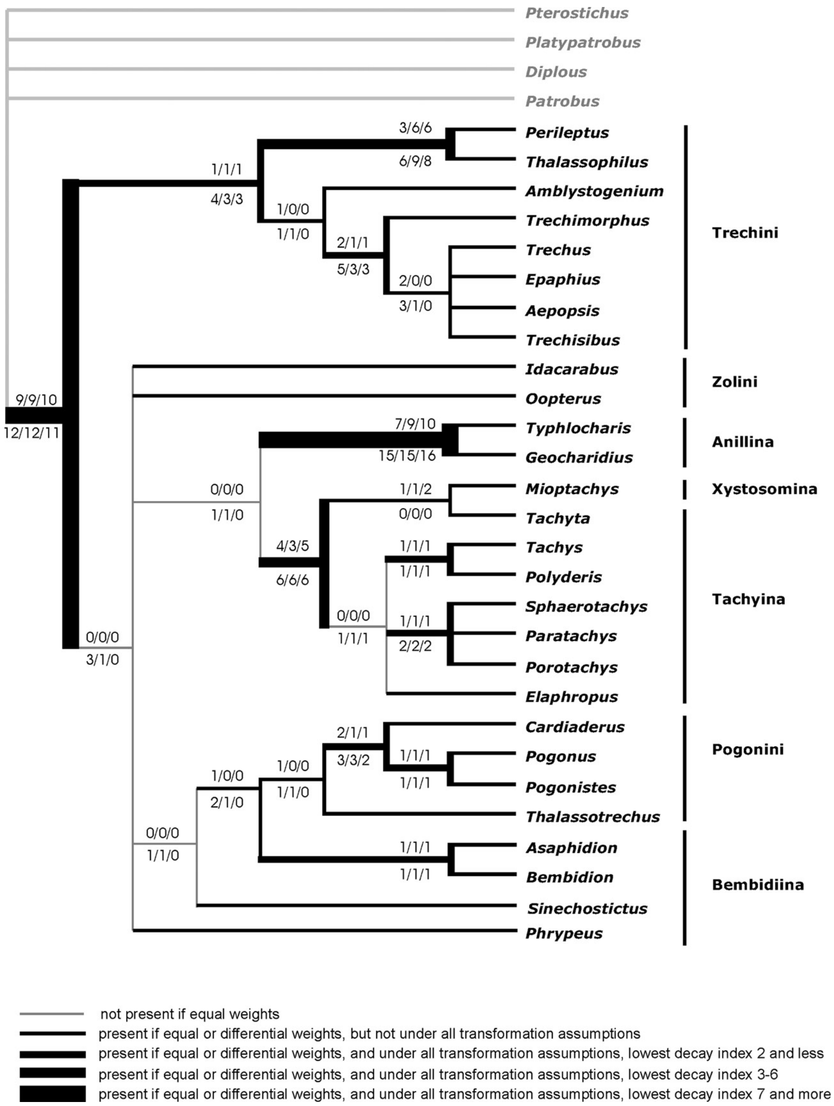

Fig. 11. The strict consensus tree of most parsimonious trees found with the most complex weighting of characters (sensillar characters were given half the weight of nonsensillar characters) and transformation assumptions (number of claws treated as irreversible and some other characters treated as ordered). The numbers around the branches, and the thickness and shading of the branches, indicate support for the clade under this and other assumptions. The numbers above the branches indicate decay indices if characters are equally weighted, with the first number indicating the value with characters treated as irreversible (number of claws), ordered, and unordered; the second number with the number of claws treated as ordered; the third number with all characters treated as unordered. The numbers below the branches indicate decay values similarly, but with nonsensillar characters given a weight of two.

ratio of distances of setae FR1–FR2 and FR2–FR3 on the frontale (character 7; Fig. 12). A possible sister group relationship with *Asaphidion* + *Bembidion* indicated in Figs 11 and 12 is weakly supported and is not advocated in this paper (see below).

Trechini

The monophyly of the tribe Trechini is well supported with at least two unique larval synapomorphies: the lateral surface of the penultimate antennomere above the sensorium is sclerotized (character 14) and the frontale with secondary setae in older instars (character 58) (Fig. 12).

Trechini: Trechodina (Perileptus with Thalassophilus)

Classical trechine classification treats trechines as containing two major lineages: Trechina and Trechodina (Casale & Laneyrie, 1982), based on a difference in the male genitalia. Only *Thalassophilus* belongs in the

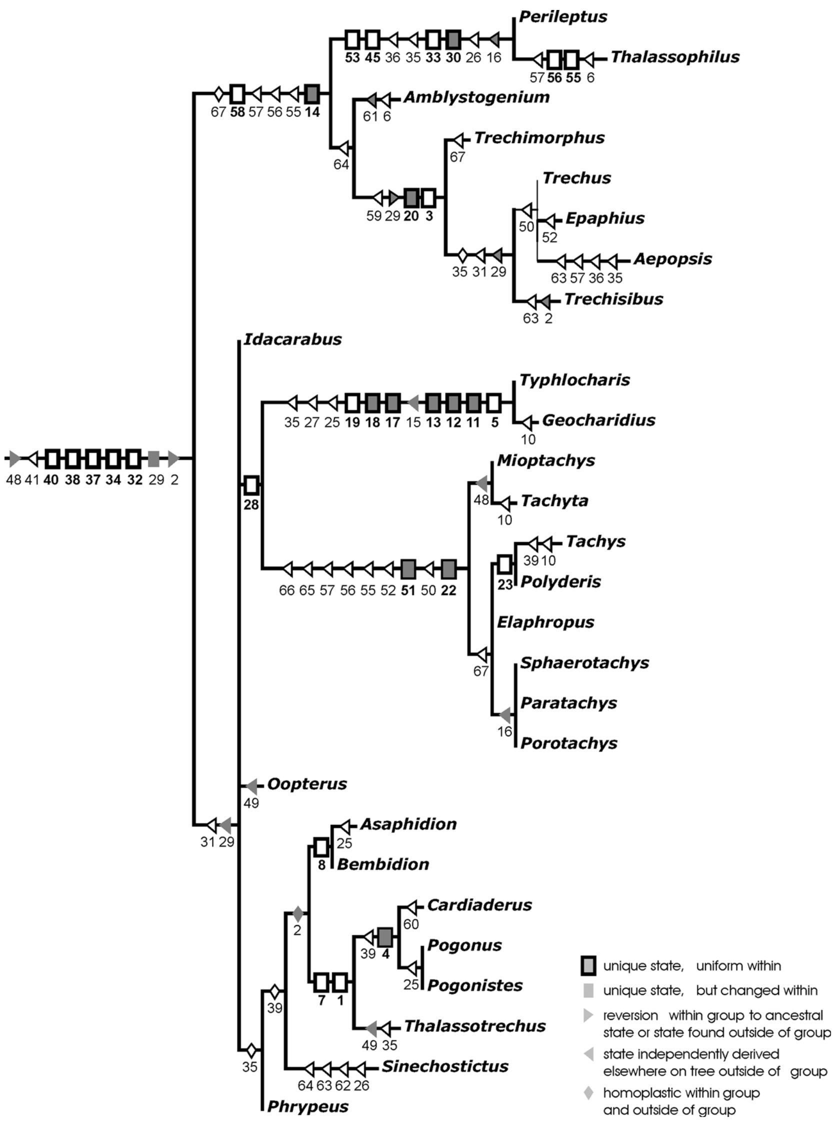

Fig. 12. Reconstruction of possible character evolution on one of the most parsimonious trees. Only unambiguously reconstructed character changes are shown. Only the character numbers are shown. Nonsensillar characters are dark grey; sensillar characters are white. The symbols indicate which changes represent the origin of unique states, or homoplastic states.

trechodines among those treated here. *Perileptus* is viewed as a Trechina (e.g. Casale & Laneyrie, 1982) and it might appear surprising that *Thalassophilus* grouped with *Perileptus*. However, Uéno (1989) stated that previous interpretation of male genitalia of *Perileptus* was incorrect, and that *Perileptus* was instead a trechodine, the opinion supported in the present study. The monophyly of *Perileptus* and *Thalassophilus* is supported by four unique synapomorphies: the presence of a hyaline structure on the dorsal surface of a claw (character 30); long and flat claw seta (character 33); seta UR3 on urogomphi located near seta UR4 (character 45) and sensillum ES1 on the mesothorax absent (character 53). Additionally, two more synapomorphic characters of *Perileptus* and *Thalassophilus*, namely the presence of terebral teeth (character 16) and the flat shape of seta LA6 on the ligula, are also derived independently in some members of the tribes Tachyina (*Sphaerotachys*, *Paratachys*, *Porotachys*) and Bembidiina (*Sinechostictus*), respectively.

Trechini: Trechina

The monophyly of the subtribe Trechina is supported by only one synapomorphy: the presence of secondary femoral setae in older-instar larvae (character 64). The same derived character state was also found in larvae of Bembidiini (*Sinechostictus*) and Pogonini (at least one species within the genus *Pogonus*). However, there is a difference in the way these secondary setae are arranged on the femur. In Trechina, these setae are rather stout, located on the ventral surface and always constant in number between species and among different specimens. In *Sinechostictus* and *Pogonus cumanus* Lutshnik, the secondary setae on the femur are thin, not restricted to the ventral surface and vary in number between species (in *Sinechostictus*) and also among different specimens and different legs of the same larva. Therefore, it might be assumed that the conditions of these setae in Trechina are unique and therefore this is a unique synapomorphy of the group.

Trechini: Trechina minus Amblystogenium

The monophylum containing the Trechina genera *Trechisibus*, *Aepopsis*, *Aepopsis*, *Trechus* and *Trechimorphus* is well supported by two unique synapomorphies: two setae at anterior angles of the epipharynx (setae CI1; character 3) and apical palpomeres of maxillary and labial palp subdivided on three and two subsegments, respectively. Moreover, the clade is supported by a partial reduction of the second claw (character 29, state 2) and the presence of one secondary seta on the apex of the second antennomere in older-instar larvae (character 59). The last character is unique within Trechitae and is probably a good synapomorphy for the monophylum in question. It is present, however, in one of the outgroups (*Pterostichus adstrictus* Eschscholtz) and therefore is shown in Fig. 12 as independently derived elsewhere in the tree.

Trechini: Trechina: Trechisibus, Aepopsis, Epaphius and Trechus

This monophylum is one of two groups within Trechitae supported by two synapomorphies: only one claw (character 29, state 3) and attachment to claw seta on the base of the claw (character 31). Such correlation of these two characters suggests that they might be genetically or developmentally connected and therefore not independent evidence of a relationship.

Lack of evident monophyly of Bembidiini (Bembidiina + Tachyina + Xystosomina + Anillina)

The tribe Bembidiini (*s. lato*; including subtribes Bembidiina, Tachyina, Xystosomina, and Anillina) has no support based on larval morphology. However, both Bembidiina, on one hand (see below), and Tachyina + Xystosomina + Anillina, on the other hand (see below, also Grebennikov, 2002), are supported. This result is consistent with the opinion expressed by Kryzhanovskij (1983) that these two groups are separate and not necessarily related. However, it is also consistent with the two being each other's sister groups, but with their common ancestral branch having acquired no evident, derived features during its history.

Bembidiini: Anillina

The subtribe Anillina appears in our study as a well-defined monophylum (Fig. 12), which supports the opinion of Jeannel (1937, 1963). Five unique larval apomorphies strongly corroborate that Anillina is indeed a monophylum: the basal antennomere with two pores (character 11); antennomere 2 markedly reduced in length or absent (character 12); antennal fossa separated from pleurosoma by a wide strip of sclerotized cuticle (character 13); terebra with two teeth, each not less than the retinaculum (character 17), and the retinaculum markedly reduced (character 18). It should be kept in mind that larvae of only two of sixty Anillina genera are known (Arndt *et al.*, 1999; Grebennikov, 2002). Adults of Anillina are markedly diverse and recorded from all zoogeographical regions. It might be expected that such strong support of the monophyly of Anillina will gradually weaken when more larvae of the group are known.

Bembidiini: Anillina + (Tachyina + Xystosomina)

Anillina and Tachyina + Xystosomina share at least one unique synapomorphy: the absence of seta LA5 on ligula (character 28). This grouping, however, is suggested only weakly if sensillar characters are downweighted as compared with nonsensillar characters, and this group completely disappears when all characters are treated as equally weighted (Fig. 11). With equal weighting, it is equally parsimonious to place Tachyina + Xystosomina with Trechini (and Anillina with Bembidiina + Pogonini) as it is to place Tachyina + Xystosomina with Anillina. Recovery of Anillina + Tachyina + Xystosomina does not depend upon downweighting all sensillar characters, however. Downweighting only four (characters 53, 55–57) will yield the same MPTs as downweighting all sensillar characters. Characters 53 and 55–57 represent a common reduction in four setae of the thorax and abdomen in Tachyina + Xystosomina and Trechina. If these four characters are genetically related, as is possible, and thus not fully independent, then they may not be providing the independent evidence of a relationship that the equally weighted analysis assumes. If this assumption is true, than Anillina and Tachyina + Xystosomina would become a more strongly supported clade, as it is believed by Grebennikov (2002).

Bembidiini: Bembidiina: Sinechostictus

Larvae of the bembidiine genus *Sinechostictus* were studied recently in detail (Grebennikov, 1997) and it was concluded that it did not belong within *Bembidion*. The current study supports this view, as *Sinechostictus* is outside of a monophylum containing *Asaphidion* and *Bembidion*;

the unique synapomorphy supporting this clade is the placement of FR4 very close to FR5 (character 5).

However, *Sinechostictus* may still be a bembidiine based on a larval synapomorphy: the absence of pore PRh (character 39 in the present study). This character state was discovered later in larvae of *Tachys* and *Thalassotrechus*, the members of the tribes Tachyini and Pogonini, respectively, and is very likely a convergence. In the present study, *Sinechostictus* does not group with Bembidiina and instead lies as a sister group to Bembidiina + Pogonini based on the absence of pore PRh, whereas the larvae of the pogonine genera *Cardiaderus*, *Pogonus* and *Pogonistes* are assumed to regain the presence of this pore (Fig. 12; character 39). The secondary reappearance of pore PRh seems to be a rather unlikely scenario. Therefore, sister group relationships of *Asaphidion* + *Bembidion* and Pogonini, as well as *Sinechostictus* being a sister to them all, are not considered well supported. For a detailed description of the *Sinechostictus* larvae see Grebennikov (1997).

Bembidiini: Bembidiina: Phrypeus

Larvae of the North American genus *Phrypeus* were unknown previously. The genus was treated as a Bembidiina (see Lindroth, 1963), although Erwin (1972) notes some unusual (and possibly primitive) features of adults, including the nearly symmetrical basal lobes of the male genitalia and the relatively deep frontal furrows on the head. Our study does not firmly solve the relationships of the genus. It is not within the group *Asaphidion* + *Bembidion* + *Sinechostictus*, as it has pore PRh on the prothorax (character 39) and, moreover, setae FR4 and FR5 on the frontale are not drawn together (the advanced state of character 8 is also missing in *Sinechostictus*, which might also belong to Bembidiina). However, we have no evidence that *Phrypeus* is not within Bembidiina. Larvae of *Phrypeus* have a remarkable number of plesiomorphic character states and, therefore, along with zoline genera *Oopterus* and *Idacarabus*, come out from a 'basal' Trechitae (exclusive of Trechini) polytomy.

Evolution of claws and associated structures

The current study supports a hypothesis that a reduction in the number of claws in Trechitae from two to one has taken place twice: in 'advanced' Trechini (genera *Trechus*, *Epaphius*, *Aepopsis* and *Trechisibus*) and in a clade of Zolini + Bembidiini + Pogonini. Trechini larvae demonstrate a transformation series from two almost equally long claws (*Thalassophilus* and *Perileptus*) towards the posterior claw being three quarters of the anterior (*Amblystogenium*), one half of the anterior (*Trechimorphus*) and finally complete reduction (*Trechus*, *Epaphius*, *Aepopsis* and *Trechisibus*). We hypothesize that larvae of other Trechodina taxa also have two claws. No such transformation series is known among larvae of other Trechitae tribes; all have one-clawed legs. On both occasions the complete reduction of the posterior claw (character 29/4) was accompanied by the migration of the claw seta from the basal claw membrane on to the base of the claw (character 31). It is possible that these two characters are genetically related and, therefore, should be treated as a single character.

It should be noted that a similar process of the reduction from two claws to one has taken place apparently independently in the carabid tribe Clivinini. The majority of Clivinini larvae have a single claw, except for the two-clawed larva of the genus *Schizogenius* Putzeys, recently described by Bousquet (1996). It should also be noted that *Schizogenius* larvae have a hyaline structure on the dorsal surface of the claw, rather similar to that discovered in *Thalassophilus* and *Perileptus* larvae (character 30).

Concluding remarks

Larvae of the several Trechitae taxa are unknown and could greatly contribute to our knowledge of the phylogeny of the group. Of particular interest are the cave trechodines *Canarobius* Machado, and *Spelaeovulcania* Machado from the Canary Islands (Machado, 1987b); the tachyine *Tasmanitachoides* Erwin, from Australia (Erwin, 1972); *Lymnastis* and *Micratopus*; the bembidiines *Amerizus* Chaudoir, *Bembidarenas* Erwin from South America, *Orzolina* Machado from the Canary Islands, *Hoquedela* Müller-Motzfeld from the Himalayas and *Caecidium* Uéno, from Japan (Uéno, 1971; Machado, 1987a; Müller-Motzfeld, 1988; Müller-Motzfeld & Schmidt, 2001); any additional anilline genus; the zolines *Chaltenia* from Argentina and *Sinozolus* from China; the pogonine *Olegius* from Turkmenistan. In addition, *Lissopogonus* Andrewes, from South East Asia, as an unusual member of the outgroup taxon Patrobini, would provide additional data to confirm the root of the Trechitae tree.

Acknowledgements

We are grateful to the collectors and curators who made Trechitae larvae under their care available for our study. Vasily Grebennikov's interest in Trechitae was initiated and generously supported by Igor A. Belousov in St. Petersburg, Russia. Vasily Grebennikov would like to thank Inessa Khristianovna Sharova (Moscow, Russia) and Yves Bousquet (Ottawa, Canada) for their support during and after the preparation of his PhD thesis on Trechitae larvae in 1994–98 in Moscow and Ottawa. His 1 year stay in Ottawa was sponsored by the Russian Federation Presidential Fellowship. He would also like to acknowledge the subsequent financial support contributing to finishing this paper: Visiting Fellowship (Canadian Museum of Nature, Ottawa, Canada), Visiting Fellowship (Field Museum of Natural History, Chicago, U.S.A.), Ernst Mayr Fellowship (Museum of Comparative Zoology, Cambridge, U.S.A.), Alexander von Humboldt Fellowship (Bonn, Germany) and Postdoctoral Fellowship (University of Pretoria, South Africa). Much of David Maddison's work raising trechite larvae was carried out while an MSc student at the University of Alberta with George E. Ball; for the inspiration George provided then, as he does now, David is ever grateful.

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Accepted 26 February 2004
First published online 10 December 2004

Appendix 1

List of terminal taxa autapomorphies.

1. Genus *Perileptus* Schaum, 1860

Autapomorphies: Antennomere 3 with nearly round sensorium (L1–3). See also Grebennikov & Luff (1999).

2. Genus *Thalassophilus* Wollastone, 1854

Autapomorphies: Antennomere 3 with markedly elongated sensorium (L1); abdominal segments 2–7 with additional seta on each side of medial ventral sclerite (L1). See also Grebennikov (1996).

3. Genus *Amblystogenium* Enderlein, 1905

Autapomorphies: Not found.

4. Genus *Trechimorphus* Jeannel, 1927

Autapomorphies: Not found. See also Arndt (2000).

5. Genus *Trechus* Clairville, 1806

Autapomorphies: Not found. See also Jeannel (1920).

6. Genus *Epaphius* Stephens, 1827

Autapomorphies: Not found. See also Jeannel (1920).

7. Genus *Aepopsis* Jeannel, 1922

Autapomorphies: Apex of fourth antennomere with one conical sensillum instead of two (L1–3); setae FR10 and FR11 removed basally on dorsal surface from the apical margin of frontale (L1–3); terga of meso- and metathorax lack pore MEa, and abdominal terga 1–8 lack pore TEa (L1–3). See also Grebennikov & Luff (1998).

8. Genus *Trechisibus* Motschulsky, 1863

Autapomorphies: Not found. See also Arndt (2000).

9. Genus *Idacarabus* Lea, 1910

Autapomorphies: Third antennomere present with one campaniform sensillum near sensorium instead of two (L3); fourth antennomere with seta AN7 reduced in size to nontrichoid sensillum (L3). See also Grebennikov (1999).

10. Genus *Oopterus* Guérin-Méneville, 1841

Autapomorphies: Not found. See also Johns (1974), Grebennikov (1999) and Arndt (2000).

11. Genus *Typhlocharis* Dieck, 1869

Autapomorphies: Apically rounded nasale without serration (L3); seta PA5 absent (L3); second antennomere absent (L3). See also Arndt *et al.* (1999).

12. Genus *Geocharidius* Jeannel, 1963

Autapomorphies: Not found. See also Grebennikov (2002).

13. Genus *Mioptachys* Bates, 1882

Autapomorphies: Not found. See also Grebennikov & Maddison (2000).

14. Genus *Tachyta* Kirby, 1837

Autapomorphies: Claw with seta UN1 long and thick, as long as proximal width of claw (L1–3); antennomere III with sensorium markedly reduced in size (L1–3); stipes with four setae in gMX (L1). See also Grebennikov & Maddison (2000).

15. Genus *Tachys* Stephens, 1829

Autapomorphies: Not found. See also Grebennikov & Maddison (2000).

16. Genus *Polyderis* Motschulsky, 1862

Autapomorphies: Not found. See also Grebennikov & Maddison (2000).

17. Genus *Sphaerotachys* G. Müller, 1926

Autapomorphies: Not found. See also Grebennikov & Maddison (2000).

18. Genus *Elaphropus* Motschulsky, 1839

Autapomorphies: Not found. See also Grebennikov & Maddison (2000).

19. Genus *Paratachys* Casey, 1918

Autapomorphies: Not found. See also Grebennikov & Maddison (2000).

20. Genus *Porotachys* Netolitzky, 1914

Autapomorphies: Not found. See also Grebennikov & Maddison (2000).

21. Genus *Asaphidion* Des Gozis, 1886

Autapomorphies: Frayed setae present (L1–3); posterior angles of all thoracic tergites with conical sensillae (L1); setae LA6 on ligula divergent anteriorly with angle about 30° between them (L1–3); hypopleurites with additional seta (L1). See also Maddison (1993).

22. Genus *Bembidion* Latreille, 1802

Autapomorphies: Not found. See also Maddison (1993).

23. Genus *Sinechostictus* Motschulsky, 1864

Autapomorphies: Combination of strongly sclerotized reddish-brown head and poorly pigmented whitish body (L1–3); teeth of epipharynx very small, subequal, arranged in parallel rows (L1–3); dorsal side of claws with two furrows (L1–3); lateral sides of maxillae with different number of secondarily setae in second (1) and third (2) instars (L3); parietale with secondary setae vassal of PA15 (L3); epipleurite with long seta EP2 and very short additional seta near EP1 (L3); secondary seta near UR2 short, not longer than UR3. See also Grebennikov (1996).

24. Genus *Phrypeus* Casey, 1924

Autapomorphies: Not found.

25. Genus *Cardiaderus* Dejean, 1829

Autapomorphies: Terga of meso-, metanotum and abdominal segments I–VIII with numerous secondary setae on their medial parts close to central line. See also Grebennikov & Bousquet (1999).

26. Genus *Pogonus* Dejean, 1822

Autapomorphies: Not found. See also Grebennikov & Bousquet (1999).

27. Genus *Pogonistes* Chaudoir, 1870

Autapomorphies: Not found. See also Grebennikov & Bousquet (1999).

28. Genus *Thalassotrechus* Van Dyke, 1918

Autapomorphies: Medial margin of terebra slightly convex near base (L1). See also Grebennikov & Bousquet (1999).

Appendix 2

Identification key to larvae of the supertribe Trechitae (Coleoptera: Carabidae). Symbols (L1) and (L2–3) before a character in the key 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; hypopleural plates without setae .... first-instar larva (L1)

1*. Lateral side of stipes with three and more setae; uro-gomphi with six to seven (rarely more) long setae; hypo-pleural plates with setae ....second- or third-instar larva (L2–3)

Identification key to tribes and genera of the supertribe Trechitae

1. One claw 5

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

2(1*). Claw seta not longer than one fifth of claw's length; longest claw without hyaline structure on dorsal surface; urogomphi with seta UR3 near seta UR2; incisor area of mandibles without serration........... 3

2*. Claw seta longer than one half of claw's length; longest claw with hyaline structure on dorsal surface; urogomphi with seta UR3 near seta UR4; incisor area of mandibles with serration................ 4

3(2). Antennomere 2 with one long seta at apex .... *Trechimorphus* (only older instars known)

3*. Antennomere 2 without setae................................. ....*Amblystogenium* (only older instars known)

4(2*). Pore PAb on parietale present; antennomere 3 with round sensorium; (L1) sensillum EM1 on meso- and metathorax present, porelike; (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 porelike sensilla ....*Perileptus*

4*. 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*

5(1). Mandible in addition to retinaculum with two teeth in apical part ....6 (Anillina)

5*. Mandible in addition to retinaculum with no apical teeth (rarely with even and small serration along terebra) 7

6(5). Antenna three-segmented .... *Typhlocharis*

6*. Antenna four-segmented .... *Geocharidius*

7(5*). Head width about 0.29 mm; nasale as in Fig. 10; distance between setae FR3 and FR4 about two times longer than between FR4 and 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)

7*. At least one of the characters is different 8

8(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......................... 9 (Trechini, in part)

8*. 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 10

9(8). Pores MEa on meso- and metathorax and TEa on abdominal terga 1–8 absent .... *Aepopsis*

9*. Pores MEa on meso- and metathorax and TEa on abdominal terga 1–8 present ....*Trechus, Epaphius* and *Trechisibus*

10(8). Base of stipes on medial side with one or more teeth; seta LA5 on ligula always absent; (L2–3) urogomphi with six long setae; (L1) epicranial stem sorter than diameter of proximal antennomere or absent .... (Tachyina and Xystosomina)

10*. Base of stipes on medial side without teeth; seta LA5 on ligula present (except *Idacarabus*); (L2–3) urogomphi with seven (rarely more) long setae; (L1) epicranial stem longer than diameter of proximal antennomere 19

11(10). 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) group gMX on stipes with five setae; (L2–3) lateral sides of tergum 9 without long secondary seta at middle 12

11*. 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) group gMX on stipes with six setae; (L2–3) lateral sides of tergum 9 with long secondary seta at middle 13

12(11). (L1) Parietale near seta PA6 with meshed microsculpture; (L1) distal seta of group gMX on stipes situated proximad of level of seta MX5.. *Tachyta*

12*. (L1) Parietale near seta PA6 smooth, without microsculpture; (L1) distal seta of group gMX on stipes situated distad of level of seta MX5 .... *Mioptachys* (only first instar known)

13(11*). Mandible with serration on incisor area 14

13*. Mandible without serration on incisor area 16

14(13). Incisor area with about ten small and equal teeth; (L1) frontale near pore FRb smooth, without microspines ....*Sphaerotachys*

14*. Incisor area with three to five large teeth in proximal half and some small teeth distally; (L1) frontale near pore FRb with microspines 15

15(14). 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*

15*. 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*

16(13*). Pore PRh on protergum absent................. *Tachys*

16*. Pore PRh on protergum present 17

17(16*). Pore PAb on parietale absent....*Polyderis* (in part)

17*. Pore PAb on parietale present......................... 18

18(17*). (L1) Seta FR9 on frontale more than two times longer than FR5; parietale laterad of seta PA3 with microspines ....*Elaphropus*

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

19(10*). Spindlelike 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 ....20 (Pogonini)

19*. Spindlelike setae absent; frontal arms curved; nasale only rarely with two protruding parts... 23

20(19). 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 spindlelike .... *Thalassotrechus*

20*. 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

21(21*). Length of setae MX11 and MX12 less than one quarter 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*

21*. 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 22

22(21*). (L1) Dorsal surface of mandible between MN1 and MNb with one to eight (usually two to four) microspines; (L1) seta PY6 on pygidium spindlelike .... *Pogonus*

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

23(19*). 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 .... 24 (Bembidiina, in part: without *Phrypeus*)

23*. 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......................... 26 (Zolini)

24(23). Setae FR4 and FR5 on frontale somewhat distantly located, distance between them not less than half 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*

24*. Setae FR4 and FR5 on frontale drawn together, distance between them less than one third 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 25

25(24*). 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 about 30° between them; (L1) posterior angles of thoracic and abdominal terga with conical sensillae .... *Asaphidion*

25*. Dorsal and lateral sclerites of body with simple setae only; setae MX11 and MX12 shorter than one quarter width of maxillary palpomere 3; setae LA6 on ligula parallel to each other; (L1) posterior angles of thoracic and abdominal terga without conical sensillae .... *Bembidion*

26(23*). Ligula with setae LA5; posterior row of stemmata with single stemma; seta FR2 about two times 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 thirty to thirty-three setae; seta MX6 subequal in length to MX5; (L2–3) lateral side of stipes with four setae; (L2–3) lateral side of labium with five to six setae .... *Oopterus*

26*. 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 than one twentieth length of apical antennomere; (L2–3) stipes with gMX consisting of eight setae; seta MX6 two times longer than MX5; (L2–3) lateral side of stipes with three setae; (L2–3) lateral side of labium with two to three setae.. *Idacarabus*

Appendix 3. List of taxa studied, current depository of the material and indication of whether the larvae were reared *ex ovo* '+' or identified by association '(+)'.

Tribe or subtribe	Genus	Species	L1	L2–3	Depository
Pterostichini	*Pterostichus* Bonelli, 1810	*P. adstrictus* Eschscholtz, 1823	+		DRM
Patrobini	*Platypatrobus* Darlington, 1938	*P. lacustris* Darlington, 1938	+	+	CNC, DRM
	Diplous Motschulsky, 1850	*D. aterrimus* Dejean, 1828	+	+	CNC, DRM
	Patrobus Dejean, 1821	*P. longicornis* Say, 1823	+	+	CNC, DRM
Zolini	*Oopterus* Guérin-Méneville, 1841	*O. soledadinus* (Guérin-Méneville, 1832)		(+)	NHML
	Idacarabus Lea, 1910	*I. cordicollis* Moore, 1967		(+)	ANCI
Trechini	*Perileptus* Schaum, 1860	*P. areolatus* (Creutzer, 1799)	+	+	VVG
		P. mesasiaticus Uéno, 1976	+	+	VVG
	Thalassophilus Wollastone, 1854	*T. longicornis* (Sturm, 1825)	+		VVG
	Amblystogenium Enderlein, 1905	*A. minimum* Luff, 1972		+	MLL, VVG
	Trechimorphus Jeannel, 1927	*T. diemenesis* Bates, 1878		(+)	ANCI
	Trechus Clairville, 1806	*T. quadristriatus* (Schrank, 1781)		(+)	MPGU
		T. fischtensis Reitter, 1883		(+)	VVG
		T. gravidus Putzeys, 1870		(+)	MPGU
		Trechus sp.	+		DRM
	Epaphius Stephens, 1827	*E. secalis* (Paykull, 1790)	(+)	(+)	MPGU
	Aepopsis Jeannel, 1922	*A. robinii* (Laboulbene, 1849)	(+)	(+)	MLL
	Trechisibus Motschulsky, 1863	*T. angularis* Jeannel, 1962	+		JRC
Anillina	*Typhlocharis* Dieck, 1869	*Typhlocharis* sp.		(+)	EAC, VVG
	Geocharidius Jeannel, 1963	*Geocharidius* sp.	(+)		MCZ
Xystosomina	*Mioptachys* Bates, 1882	*M. flavicauda* (Say, 1823)	+		DRM
Tachyina	*Tachyta* Kirby, 1837	*T. nana* s.str. (Gyllenhal, 1810)	+	+	VVG
	Tachys Stephens, 1829	*T. scutellaris* (Stephens, 1829)	+	+	VVG
		T. vittatus Motschulsky, 1850		+	VVG
		T. centriustatus Reitter, 1874	+	+	VVG
		T. halophilus Lindroth, 1966	+		DRM
	Polyderis Motschulsky, 1862	*P.?rufotestacea* (Hayward, 1900)	+		DRM
		P. laevis (Say, 1823)		+	DRM
	Sphaerotachys G. Müller, 1926	*S. haemorrhoidalis* (Ponza, 1805)	+	+	VVG
	Elaphropus Motschulsky, 1839	*E. tripunctatus* (Say, 1830)	+	+	DRM
		E. diabrachys Kolenati, 1845	+	+	VVG
	Paratachys Casey, 1918	*P. bistriatus* Duftschmid, 1812	+	+	VVG
	Porotachys Netolitzky, 1914	*P. bisulcatus* (Nicolai, 1822)	+	+	VVG
Bembidiina	*Asaphidion* Des Gozis, 1886	*A. caraboides* (Schrank, 1781)	+	+	VVG
		A. alaskanum Wickham, 1919	+		DRM
		A. transcaspicum Senemov, 1889	+	+	VVG
		A. flavipes (Linnaeus, 1761)	+	+	VVG
		A. austriacum Schweiger, 1975	+	+	VVG
		A. curtum (Heyden, 1870)	+	+	DRM
		A. pallipes (Duftschmid, 1812)	+	+	VVG
		A. yukonense Wickham, 1919	+		CNC
	Bembidion Latreille, 1802	*B. (Bracteon) foveum* Motschulsky, 1845	+		DRM
		B. (B) balli Lindroth, 1962	+	+	DRM
		B. (B) argenteolum (Ahrens, 1812)	+	+	VVG
		B. (B) alaskense Lindroth, 1962	+	+	DRM
		B. (B) carinula Chaudoir, 1868	+	+	DRM
		B. (B) lapponicum Zetterstedt, 1828	+	+	DRM
		B. (B) punctatostriatum Say, 1823	+	+	DRM
		B. (B) hesperium Casey, 1918	+	+	DRM
		B. (B) lorquinii Chaudoir, 1868	+	+	DRM
		B. (B) zephyrum Fall, 1910	+	+	DRM
		B. (B) levettei Casey, 1918	+	+	DRM
		B. (B) inaequale Say, 1823	+	+	DRM
		B. (Odontium) striatum (Fabricius, 1792)	+	+	VVG
		B. (O) bowditchii LeConte, 1878	+		DRM
		B. (O) coxendix Say, 1823	+	+	DRM
		B. (O) confusum Hayward, 1897	+	+	DRM
		B. (O) aenulum Hayward, 1901	+	+	DRM
		B. (Ochthedromus) bifossulatum LeConte, 1851	+		DRM

		B. (Pseudoperyphus) chalceum Dejean, 1831	+		DRM
		B. (P) antiquum Dejean, 1831	+	+	DRM
		B. (P) integrum Casey, 1918	+		DRM
		B. (Eurytrachelus) laticolle (Duftschmid, 1812)	+	+	VVG
		B. (E) interventor Lindroth, 1963	+	+	DRM
		B. (Metallina) properans (Stephens, 1829)	+	+	VVG
		B. (M) lampros (Herbst, 1784)	(+)		VVG
		B. (Phyla) obtusum Serville, 1821	+	+	DRM
		B. (Princidium) punctulatum Drapiez, 1820	+	+	VVG
		B. (Testedium) bipunctatum (Linnaeus, 1761)	+	+	VVG
		B. kuprianovi Mannerheim, 1843	+		DRM
		B. (Plataphus) planatum LeConte, 1848	+		DRM
		B. (Hirmoplataphus) salebratum LeConte, 1848	+	+	DRM
		B. (H) concolor Kirby, 1837	+	+	DRM
		B. (Notaphus) obliquum Sturm, 1825	+	+	VVG
		B. (N) varium (Oliver, 1795)	+	+	VVG
		B. (N) umbratum LeConte, 1848	+	+	DRM
		B. (N) graphicum Casey, 1918	+	+	DRM
		B. (Furcacampa) timidum LeConte, 1848	+		DRM
		B. (Eupetedromus) dentellum (Thunberg, 1787)	+	+	VVG
		B. (Notaphemphanes) ephippium (Marsham, 1802)	+	+	VVG
		B. (Philochtus) biguttatum (Fabricius, 1779)	+	+	VVG
		B. (P) guttula (Fabricius, 1792)	+	+	VVG
		B. (Talanes) aspericolle (Germar, 1812)	+	+	VVG
		B. (Leja) articulatum (Panzer, 1796)	+	+	VVG
		B. (L) octomaculatum (Goeze, 1777)	+	+	VVG
		B. (Trepanedoris) doris (Panzer, 1797)	+	+	VVG
		B. (Semicampa) gilvipes Sturm, 1825	+	+	VVG
		B. (S) schuppelii Dejean, 1831	+	+	VVG
		B. (Diplocampa) assimile Gyllenhal, 1810	+	+	VVG
		B. (s. str.) *quadrimaculatum* (Linnaeus, 1761)	+	+	VVG,DRM
		B. (Nepha) caucasicum (Motschulsky, 1844)	+	+	VVG
		B. (N) glabrum Motschulsky, 1850	+	+	VVG
		B. (N) menetriesi Kolenati, 1845	+	+	VVG
		B. (N) seriatum (Motschulsky, 1844)	+	+	VVG
		B. (N) tetragrammum Chaudoir, 1846	+	+	VVG
		B. (N) tetrasemum Chaudoir, 1846		+	VVG
		B. (Bembidionetolitzkya) tibiale (Duftschmid, 1812)	+	+	VVG
		B. (B) depressum Menetries, 1832		(+)	VVG
		B. (B) kartalinicum Lutshnik, 1935	+	+	VVG
		B. (Ocydromus) andreae (Fabricius, 1787)	+	+	VVG
		B. (O) femoratum Sturm, 1825	+	+	VVG
		B. (O) parallelipenne Chaudoir, 1850	+	+	VVG
		B. (O) tetracolum Say, 1823	+	+	VVG
		B. (O) petrosum Gebler, 1833	+	+	DRM
		B. (O) obscurellum Motschulsky, 1845	+	+	DRM
		B. (O) scopulinum Kirby, 1837	+		DRM
	Sinechostictus Motschulsky, 1864	*S.* (s. str.) *ruficolle* Sturm, 1825	+	+	ZISP, VVG
		S. (s. str.) *nordmanni* Chaudoir, 1844	+	+	VVG
		S. (s. str.) *millerianum* Heyden, 1883		+	VVG
		S. (s. str.) *atroviolaceum* Dufour, 1820		+	VVG
		S. (Pseudolimnaeum) lederi Reitter, 1888		+	VVG
	Phrypeus Casey, 1924	*Phrypeus rickseckeri* Hayward, 1897	+		DRM
Pogonini	*Pogonus* Dejean, 1822	*Pogonus luridipennis* (Germar, 1822)	+	+	VVG
		Pogonus iridipennis Nicolai, 1822	+	+	VVG
		Pogonus transfuga Chaudoir, 1870	+	+	VVG
		Pogonus meridionalis Dejean, 1828	+	+	VVG
		Pogonus punctulatus Dejean, 1828	+	+	VVG
		Pogonus cumanus Lutshnik, 1916	+	(+)	VVG
	Pogonistes Chaudoir, 1870	*Pogonistes rufoaeneus* (Dejean, 1828)	+	+	VVG
		Pogonistes convexicollis Chaudoir, 1871	+	+	VVG
		Pogonistes angustus (Gebler, 1830)	+	+	VVG
	Cardiaderus Dejean, 1829	*Cardiaderus chloroticus* (F. von Waldheim, 1823)	+	+	VVG
	Thalassotrechus Van Dyke, 1918	*Thalassotrechus barbarae* (G. H. Horn, 1892)	+		CNC, CAS

Appendix 4

Characters of Trechitae (Coleoptera: Carabidae) larvae and their states as coded in the matrix. Unless otherwise indicated, characters were treated as unordered.

1. *Spindlelike setae on body*: (0) absent; (1) present (Grebennikov & Bousquet, 1999: fig. 17).
2. *Number of stemmata*: (0) six (Fig. 1); (1) zero to five (Figs 2, 5, 8).
3. *Number of setae in anterior angles of epipharynx (seta or setae CI1)*: (0) one (Fig. 10); (1) two.
4. *Frontal suture*: (0) sinuate (Figs 3, 5); (1) nearly straight (Grebennikov & Bousquet, 1999: figs 2–5, 7–9, 24–26).
5. *Pore FRa on frontale*: (0) present (Fig. 5); (1) absent (Arndt *et al*., 1999: fig. 1; Grebennikov, 2002: fig. 1).
6. *Pore PAb on parietale*: (0) present (Fig. 5); (1) absent (Fig. 3; Grebennikov, 1996: fig. 2).
7. *Ratio of distances FR2–FR3 to FR1–FR2*: (0) 1.5 and less (Fig. 5); (1) 2 and more (Grebennikov & Bousquet, 1999: figs 2–9).
8. *Ratio of distances FR3–FR4 to FR4–FR5*: (0) 1–4 (Fig. 5); (1) 5 and more (Maddison, 1993: fig. 194).
9. *Location of seta FR6 on frontale*: (0) at lateral margins (Fig. 5); (1) mediad from lateral margins (Grebennikov & Maddison, 2000: figs 3–10).
10. *Location of pore PAb on parietale*: (0) distal of level PA2 (Fig. 5); (1) at level of PA2 (Grebennikov & Maddison, 2000: fig. 5).
11. *Basal antennomere*: (0) with five pores (Fig. 5); (1) with two pores (Grebennikov, 2002: fig. 1).
12. *Antennomere 2*: (0) of normal size (Figs 3, 5); (1) markedly reduced in length (Grebennikov, 2002: fig. 1) or absent (Arndt *et al*., 1999: fig. 1).
13. *Antennal fossa separated from pleurosoma by*: (0) a weak membrane (Figs 3, 5); (1) a wide strip of sclerotized cuticle (Arndt *et al*., 1999: fig. 1; Grebennikov, 2002: fig. 1).
14. *Lateral surface of penultimate antennomere above base of sensorium*: (0) membranous (Fig. 5); (1) sclerotized (Fig. 3; Grebennikov, 1996: fig. 5).
15. *Penicillus*: (0) present (Grebennikov & Maddison, 2000: fig. 19); (1) absent (Arndt *et al*., 1999: figs 3, 5).
16. *Small and numerous (more than three) teeth on terebra*: (0) absent (Figs 3, 5); (1) present (Grebennikov & Maddison, 2000: figs 54–56).
17. *Two teeth on terebra, each not less than retinaculum*: (0) absent (Figs 3–6); (1) present (Arndt *et al*., 1999: figs 1, 3, 5; Grebennikov, 2002: fig. 1).
18. *Size of retinaculum*: (0) of normal size (Figs 3–6); (1) markedly reduced (Arndt *et al*., 1999: figs 1, 3, 5; Grebennikov, 2002: fig. 1).
19. *Seta MD2 on mandible*: (0) much shorter than retinaculum (Grebennikov, 1996: fig. 6); (1) as long as retinaculum (Grebennikov, 2002: fig. 1).
20. *Apical labial and maxillar palpomere*: (0) complete (Figs 3–6); (1) subdivided on three and two subsegments, respectively.
21. *Presence of lacinia*: (0) present; (1) absent (Figs 3–6).
22. *One or more teeth at base of stipes*: (0) absent (Figs 6, 8); (1) present (Grebennikov & Maddison, 2000: figs 40–48).
23. *Location of pore MXc on ventral surface of stipes*: (0) in distal fourth (Grebennikov, 1996: fig. 7); (1) at middle (Grebennikov & Maddison, 2000: fig. 45).
24. *Length of seta MX6 to MX5 (ordered)*: (0) about ten times shorter (Bousquet & Grebennikov, 1999: fig. 13); (1) about half (Grebennikov, 1996: fig. 7); (2) not shorter (Arndt *et al*., 1999: figs 7, 8).
25. *Length of setae MX11 and MX 12*: (0) shorter than quarter of width of maxillary palpomere 3 (Grebennikov, 1996: fig. 7); (1) longer than half as wide (Arndt *et al*., 1999: figs 7, 8).
26. *Shape of seta LA6 on ligula*: (0) conical (Arndt *et al*., 1999: fig. 2); (1) flat (Grebennikov, 1996: fig. 10; Grebennikov & Luff, 1999: figs 9–11).
27. *Seta LA4 on labium*: (0) present (Grebennikov, 1996: fig. 6); (1) absent (Arndt *et al*., 1999: fig. 2).
28. *Seta LA5 on labium*: (0) basal, close to LA4; (1) proximal, on ligula, close to LA6 (Grebennikov, 1997: figs 5, 6, 10); (2) absent (Grebennikov & Maddison, 2000: figs 40–48).
29. *Number and shape of claws (irreversible)*: (0) two, equal (Bousquet & Grebennikov, 1999: fig. 11); (1) two, posterior about three quarters of anterior (Grebennikov, 1996: fig. 11); (2) two, posterior less than one half of anterior; (3) one (Fig. 7).
30. *Hyaline structure on dorsal surface of claw*: (0) absent (Grebennikov & Maddison, 2000: figs 18, 21); (1) present (Grebennikov & Luff, 1999: figs 13, 14).
31. *Attachment of claw setae*: (0) on basal claw membrane (Fig. 7); (1) on base of claw (Bousquet & Grebennikov, 1999: fig. 11; Grebennikov & Luff, 1999: fig. 14).
32. *Number of claw setae*: (0) two (Bousquet & Grebennikov, 1999: fig. 11); (1) one (Fig. 7).
33. *Claw seta*: (0) short and conical (Fig. 7); (1) long and flat (Grebennikov & Luff, 1999: figs 13, 14).
34. *Setae TA3–6*: (0) present (Bousquet & Grebennikov, 1999: fig. 11); (1) absent (Grebennikov & Maddison, 2000: fig. 18).
35. *Location of seta TA1 on tarsus*: (0) in basal third (Grebennikov, 1996: fig. 11); (1) in middle (Grebennikov & Maddison, 2000: fig. 18).
36. *Length of setae TI1 and TI2*: (0) not longer than other apical setae on tibia (Grebennikov & Maddison, 2000: fig. 21); (1) more than 1.5× longer (Grebennikov & Luff, 1999: fig. 12).
37. *Pore PRc on prothoracic tergum*: (0) present; (1) absent (Fig. 7).
38. *Pore PRe on prothoracic tergum*: (0) present; (1) absent (Fig. 7).
39. *Pore PRh on prothoracic tergum*: (0) present (Fig. 7); (1) absent.
40. *Pore PRi on prothoracic tergum*: (0) present; (1) absent (Fig. 7).

41. *Pore PRj on prothoracic tergum*: (0) present; (1) absent (Fig. 7).
42. *Pore MEd on meso- and metathoracic terga*: (0) present; (1) absent (Fig. 7).
43. *Pore MEe on meso- and metathoracic terga*: (0) present; (1) absent (Fig. 7).
44. *Pore TEb on abdominal terga 1–8*: (0) present; (1) absent (Fig. 7).
45. *Location of UR3 on urogomphi*: (0) near UR2 (Fig. 8); (1) near UR4 (Grebennikov, 1996: fig. 12).
46. *Shape of frontal arms*: (0) weakly or not sinuate, closer to V (Fig. 5); (1) markedly sinuate, closer to U (Grebennikov & Maddison, 2000: figs 3, 4).
47. *Epicranial stem*: (0) present (Fig. 5); (1) absent (Grebennikov, 2002: fig. 1).
48. *Egg-bursters on frontale*: (0) present as a keel (Bousquet & Grebennikov, 1999: fig. 8); (1) present as very faint teeth of microsculpture or absent (Fig. 5); (2) present as separate teeth (Fig. 1; Grebennikov & Maddison, 2000: figs 3, 4).
49. *Egg-bursters on parietale*: (0) absent (Fig. 5); (1) present (Grebennikov & Bousquet, 1999: fig. 6).
50. *Number of setae in gMX*: (0) more than six (Bousquet & Grebennikov, 1999: fig. 13); (1) six and less (Grebennikov & Maddison, 2000: figs 40–44).
51. *Teeth on coxa*: (0) absent; (1) present.
52. *Sensillum EM1 on prothorax (ordered)*: (0) seta (Fig. 7); (1) pore; (2) absent.
53. *Sensillum ES1 on mesothorax (ordered)*: (0) seta (Fig. 7); (1) pore; (2) absent (Grebennikov, 1996: fig. 13).
54. *Sensillum ES1 on metathorax (ordered)*: (0) seta; (1) pore; (2) absent.
55. *Sensillum EM1 on mesothorax (ordered)*: (0) seta; (1) pore; (2) absent.
56. *Sensillum EM1 on metathorax (ordered)*: (0) seta; (1) pore; (2) absent (Grebennikov, 1996: fig. 13).
57. *Sensillum EP1 on IX abdominal segment (ordered)*: (0) seta; (1) pore (Grebennikov & Luff, 1999: fig. 17); (2) absent (Grebennikov, 1996: fig. 12).
58. *Secondary setae on frontale*: (0) absent; (1) present (Grebennikov & Luff, 1999: fig. 3).
59. *One long secondary seta at apex of antennomere II*: (0) absent (Fig. 7); (1) present.
60. *Two and more secondary setae on antennomere 2*: (0) absent (Fig. 7); (1) present (Grebennikov & Bousquet, 1999: figs 22, 23, 26).
61. *Length of galea*: (0) markedly longer than two proximal palpomeres combined (Grebennikov & Maddison, 2000: figs 47, 48); (1) not longer than two proximal palpomeres combined (Fig. 3; Grebennikov & Maddison, 2000: fig. 46).
62. *Secondary setae on tarsus*: (0) absent; (1) present (Grebennikov, 1997: fig. 19).
63. *Secondary setae on tibia*: (0) absent; (1) present (Grebennikov & Luff, 1999: fig. 9).
64. *Secondary setae on femur*: (0) absent; (1) present (Grebennikov & Luff, 1999: fig. 9).
65. *Secondary pores on abdominal ventrites*: (0) absent; (1) present.
66. *Number of long setae on urogomphi (ordered)*: (0) six (Grebennikov & Maddison, 2000: figs 57–60); (1) seven (Grebennikov, 1997: fig. 24); (2) nine; (3) ten (Maddison, 1993: fig. 260).
67. *Secondary seta on lateral sides of tergum 9*: (0) absent (Grebennikov & Maddison, 2000: fig. 57); (1) present (Grebennikov & Maddison, 2000: figs 58–60).
68. *One to three short secondary setae at base of UR*: (0) absent; (1) present.
69. *Seta URalpha (ordered)*: (0) long (Grebennikov, 1997: fig. 24); (1) reduced in length (Bousquet & Grebennikov, 1999: figs 14, 15); (2) absent.

Appendix 5. Matrix of larval characters used in the analysis. Characters present in all instars (characters 1–45), in only first instars (characters 46–57) or only later instars (characters 58–69) of Trechitae and outgroups. The codes used for states are given in Appendix 4.

			1 2 3 4		5		6					
	1 2	345 6	789012345678901234567890123456789012345678	9	0 1	23456789	0	1 2	3	4	56	7 89
Pterostichus	0 0	000 0	000000000000000001001000000010000000000000	0	0 0	00200001	0	0 0	0	0	03	0 01
Platypatrobus	0 0	000 0	000000000000001000000100000010000010110000	0	0 0	00200000	0	0 0	0	0	00	0 11
Diplous	0 0	000 0	000000001000001000000100000010000000110000	0	0 0	00200000	1	0 1	1	1	01	0 11
Patrobus	0 0	000 0	000000000000001000000100000010000001110000	0	0 0	00200000	0	0 0	0	0	01	0 10
Perileptus	0 1	000 0	000100010100001001010111011101110111111001	0	0 0	02211110	0	0 0	0	0	11	1 00
Thalassophilus	0 1	000 1	000-00010100001001010111011101110111111001	0	0 0	022222??	?	? ?	?	?	??	? ??
Amblystogenium	0 1	000 1	000-00010000001002000110010110110111110???	?	? ?	??????10	0	1 0	0	1	01	1 00
Trechimorphus	0 1	100 0	000000010000011002000120010110110111110???	?	? ?	??????11	0	0 0	0	1	01	0 00
Trechus	0 1	100 0	000000010000011002000130110100110111110001	0	1 0	01211111	0	0 0	0	1	01	1 00
Epaphius	0 1	100 0	00000001000001100?000130110?00110111110001	0	1 0	11211111	0	0 0	0	1	01	1 00
Aepopsis	0 1	100 0	000000010000011001000130110111110111110001	0	1 0	0?2??211	0	0 0	1	1	01	1 00
Trechisibus	0 0	100 ?	000000010000011002000130110100110111110001	0	0 0	01211111	0	0 0	1	1	?1	? 00
Idacarabus	0 1	000 0	000000000000001002000130110110110111110???	?	? ?	??????00	0	0 0	0	0	01	0 00
Oopterus	0 1	000 0	000000000000001002000130110110110111110???	1	? ?	??????00	0	0 0	0	0	01	0 00
Typhlocharis	0 1	?01 0	00001110101110100210123011010011?11111011?	?	? ?	??????00	0	0 0	0	0	01	0 00
Geocharidius	0 1	?01 0	00111110101110100210123011010011?111110111	0	0 0	0?2000??	?	? ?	?	?	??	? ??
Mioptachys	0 1	000 0	001000000000001102000230110110110111110112	0	1 1	112111??	?	? ?	?	?	??	? ??
Tachyta	0 1	000 0	001100000000001102000230110110110111110112	0	1 1	11211100	0	1 0	0	0	10	0 00
Tachys	0 1	000 0	001100000000001112000230110110111111110011	0	1 1	11211100	0	0 0	0	0	10	1 00
Polyderis	0 1	000 0&1	001000000000001112000230110110110111110011	0	1 1	11211100	0	0 0	0	0	10	1 00
Sphaerotachys	0 1	000 0	001000000100001102000230110110110111110011	0	1 1	11211100	0	0 0	0	0	10	1 00
Elaphropus	0 1	000 0	001000000000001102000230110110110111110011	0	1 1	11211100	0	0 0	0	0	10	1 00
Paratachys	0 1	000 0	001000000100001102000230110110110111110011	0	1 1	11211100	0	0 0	0	0	10	1 00
Porotachys	0 1	000 0	001000000100001102000230110110110111110011	0	1 1	11211100	0	0 0	0	0	10	1 00
Asaphidion	0 0	000 0	010000000000001002100130110100111111110002	0	0 0	00200000	0	0 0	0	0	01	1 00&2
Bembidion	0 0&1	000 0	010000000000001002000130110100111111110000−2	0&1	0 0	00200000	0	0 0	0	0	01&3&4	1 00
Sinechostictus	0 1	000 0	000000000000001002010130110100111111110001	0	0 0	00200000	0	0 1	1	1	01	0 00
Phrypeus	0 1	000 0	000000000000001002000130110100110111110001	0	0 0	002000??	?	? ?	?	?	??	? ??
Cardiaderus	1 0	010 0	100000000000001002000130110100110111110001	0	0 0	00200000	1	0 0	0	0	01	0 00
Pogonus	1 0	010 0	100000000000001002100130110100110111110001	0	0 0	00200000	0&1	0 0&1	0&1	0&1	01	0 00
Pogonistes	1 0&1	010 0	100000000000001002100130110100110111110001	0	0 0	00200000	0	0 0	0	0	01	0 00
Thalassotrechus	1 0	000 0	100000000000001002000130110110111111110001	1	0 0	00200000	0	0 0	0	0	01	1 00