Revision of the genus *Caracladus* with the description of *Caracladus zamoniensis* spec. nov. (Araneae, Linyphiidae, Erigoninae)

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Abstract

The genus *Caracladus* Simon, 1884 with two Asian and formerly two European species is revised and one new species, *Caracladus zamoniensis* spec. nov., is described. The new species has been overlooked for over one hundred years.

All *Caracladus* species are diagnosed and described and data on their distribution, habitat and phenology are given. The phylogenetic placement of the genus *Caracladus* and the relationships between its species are discussed based on 49 morphological characters. *Caracladus* is deeply nested in the “distal erigonines” with closest relations to *Tapinocyba* Simon. Detailed illustrations are given for the type species *C. avicula* (L. Koch, 1869), *C. leberti* (Roewer, 1942), *C. tsurusakii* Saito, 1988 and *C. zamoniensis* spec. nov.

*Erigone pauperula* (Bösenberg & Strand, 1906) nov. comb. (formerly *Caracladus pauperulus*) is illustrated with some supplementary notes on its description.

Key words: dwarf spiders, Alps, new species, phylogeny, *Caracladus avicula*, *Caracladus leberti*, *Caracladus tsurusakii*, *Caracladus montanus*, *Erigone pauperula* nov. comb.
Introduction

Linyphiidae are the most diverse spider family in the northern hemisphere. More than 4300 species have been described worldwide (Platnick 2008) and many species are newly described every year. However, the assignment to genera seems sometimes very difficult. As a result, some genera are extremely heterogeneous, and others monotypic to account for special characters. It is therefore important to revise and clearly define the present genera to make assignments of new species easier.

In the present work we are revising *Caracladus*, a morphologically bizarre genus of Erigoninae with most extraordinary cephalic lobes. Ludwig Koch (1869) described the type species *Caracladus avicula* with a head looking like the one of a bird. Later, Bösenberg and Strand (1906) described a female from Japan as *C. paupe-rulus* which now belongs to *Erigone*. Thaler (1973) transferred *Diplocephalus leberti* Roewer to *Caracladus* according to the male and female genital morphology, even though the males do not have an elongated cephalic lobe with thick hairs anterior to the PME as in *C. avicula*. Recently, Sha and Zhu (1994) described *C. montanus* from China and Saito (1988) described *C. tsurusakii* from Japan. Both species have the typical cephalic lobe of the type species and also share genital characters with both European species. Up to date no more records of *Caracladus* are known in between these regions.

The comparison of SEM pictures of *C. avicula* with fresh material collected at the alpine timberlane of the Swiss Central Alps by Muff *et al.* (2007; as *Caracladus* sp. A) revealed one species new to science, *C. zamoniensis* spec. nov., which is described here. Analyses of material from museums and private collections showed that the new species has been collected but overlooked for over hundred years. The extraordinary (apparently unique) cephalic lobe of *C. avicula* and the syntopic distribution on landscape level (but not on small scale level) may have led to a negligence of detailed examinations of male and female genitals which resulted in this confusion. However, in spite of the close relationship between the two species, a number of clear-cut differences without intermediates could be found and are described here.

Material and methods

**Specimen examination.** The specimens were examined in 80% ethanol under a Leica MZ16 stereo microscope. An Axioplan 2 compound microscope was used for closer examinations of the specimens in Hoyers solvent (Kraus 1984; Crabill 1958) or glycerol gelatine (C₃H₈O₃). Illustrations were prepared by means of a camera lucida. H.F. used soft pencils (3B Caran d’Ache) and normal paper for laminar drawings and ink for line drawings. The finishing was done with Adobe Photo Shop 7.

The preparations for SEM photography were made with a Wild M8 stereo microscope. The male palps were expanded by placing them in 10% potassium hydroxide (KOH) for 1–3 minutes and were subsequently transferred into distilled water for another few minutes. For the JEOL JSM 840 scanning electron microscope with digital image processing equipment (JEOL SemAfore) the objects were prepared as follows: They were placed in a dilution series from 80% to 100% ethanol using 5% steps for 10 minutes each. They remained in absolute ethanol for 2–4 hours and were subsequently cleaned with ultrasound for approximately 1 minute before drying in a BAL-TEC CPD 030 critical point dryer. Later, the objects were mounted on aluminium rivets with transparent nail polish and subsequently coated with a 20 nm thick layer of platinum/palladium using a JEOL JFC-2300HR high resolution fine coater.

Color descriptions are based on specimens immersed in 80% ethanol, illuminated by a CLS 150 X (40 Volts) halogen lamp. The color descriptions refer to Pantone™ reference chart numbers (Pantone Color Formula Guide on uncoated paper).

**Intrageneric relationships.** Conducted using implicit enumeration in TNT with collapsing “rule 3”.
Phylogenetic placement of *Caracladus*. The examination followed the descriptions mentioned above. Additionally, the tracheal system was cleared with eye-lens cleaner (half a tablet of AMO Ultrazyme with Subtilisin A diluted in 1 ml of distilled water) over night. The tracheae were removed from the remaining tissue and stained in Toluidine blue for one minute and subsequently placed in distilled water for observation.

The scoring of morphology followed the characters given by Miller and Hormiga (2004). Incorrect coding of characters 35, 68 and 77 noted in Dupérré and Paquin (2007) were corrected accordingly prior to our analysis. Miscoding of one character in *Intecymbium* Miller, *Dolabritor* Millidge and *Gonatoraphis* Millidge were found in the character matrix available online (http://www.gwu.edu/~spiders/cladograms.htm). Character 56 is recoded as “-“ instead of “0“ in these taxa. Character 55 “anterior radical process” is coded as “0” (absent) in all three genera and can therefore not be coded as “robust” in character 56 “anterior radical process type”. They are correctly presented in Appendix B in Miller and Hormiga (2004). *Tapinocyba* was recoded from Miller and Hormiga (2004) as having a marginal suprategular apophysis (character 34, state 1 instead of 0), but see discussion for details.

The matrix was analysed using parsimony in PAUP* (Swofford 2001) as in previous analyses on Linyphiid relationships (e.g. Miller & Hormiga 2004). Additionally, we repeated the analysis with TNT (same parameters as in PAUP*) and used it also for Bremer support calculations (Goloboff et al. 2003). For the latter the shortest trees from the tree search were saved in RAM and used as starting trees for the Bremer support analysis (same parameters as for the parsimony analysis). 20'000 trees up to 10 steps suboptimal were saved and used to calculate the Bremer support values.

Characters were of equal weight and unordered. A heuristic approach was used with the random addition option, TBR branch swapping (tree bisection reconnection), and 1000 replicates, collapsing “rule 3”. WinClada 1.00.08 (Nixon 1999) calculated the strict consensus tree, ensemble consistency index (corrected for uninformative characters), ensemble retention index and the character optimisations using ACCTRAN. This option favors reversal or secondary loss over convergence, as used in Homiga (2000).

Abbreviations.

ALE: anterior lateral eyes
ALS: anterior lateral spinnerets
AME: anterior median eyes
C: cymbium
CD: copulatory duct
CO: copulatory opening
CP: copulatory pouch
DP: dorsal plate
DSA: distal suprategular apophysis
E: embolus
ED: ejaculatory duct
FD: fertilisation duct
EM: embolic membrane
GF: glabrous field on leg tibia I
GB: glabrous band on palpal tibia
MS: macroseta
MSA: marginal suprategular apophysis
PC: paracymbium
PLE: posterior lateral eyes
PLS: posterior lateral spinnerets
PME: posterior median eyes
PMS: posterior median spinnerets
PT: protegulum
PTA: prolateral tibial apophysis
PTB: tibia prolateral trichobothrium
PTP: protegular papilla
R: radix
RTA: retrolateral tibial apophysis
RTB: tibia retrolateral trichobothrium
S: spermatheca
SPT: suprategulum
ST: subtégulum
SU: sulcus
T: tegulum
Tm I: relative position of trichobothrium on metatarsus I
TP: radical tailpiece
TB: trichobothrium
VP: ventral plate

Institutional abbreviations appear in the acknowledgements.

Taxonomy

**Caracladus** Simon, 1884

*Type species.* *Caracladus avicula* (L. Koch, 1869).

**Diagnosis.** *Males:* Cephalothorax with distinct lobe facing forward, PME situated on its topmost position. This lobe bears many stout, short and few thin, long hairs anterior to the PME (Fig. 11). Simon (1884) describes this lobe as a swelling that looks like a birds head, resembling to what can be seen in *Walckenaeria acuminata* Blackwall, 1833. Protegulum with short and/or long papilla, radix simple without any processes other than the radical tailpiece and the embolus.

*Females:* Dorsal plate of epigyne totally visible in ventral view, forming a more (Fig. 26) or less (Fig. 40) distinct copulatory pouch, receptacula laterally to the dorsal plate.

**Description.** *Males:* Total length: 1.85–2.50 mm. Cephalothorax: honey brown; reticulated in all known species (unknown for *C. montanus*); broad oval; 0.89–1.26 mm long including the cephalic lobe; 0.61–0.83 mm wide. Cephalic lobe: in most cases very distinct, forming a neck with a swollen forward facing tip (e.g.: Fig. 9; not in *C. leberti*, Fig. 35); Cephalic lobe with many stout, short hairs (Fig. 12) and some slender, long hairs anterior to the PME (Fig. 11); sulcus with pit in all European species present. Eyes: PME topmost on the cephalic lobe; AME projecting forward; one long macroseta (some setae in *C. leberti*, Fig. 35) projecting forward between AME in most species (e.g. Fig. 54). Clypeus: directed obliquely backwards. Sternum: very fine brown pigmentation on yellow ground, darker at the margins; shield-shaped (“wappenförmig”) in all known species (unknown for *C. montanus*). Chelicerae: honey brown; promargin with five to six teeth, of which the 3rd and 4th are strongest; retromargin with four to six denticles; stridulatory striae imbricated in all known species (unknown for *C. montanus*), numerous striae, in most species very densely arranged (Fig. 13). Legs: yellow; formula 4-1-2-3 in all known species; tibia III–IV with one proximal macroseta (0-0-1-1), sometimes
FIGURES 1–8. Caracladus avicula (L. Koch, 1869). Male: palp retrolateral (1), prolateral (2), distal (3); palpal tibia dorsal (4); embolic tip (5). Female: right spinnerets (6); epigyne ventral (7), aboral (8). Scale: 100 μm if not stated differently.
FIGURES 9–16. Caracladus avicula (L. Koch, 1869). Male: cephalothorax lateral (9), frontal (10), cephalic lobe lateral (11); thick hair on cephalic lobe anterior to the PME (12); chelicerae lateral (13); sulci frontal (14); booklung cover ventral (15); left spinnerets (16). Scale: 100 μm if not stated differently.
also present on tibia I-II; tibial macrosetae quite robust, longer than the diameter of the tibia (Simon 1884); metatarsi I–III with one trichobothrium (Tm I: 0.50–0.63) and metatarsus IV without trichobothria in all known species. Pedipalp: patella at least two times longer than broad; tibia with one prolateral and one retrolateral trichobothrium in all known species (unknown for C. montanus); form of the prolateral tibial apophysis ranging from a small knob (Fig. 20) to a distinct triangle (Fig. 32); retrolateral tibial apophysis small (Fig. 20), big (Fig. 42) or absent (Fig. 32); paracymbium simple, basally mostly with five distinct setae (Fig. 17) (three in C. tsurusakii); tegulum with short and/or long papilla on top of protegulum (Figs 1–3, 48); suprategulum, semi circular, marginal suprategular apophysis present (Fig. 31), but often minute and shifted to the distal suprategular apophysis (Fig. 19); distal suprategular apophysis highly sclerotised, facing distally; embolic membrane slender without (Fig. 19) or with (Fig. 41) papillae, emerging close to the distal apophysis (Fig. 19); radix simple without any processes other than the radical tailpiece and the strongly sclerotised embolus, rising in the opposite end (Fig. 18). Abdomen: variable in color, often dark olive green.

**Females:** Total length: 1.62–2.72 mm. Cephalothorax: honey brown; reticulated; 0.75–1.08 mm long; 0.58–0.83 mm wide. Eyes: posterior row procurred in all known species; anterior row straight to slightly recurved (seen from above). Sternum: very fine brown pigmentation on yellow ground, darker at the margins; shield-shaped (“wappenförmig”) in all known species (unknown for C. montanus). Chelicerae: honey brown; promargin with five to six teeth of which the 3rd and 4th are the strongest (Simon 1884); retromargin with four to six denticles; stridulatory striae imbricated, numerous striae. Legs: yellow; formula 4-1-2-3; tibia I–IV with one dorsal proximal macroseta (1-1-1-1); tibial macrosetae quite robust, longer than diameter of tibia (Simon 1884); metatarsus I–III with one trichobothrium (Tm I: 0.48–0.63), metatarsus IV without trichobothria. Epigyne: dorsal plate fully visible in ventral view, copulatory pouch present (e.g. Fig. 26), sometimes reduced to some extent (Fig. 40); receptacula positioned lateral to dorsal plate (e.g. Fig. 26). Vulva: receptacula globular, incoming dorsally (Fig. 28), copulatory duct present in most species (C. avicula, C. leberti and C. montanus) but absent in C. zamoniiensis spec. nov. and C. tsurusakii. Abdomen: variable in color, often dark olive green; tracheal system with two thick median and two thin lateral tracheae (Fig. 25).

**Distribution.** All European species are endemic to the Alps (Fig. 59). C. avicula and C. zamoniiensis spec. nov. are restricted to areas above circa 1200 m a.s.l. (one unpublished record at 800 m), whereas C. leberti occurs below 1300 m. C. montanus was found at circa 2000 m and C. tsurusakii at circa 1200 m.

**Habitat.** The European species prefer litter of deciduous forests (Thaler 1973; Maurer & Hänggi 1990; Frick et al. 2006). The information on the Asian species is very limited, C. tsurusakii occurs under leaf litter (Saito 1988).

**Remarks.** On the Asian species only three publications are available concerning mainly the type localities, which makes a more precise ecological characterisation difficult. C. tsurusakii and C. zamoniiensis spec. nov. lack a copulatory duct. The insertion of sperm is assumed to take place through a space between the ventral and the dorsal plates, which are supposed to be pressed apart during copulation.

Characters that are invariant in all Caracladus species are not specifically mentioned in the species descriptions with the exception of C. zamoniiensis spec. nov.

**Caracladus avicula** (L. Koch, 1869)
(Figs 1–28)

_Erigone avicula_ L. Koch, 1869: 30.
_Caracladus avicula_ Simon 1884: 590, figs 408–409; Simon 1894: 658, fig. 657; Simon 1926: 387, 498, fig. 690.
**Type material.** **HOLOTYPE:** Austria: Tyrol: Kühtai, next to the chapel, ca. 1950 m [47°12'45" N, 11°00'50" E], σ 08.vii, under a stone, leg. A. Ausserer (Koch 1869). Koch (1869) notes that Anton Ausserer found both sexes together. The whereabouts of the material is not known to the authors. Parts of the collection of Ludwig Koch are stored in the BMNH (Horn et al. 1990), but the material from Kühtai was untraceable. Instead, there is one tube with two intact males and one tube with several legs, one abdomen, two right and two left palps in the collections of the BMNH. They are tagged as “coll. Koch” but with notes saying “E. Simon” and “Hautes-Alpes”. As Simon (e.g. 1884) usually used the term “Hautes-Alpes” for a province in France, these specimens most probably are not Koch’s original types.


**Unexamined literature records. Austria: Tyrol**: Lech, Forchach, ca. 900 m [47°25'48" N, 10°35'26" E], Blockau, (Steinberger 1996); Obergurgl, 1960 m [46°52' N, 11°02' E], 5♂ 2♂ 02.ix.1976–08.x.1976, hey meadow, leg. S. Puntcher (Puntcher 1980). **Germany**: Bavaria: Mangfallgebirge, Hochmiesing, Alp Spitz, Hoher Fricken, ca. 1500–1700 m [47°39' N, 11°57' E] (Staudt 2008). Italy: Aosta valley: La Thuile, 1800 m [45°42'53" N, 6°56'56" E], 2♂ , leg. Focarile (MSNM) (Pesarini 1996). Lombardia: Presolana [45°53' N, 10°03' E], 1♂ 23.vii.1989, leg. Sciały (MSNM) (Pesarini 1996). Trentino: close to Corvara, 1700–1800 m [46°33'10" N, 11°53'00" E], 2♂ many ♀ vii.1973, Dolomites, leg. A. F. Millidge (Millidge 1979). Switzerland: *Grison*: Engadin, Sils, Basligia, ca. 1800 m [46°26'03" N, 9°45'22" E], leg. Kummer (Vogelsanger 1947); Frauenkirch, Aebibwald, 1600 m–2000 m [46°45'39" N, 9°48'58" E], vi.–vii., subalpine zone, leg. T. Vogelsanger (Vogelsanger 1947); Pontresina, Belvoir, ca. 1850 m [46°29'30" N, 9°54'20" E], subalpine zone, leg. Kummer (Vogelsanger 1947); Trins, Flims, ca. 900–1200m [46°50' N, 9°19' E], vii, leg. E. Schenkel (Vogelsanger 1947). *Valais*: path to Saas-Fee [46°06'30" N, 7°55'40" E], 1♂ 12./18.vii.1929, forest zone, left valley slope, leg. E. Schenkel (Schenkel 1933); Saas-Fee, Egg or Bärenfälle or Fluh or Imseng or Bider, 1700–1900 m [46°07'30" N, 7°55'40" E], 4♂ 8♀ 07.vii.1926, leg. E. Schenkel (Schenkel 1927); Saas-Fee, Gletscheralp, around the hut, 2135 m [46°04'51" N, 7°55'01" E], 1♂ 05.viii.1926, leg. E. Schenkel (Schenkel 1927); Vassorey, close to Bourg-Saint-Pierre, lower border of forest, ca. 1633 m [45°56'50" N, 7°12'30" E], vii, leg. Simon (MNHN) (Simon 1884); Zermatt, äußere Wälder, ca. 2000 m [46°01' N, 7°44' E], 5♀, leg. T. Vogelsanger (Vogelsanger 1944).

**Diagnosis. Males**: Koch (1869) describes the cephalic lobe in detail as “similar to a bird head, placed on a long neck” which is indicated in the species epithet “avicula”. This lobe has been considered to be typical for *C. avicula* but is also present in *C. zamoniensis* spec. nov. However, *C. avicula* with long, straight, whip-like
FIGURES 17–24. Caracladus avicula (L. Koch, 1869). Male: palp retrolateral (17), prolateral (18), embolic division prolateral (19); palpal tibia dorsal (20); cephalothorax dorsal (21), frontal (22) and lateral (23); right leg tibia I retrolateral (24). Scale: 200 μm.
embolus that narrows constantly towards the end (Figs 18, 19). Cephalic lobe much thinner below the eye-field than above. Distance between channel-like sulcus and AME above 0.12 mm (Fig. 22).

**Females:** Dorsal plate rectangular without sclerotised parts visible in transparency through the dorsal plate but lateral to it (Fig. 26). Epigyne with two anterior pouches formed by the ventral and the dorsal plate (Fig. 26). They are much larger and less sclerotised than in *C. zamoniensis* spec. nov. (Fig. 56). Vulva with a rather complex copulatory duct (Figs 27, 28).

**Description. Male** (NMBE Ar 5292): Total length 2.02 mm. Cephalothorax: honey brown (138 U); reticulated; 0.84 mm long without cephalic lobe, 1.19 mm long with cephalic lobe, 0.71 mm wide. Cephalic lobe: light brown (124 U); Thaler (1969) describes this lobe as slim elongated shaft which is sloped forwardly, originating at the position of the median eyes (Fig. 23), with a hairy tip that is laterally compressed (Fig. 21); smallest diameter below the eye-field 0.06 mm wide laterally, 0.07 mm wide dorsally; ventral side of the shaft with channel-like depression bearing a sulcus (Thaler 1969), margin of sulcus 0.16 mm below the AME (Fig. 22). Eyes: PME dorsally on tip of lobe; AME projecting forward from the shaft (Fig. 23); one long macroseta
projecting forward between AME (Fig. 23). Clypeus: directed obliquely backwards (Fig. 23). Sternum: very fine brown (469 U) pigmentation on yellow (124 U) ground, dark brown (469 U) on the margins; 0.47 mm long; 0.47 mm wide. Chelicerae: light brown (124 U); stridulatory striae fine and dense (Fig. 13); promargin with five big teeth; retromargin with five denticles. Legs: yellow (120 U); tibia I–IV with one dorsal proximal macroseta (1-1-1-1), 1.3–1.6 times longer than diameter of tibia; Tm I: 0.58 mm. Pedipalp: yellow (120 U); patella cylindrical; tibia nearly two times longer than broad, with glabrous band retrolaterally (Fig. 20), dorsal with highly sclerotised small tip facing forward (Fig. 20); paracymbium simple clasp (Fig. 17); tegulum distal with short and long papillae on protegulum (Figs 17, 18); suprategulum kneed; column broad; marginal suprategular apophysis present (Thaler 1969: Figs 17, 18); distal suprategular apophysis pointed (Thaler 1969: Figs 17, 18); embolic membrane slender; radix simple without any processes other than the short radial tailpiece and the strongly sclerotised, slim, terminal, whip-like embolus (Figs 18, 19). Abdomen: dark olive green to brown (125 U), ventral darker (117 U); booklung covers brown (125 U), scaly (Fig. 15).

**Female** (NMBE Ar 5315): Total length: 1.79 mm. Cephalothorax: honey brown (138 U); broad egg-shaped (Thaler 1972); 0.77 mm long, 0.62 mm wide. Eyes: eye-field steep (Thaler 1972); posterior eyes separated by their diameter; AME separated by their radius. Clypeus: concave. Sternum: very fine brown (469 U) pigmentation on yellow (124 U) ground, dark brown (469 U) on the margins; 0.47 mm long; 0.47 mm wide. Legs: yellow (122 U); tibia I–IV with one dorsal proximal macroseta (1-1-1-1), 1.4–1.8 times longer than diameter of tibia; Tm I: 0.56. Chelicerae: light brown (124 U); promargin with five teeth; retromargin with five denticles; stridulatory striae indistinct and scaly. Epigyne: rectangular dorsal plate visible in ventral view; receptaculum laterally to dorsal plate, visible in transparency trough ventral plate (Fig. 26). Vulva: copulatory pouch narrows in the middle of the vulva forming a copulatory duct (Figs 26, 27); receptaculum globular, incoming dorsally. Abdomen: dark olive green to black (147 U). Tracheal system with two thick median and two thin lateral tracheae (Fig. 25).

**Variation.** The measurements are based on specimens from the NMBE (Ar5281, Ar5290, Ar5292, Ar5298, Ar5304, Ar5315, Ar5318, Ar5324, Ar5329, Ar5352, Ar5356: 6♂ 6♀) and the NB (P-G 1-4 H, P-G 1-4 I, coll. Zingerle: 4♂ 3♀).

**Males** (n=10, means in brackets): The coloration is variable. Total length 1.95–2.31 mm (2.10 mm). Cephalothorax: 0.76–0.89 mm (0.82 mm) long without cephalic lobe, 1.10–1.26 mm (1.17 mm) long with cephalic lobe, 0.65–0.71 mm (0.69 mm) wide. Cephalic lobe: smallest diameter below the eye-field 0.06–0.07 mm (0.06 mm) wide laterally, 0.06–0.08 mm (0.07 mm) wide dorsally; margin of sulcus 0.12–0.16 mm (0.14 mm) below the AME. Legs: dorsal proximal macroseta on tibia 1.3–1.6 times longer than diameter of tibia (Thaler 1969); Tm I: 0.50–0.61 mm (0.56 mm).

**Females** (n=9, means in brackets): The colorations are variable. Total length: 1.68–1.91 mm (1.80 mm). Cephalothorax: 0.77–0.84 mm (0.81 mm) long, 0.62–0.67 mm (0.65 mm) wide. Legs: dorsal proximal macroseta on tibia 1.4–1.8 times longer than diameter of tibia; Tm I: 0.53–0.60 mm (0.57 mm).

**Distribution.** Endemic to the Alps, distributed between the Western- and the Eastern Alps (Thaler 1969) in France, Switzerland, Germany, Austria and Italy (Fig. 59). The records in Romania (Fuhn & Oltean 1970) are questionable (Thaler 1972). Bonnet (1956) erroneously lists *C. avicula* as present in Hungary citing Kolossváry (1939) who mentioned this species as a characteristic subalpine spider of Switzerland (Thaler 1972).

**Habitat.** Subalpine region, in moss of coniferous forests (Lessert 1910; Maurer & Hänggi 1990). Records between 1150–2160 m (Muster 2001) in litter of coniferous forests (mainly Norway spruce, *Picea abies*, sporadically mixed with larch, *Larix decidua*) (Zingerle 1999a). Extensive sampling at the alpine timberline at 1960 m a.s.l. showed that *C. avicula* occurs in the litter of subalpine Norway spruce forests and is also common under stand alone trees in the dwarf-shrub heath (Frick et al. 2006). However, it is more or less absent in the surrounding open areas like meadows and dwarf-shrub heath (Muff et al. 2007).
Phenology. Adults eurychronous in lower altitudes (Thaler 1972). However, alpine records (Zingerle 1999a; Frick et al. 2006; Muff et al. 2007; together sampled app. 80% of the collected specimens) indicate winter activity between September and April.

Remarks. Our discovery of two sympatric Caracladus species (the first with a male cephalic lobe that is wider above the eye-field (AME, ALE, PLE) than below and with a longitudinal channel-like sulcus, the second one with an equally broad “neck” above and below the eye-field with a transverse cup-like sulcus) leads to the question, which species L. Koch had described as C. avicula. From Koch’s (1869: 31) original description it is clear that the name C. avicula refers to the first species (“... über diesen Augen [AME, ALE, PLE] wird der Fortsatz dicker”; “...die Basis ... ist an der Unterseite rinnenartig ausgehöht, wo diese Rinne aufhört, sitzen die beiden vorderen Mittelaugen...”). The second species is here newly described. The original description of the female in Koch (1869) is ambiguous and was therefore redescribed in Thaler (1969).

Lessert (1907) noted that his specimens from Valais and Bern differ slightly from Simon’s (1884) drawings. According to Thaler (1972), Lessert’s (1907: Fig. 7; 1910: Fig. 100) females belong to Diplocentria bidentata (Emerton, 1882). Lessert’s (1907: Figs 5–6; 1910: Figs 98–99) males belong to C. zamoniensis spec. nov.

Caracladus leberti (Roewer, 1942)
(Figs 29–39)

Plaesiocraerus kochi, Simon 1884: 770, figs 675–678.
Diplocephalus kochi, Lessert 1910: 152, fig. 93.
Plaesiocraerus leberti, Roewer 1942: 696, replacement name for Erigone kochii Lebert, 1877.
Caracladus leberti, Thaler 1973: 45, figs 10–18 (transferred from Plaesiocraerus=Diplocephalus); Heimer and Nentwig 1991: 124, figs 351.1–351.5.

Type material. HOLOTYPE: Switzerland: Vaud: Lausanne, Cery, close to psychiatric clinic, ca. 600 m [46°32'50" N, 6°36'20" E], 2♂ xii, (Lebert 1877). The whereabouts of Lebert’s collection and consequently the type material is unknown to the authors.

Examined material. France: Rhône-Alpes: Haute-Savoie, Sallanches, Nant-Cruy, ca. 900 m [45°55'10" N, 6°37'10" E], 5♂ 06.vii.1952, leg. A. Comellini (MHNG) (Comellini unpubl.). Liechtenstein: Unterland: Benders, Brunaböchkl, stone pit, 460 m [47°11'21.39" N, 9°32'24.66" E], 1♀ 24.vii.2008, west exposed slope with beech and ash on debris, in leaf litter with moss, leg., det. and coll. H. Frick (SP_0436). Switzerland: Basel: Reichenstein, ca. 450 m [47°29’48” N, 7°37’44” E], x., leg. E. Schenkel (NMB 1601a) (Schenkel 1918); Oberdorf, Wintenberg, ca. 650 m [47°23’20” N, 7°44’40” E], 10% 14& x., leg. E. Schenkel (NMB 1601a) (Schenkel 1923); close to Dornach, Ingelstein, ca. 550 m [47°28’22” N, 7°38’16” E], x., leg. E. Schenkel (NMB 1601a) (Schenkel 1918); Eggfluehberg southern slope, ca. 500 m [47°26’50” N, 7°35’0” E], xi, leg. E. Schenkel (NMB 1601a) (Schenkel 1923); Huzmannshulf and Falkenfluh, ca. 600 m [47°26’30” N, 7°36’50” E], x./xii, leg. E. Schenkel (NMB 1601a) (Schenkel 1923). Valais: Fiesch, Binneleggen, 1300 m [46°23’07” N, 8°08’13”E], 7♀ 22.vii.1925, leg. E. Schenkel (NMB 1601b) (Schenkel unpubl.).

France: Alpes Maritimes: Saint-Martin-Lantosque, Saint-Martin-Vésubie, Venançon, ca. 1000 m [44°03'10'' N, 7°15'10'' E], in moss of spruce forests (Simon, 1884). Provence-Alpes-Côte d’Azur: Hautes-Alpes (Simon 1914). Rhône-Alpes: Haut-Savoie, Chamonix, path from la Joux to Argentière (small south exposed balcony) [45°58'50'' N, 6°55'30'' E], 1% 02.ix.1995, spruce forest, in soil, coll. J.-C. Ledoux (Ledoux unpubl.); Isère, Massif de la Chartreuse, le Sappey, le Bourg-d’Oisans, ca. 750 m [45°03'10'' N, 6°01'50'' E], in moss of spruce forests (Simon 1884). Italy: Trentino: Bruneck, Amaten, ca. 1000 m [46°48'50'' N, 11°57'40'' E], 1% 23.iii.1962, leg. and coll. K. Thaler (Thaler 1973); Burgstall, ca. 440 m [46°36'40.44'' N, 11°11'49.96'' E], 1% 01.i.–09.iii.2007, on sweet cherry in SW-exposed pubescent oak forest, leg. S. Ballini (Ballini unpubl.); Lana, ca. 550 m [46°36'26.93'' N, 11°07'24.5'' E], 2% 07.xii.2006–29.i.2007, sweet chestnut forest, leg. S. Ballini (Ballini unpubl.).

Switzerland: Basel: Pfeffingen, ca. 400 m [47°27'33'' N, 7°35'25'' E], (Schenkel 1918). Geneva: Geneva, ca. 400 m [46°12' N, 6°08' E], (Cambridge 1912). Ticino: Val Vergeletto (valley of V.) [no coordinates available for distribution map], leg. P. Pronini (Pronini unpubl.; Maurer & Hänggi 1990). Valais: Col de la Forclaz, Northern slope, 1100 m [46°04'50'' N, 6°59'30'' E], 8% 16&ix.1983, Norway spruce forest edge in mossy litter (Müller 1985); Lavigny, ca. 500 m [46°30'4'' N, 6°24'14'' E], v., x., xi., (Lessert 1904); St-Livres, 600 m [46°30'34'' N, 6°22'58'' E], xii, forest (Lessert 1907).

**Diagnosis.** Males: Characteristic male cephalic lobe (Thaler 1973) with a small upwards and forwards facing bump between the PME (Figs 33–35). Thaler (1973) noted that the tegulum, suprategular apophysis, embolic division, vulva and chaetotaxy are similar to *C. avicula*. However, the embolus is rather robust and straight in *C. leberti* (Fig. 30) whereas it is thin and whip-like in *C. avicula* (Fig. 18). Its tailpiece is much shorter than in *C. avicula* and the marginal suprategular apophysis can clearly be seen (Figs 29, 30).

Females: The dorsal plate of the epigyne is nearly triangular (Fig. 37) and has a small copulatory opening compared to *C. avicula* (Fig. 26). The form of the copulatory pouches are barely visible in ventral view and the copulatory duct is much more robust in *C. leberti* (Fig 39) than in *C. avicula* (Fig. 28).

**Description.** Male (NMB 1601a): Total length: 1.62 mm. Cephalothorax: honey brown (138 U); broadly oval; 0.83 mm long without cephalic lobe, 0.85 mm long with cephalic lobe (Fig. 35); 0.62 mm wide. Cephalic lobe: frontally steeply declining, rounded protuberance between and lateral to the PME (Thaler 1973), lobe at PME 0.23 mm wide dorsally; fine, short pubescence with some long hairs; broad lateral sulci (Thaler 1973). Eyes: PME upmost on the cephalic lobe (Fig. 34); AME projecting forward; long, upwards facing hairs between AME (Fig. 35). Clypeus: directed obliquely backwards. Sternum: very fine brown (469 U) pigmentation on yellow (124 U) ground, dark brown (469 U) on the margins; 0.50 mm long; 0.46 mm wide. Chelicerae: honey brown (138 U); fine and dense stridulatory striae. Legs: yellow (122 U); Tibia III–IV with one dorsal proximal macroseta (0-0-1-1), 1.1–1.3 times longer than diameter of tibia; Tm I: 0.57. Pedipalp: patella three times longer than wide; tibial apophysis directing distally with retrolaterally curved tip; paracymbium simple; tegulum with short and long protargel papillae on protegulum; suprategular apophysis with marginal suprategular apophysis and pointed distal suprategular apophysis; embolic membrane slender without papillae; radix simple without any processes other than the short radical tailpiece and a strongly sclerotised embolus. Abdomen: light brown (125 U); booklung covers yellow (122 U), scaly.

Female (NMB 1601a): Total length: 1.51 mm. Cephalothorax: honey brown (138 U); 0.77 mm long, 0.57 mm wide. Eyes: posterior eyes separated by their diameter. Sternum: very fine brown (469 U) pigmentation on yellow (124 U) ground, dark brown (469 U) on the margins, 0.49 mm long, 0.45 mm wide; coxa separated by their diameter. Chelicerae: honey brown (138 U); promargin with six big teeth; retromargin with five to six denticles; stridulatory striae fine and dense. Legs: yellow (122 U); formula 4-1-2-3; tibia I–IV with one dorsal proximal macroseta (1-1-1-1); Tm I: 0.48. Epigyne: copulatory opening at anterior end of trapezoid dorsal plate (Fig. 37). Vulva: receptacula globular, incoming dorsally; copulatory duct faces forward/laterad, then aborad and finally mediad/aborad where they are stronger sclerotised (Figs 38, 39; Thaler 1973). Abdomen: light brown (125 U). **Variation.** The measurements are based on alcohol material from NMB (1601a: 5♂ 5♀).
FIGURES 29–36. Caracladus leberti (Roewer, 1942). Male: palp retrolateral (29), prolateral (30), embolic division prolateral (31); palpal tibia dorsal (32); cephalothorax dorsal (33), frontal (34) and lateral (35); mirrored left leg tibia I retrolateral (36). Scale: 200 μm.
Males (n=5, means in brackets): The coloration is variable. E.g. Thaler (1973) describes the abdomen as blackish and the legs as brownish whereas our specimens were much brighter presumably due to the long storage in alcohol. Total length 1.55–1.68 mm (1.61 mm). Cephalothorax: 0.81–0.85 mm (0.83 mm) long without cephalic lobe, 0.84–0.89 mm (0.86 mm) long with cephalic lobe; 0.62–0.69 mm (0.65 mm) wide. Cephalic lobe: at PME 0.22–0.24 mm (0.23 mm) wide dorsally. Legs: Tm I: 0.56–0.63 mm (0.58 mm).

Females (n=5, means in brackets): The colorations are variable. Total length 1.34–1.79 mm (1.59 mm). Cephalothorax: 0.72–0.81 mm (0.76 mm) long; 0.55–0.62 mm (0.59 mm) wide. Legs: Tm I: 0.48–0.66 mm (0.57 mm).

Distribution. Several records along the Northern Alpine Arch from the foreland of the Alps up to alpine valleys in the Western and Central Alps (Fig. 59). Occasional records also in the Southern Alps.

Habitat. Altitudes between 650 m (Breuss 1994) and 1100 m (Müller 1985), unpublished records from 440 m (Ballini pers. comm. and Frick) to 1300 m (Schenkel, specimen from NMB). Occurs in moss and litter of light spruce and pine forests (Simon 1884; Thaler 1973; Maurer & Hänggi 1990). Ballini (unpubl.) also found specimens in tree eclectors in an oak, Quercus pubescens and a sweet chestnut, Castanea sativa, forest in the Southern Alps.

Phenology. Adult specimens were found throughout the year. However, they seem to be winter active (Thaler 1973) with a peak between September and April (e.g. Thaler 1973; Müller 1985).

Remarks. The close relationship of *C. leberti* with the other species of *Caracladus* is highly supported by the cladistic analysis on species level (Fig. 63), although males of *C. leberti* do not have the typical cephalic
lobe with thick hairs anterior to the PME. Thaler (1973) correctly placed this species to *Caracladus* according to the close resemblance of the male and female genitals.

*Caracladus montanus* Sha & Zhu, 1994

*Caracladus montanus* Sha & Zhu, 1994: 172, figs 1–7; Song et al. 1999: 160, figs 88M–O.

**Type material.** HOLOTYPE: China: *Jilin*: Changbai mountain [42°00' N, 128°01' E], 1♂ 1979–1990 (Sha & Zhu 1994). PARATYPES: China: *Jilin*: Changbai mountain, Baiyunfeng (“white cloud peak”) [42°00' N, 128°01' E], 1♂ 19.vi.1979, leg. Y. Zhang and C. Wang (Sha & Zhu 1994); Changbai mountain [42°00' N, 128°01' E], 1♀ 11.viii.1985, leg. C. Zhu (Sha & Zhu 1994); Changbai mountain, Xidapo (“big western slope”) [42°00' N, 128°01' E], 6♂ 9♀ 31.vii.1990, leg. Y. Sha (Sha & Zhu 1994); Changbai mountain, Xiaotianchi (“small heaven lake”) [42°05'48'' N, 128°03'50'' E], 3♂ 5♀ 04.viii.1990, leg. Y. Sha (Sha & Zhu 1994). The type material (mentioned above) is stored in the Department of Biology, Norman Bethune University of Medical Sciences in Changchun, which is now a subunit of the Jilin University, China (Sha & Zhu 1994). The material was not available for observation since establishing contacts with Jilin University was not successful..

**Diagnosis.** **Males:** Similar to *C. tsurusakii* with differences in the shape of the male palpal tibia and the embolus (Sha & Zhu 1994). In lateral view, the cephalic lobe is broadest below the eye-field (Sha & Zhu 1994: Fig. 2), but is narrowed down in *C. tsurusakii* (Fig. 45). The prolateral tibialapophysis looks like a big tooth (Sha & Zhu 1994: Fig. 4) whereas it is a glabrous blunt apophysis in *C. tsurusakii* (Fig. 42).

**Females:** The shape of the epigynum and the vulva are different to what is seen in other *Caracladus* species. E.g. the curled copulatory duct (Sha & Zhu 1994: Fig. 7).

**Description.** **Males:** Total length: 1.85–2.07 mm (Sha & Zhu 1994). Cephalic lobe: facing forward, hairy in front of the PME (Sha & Zhu 1994: Fig. 2); shaft rather thick with some hairs (Sha & Zhu 1994: Fig. 2); sulcus absent. Eyes: PME upmost on the cephalic lobe (Sha & Zhu 1994: Fig. 2). Chelicerae: promargin with five larger teeth; retromargin with five very small denticles; stridulatory striae present (Sha & Zhu 1994). Legs: tibia I–IV with one dorsal proximal macroseta (1-1-1-1); Tm I: 0.61 (Sha & Zhu 1994). Pedipalp: paracymbium simple hook (Sha & Zhu 1994: Fig. 3); retrolateral tibial apophysis small tooth; prolateral tibial apophysis long and broad (Sha & Zhu 1994: Figs 4, 5); protegulum present (Sha & Zhu 1994: Fig. 3).

**Females:** General appearance similar to males but without a cephalic lobe (Sha & Zhu 1994). Total length: 2.07–2.72 mm (Sha & Zhu 1994). Eyes: anterior row slightly recurved (Sha & Zhu 1994). Chelicerae: stridulatory striae present (Sha & Zhu 1994). Epigyne: ventral plate hourglass-like, visible in ventral view (Sha & Zhu 1994: Fig. 6, see remarks). Vulva: receptacula globular; copulatory duct spiral (Sha & Zhu 1994: Fig. 7).

**Distribution.** Only known from the type locality in Jilin, China (Song et al. 1999).

**Habitat.** The coordinates in the original publication correspond to a spot at ca. 2000 m a.s.l.

**Phenology.** All records in summer time between June and August.

**Remarks.** No specimens were available for examination. The diagnosis and description of certain structures and the coding of characters for the phylogeny on species level followed the descriptions and figures given in Sha and Zhu (1994) of which some are redrawn in Song et al. (1999). Misinterpretations of the figures can therefore not be excluded. It is assumed, for example, that *C. montanus* has no sulcus because Sha and Zhu (1994) mention the close resemblance to *C. tsurusakii* without mentioning a sulcus in the original description. The conformation of the epigyne is unclear to the authors. It is assumed that the ventral hourglass-shaped structure represents the dorsal plate.
Caracladus tsurusakii Saito, 1988
(Figs 40–46)


Diagnosis. Males: Most similar to C. avicula with differences in the structure of the male palp (Saito 1988). Cephalic lobe similar to C. avicula but more robust and lacking a neck. Embolus whip-like as in C. avicula but much longer and with a loop back, radical tailpiece long and bent (Fig. 41). Distal suprategular apophysis blunt and nearly transparent (Fig. 41). Palpal tibia with two well defined apophyses (Fig. 42).

Females: Nearly triangular dorsal plate with two copulatory pouches anterior and ventral to it and together not broader than the anterior end of the dorsal plate (Fig. 40).

Description. Male (holotype, NSMT Ar5249): Total length: 2.50 mm. Cephalothorax: chestnut brown with darker radiating lines, cervical grooves black (Saito 1988); 1.03 mm long without cephalic lobe (Fig. 45), 1.35 mm long with cephalic lobe (Fig. 45); 0.78 mm wide. Cephalic lobe: projecting forward, thick at base and sharply pointed tip with sparse stout hairs; at thinnest part below the eye-field 0.14 mm wide laterally, 0.23 mm wide dorsally (Figs 43, 45); sulcus absent (Fig. 44). Eyes: PME upmost on the cephalic lobe, separated by slightly less than 1.5 times their diameter; position of the PLE adjacent to and above the ALE; one long macroseta projecting forward between AME (Fig. 45); anterior row slightly procurred, eyes separated by their radius. Clypeus: wide, slightly convex. Chelicerae: dark brown (Saito 1988); promargin with five teeth; retromargin with six denticles; many broad stridulatory striae. Sternum: yellowish brown, strongly darker at the margins (Saito 1988). Legs: tibia I–IV with one dorsal proximal macroseta (1-1-1-1); Tm I: 0.63. Pedipalp: prolateral tibial apophysis glabrous, facing forward; retrolateral tibial apophysis hairy, facing forward (Saito 1988: Fig. 12); suprategular apophysis semi circular; marginal suprategular apophysis minute; distal suprategular apophysis thin, blunt (Fig. 41); embolic membrane with papillae; radix simple without any processes other than the long radical tailpiece and the very long, whip-like embolus that is strongly curved towards the tip (Fig. 41).

Female (paratype, NSMT Ar5250): Total length: 2.58 mm. Cephalothorax: 1.08 mm long; 0.83 mm wide; general appearance similar to males, but without cephalic lobe (Saito 1988). Eyes: anterior row slightly recurved, separated by about the radius of the AME; posterior eyes separated by at least an eye diameter (Saito 1988). Epigyne: dorsal plate visible in ventral view; receptaculalateral to the dorsal plate, barely visible in transparency trough ventral plate (Fig. 40); very small copulatory pouches (Fig. 40). Vulva: without copulatory duct (Fig. 40); receptacula globular.

Distribution. Only known from the type locality on Hokkaido, Japan (Saito 1988).

Habitat. The specimens were collected under leaf litter by sifting or with pitfall traps (Saito 1988). If we correctly located the locus typicus, this species occurs on a volcano on ca. 1300 m a.s.l.

Phenology. One record from late September, only.

Remarks. C. tsurusakii lacks a copulatory duct. The insertion of sperm is assumed to take place through a space between the ventral and the dorsal plates which are supposed to be pressed apart during copulation.
FIGURES 40–46. Caracladus tsurusakii Saito, 1988. Female: epigyne ventral (40). Male: palp prolateral (41); palpal tibia dorsal (42); cephalothorax dorsal (43), frontal (44) and lateral (45); right leg tibia I retrolateral (46). Scale: 200 μm. Specimens: Paratype, NSMT Ar5250 (female); holotype, NSMT Ar5250 (male).
Caracaladus zamoniensis spec. nov.

Caracaladus avicula, Lessert 1907: 108, figs 5–6, σ misidentified; Lessert 1910: 160, figs 98–99, σ misidentified.


**Examined material. Austria:** Vorarlberg: Montafon, Garneratal, close to Gaschurn, 1560 m [46°57'56" N, 10°00'40" E], 1♂ 19.vii.–29.viii.2000, leg., det. and coll. W. Breuss (Breuss unpubl.). **France:** Rhône-Alpes: Haute-Savoie, Chamonix, montagne des Posettes (Montroc), 1600 m [45°59'40" N, 6°56'03" E], 1♂ 18.viii.1993, spruce forest with some birch trees, ground dwelling, leg., det. and coll. J.-C. Ledoux (Ledoux unpubl.); Vallorcine, entrance to the canyon of Bérard, 1680 m [46°02'30" N, 6°56'10" E], 1♂ 01.viii.1930, leg. E. Schenkel, det. P. Muff (NMB 2795f) (Schenkel 1933); Trins, Mulins, Bar-...
Bruniswaldalp close to Alzellen, > 1400 m [46°51'20'' N, 8°23'20'' E], 1♂ 4♀ viii., leg. E. Schenkel, det. P. Muff (NMB 2795g) (Schenkel 1923). Ticino: Val Bedretto, Bedretto to Alpe di Folcra, 1400–1800 m [46°30'8'' N, 8°30'59'' E], 1♀ 11.–22.vii.1927/1928, forest slope on the right valley side, leg. E. Schenkel, det. P. Muff (NMB 2795e) (Schenkel 1929). Valais: close to Fiesch, Rafgarten – Ober Titer, 1500 m–1600 m [46°30'50'' N, 8°18'20'' E], 6♀ 15.vii.1925, leg. E. Schenkel, det. P. Muff (NMB 2795c) (Schenkel 1926); Fionnay, 1500 m [46°01'54'' N, 7°18'26'' E], 1♂ 2♀ ix.1906, in moss of spruce forest, leg. R. de Lessert, det. H. Frick (MHNG) (Lessert 1907; Thaler 1972); Leukerbad, ca. 1400 m [46°22'30'' N, 7°37'30'' E], 1♂ 4♀ viii.1930, leg. R. de Lessert, det. H. Frick (MHNG), 1♂ 1♀ viii.1930, leg. R. de Lessert, det. P. Muff (NMB 2795h) (Lessert 1930); Lötschental, close to Ried, 1500 m–1600 m [46°24'50'' N, 7°48'20'' E], 1♂ 1♀ vii.1938, leg. E. Schenkel, det. P. Muff (NMB 2795i) (Schenkel 1939); Saas-Tal, Saas-Tal below Saas-Fee, Almagell–Saas-Fee, ca. 1600 m [46°06'30'' N, 7°55'40'' E], 1♂ vii./viii., leg. E. Schenkel, det. P. Muff (NMB 810d) (Schenkel unpubl.).

**FIGURE 47.** Type locality of *C. zamoniensis* spec. nov.. Type specimens found in sieved Norway spruce litter, collected close to the tree trunk under approximately 5 cm of snow on 24 October 2007.

**Diagnosis.** *C. zamoniensis* spec. nov. is most similar to *C. avicula* but differs in the shape of the male and female genitalia and the shape of the male cephalic lobe.

**Males:** Cephalic lobe of *C. zamoniensis* spec. nov. more robust than in *C. avicula*: the neck-like prolongation of *C. zamoniensis* spec. nov. is of equal diameter directly below and above the eye-field (AME, ALE, PLE) (Fig. 54) but much thinner below the eye-field in *C. avicula* (Fig. 23); distance between sulcus and AME is below 0.11 mm in *C. zamoniensis* spec. nov. (Fig. 53) and above 0.12 mm in *C. avicula* (Fig. 22); sul-
cus cup-like in *C. zamoniensis* spec. nov. and channel-like in *C. avicula*. Embolus of *C. zamoniensis* spec. nov. short, broad and robust basally, thin and U-shaped distally (Figs 49, 50); *C. avicula* with long, straight and whip-like embolus that narrows constantly towards the end (Figs 18, 19). *C. zamoniensis* spec. nov. tibia I proximally bent and dorsally with glabrous area on the proximal half (Fig. 55) and no macroseta, in *C. avicula* with one dorsal macroseta in small glabrous field (Fig. 24).

**Females**: Epigyne of *C. zamoniensis* spec. nov. with two anterior pouches formed by the ventral and dorsal plate, anterior borders highly sclerotised (Fig. 56). Pouches in *C. avicula* much larger and less sclerotised (Fig. 26). *C. zamoniensis* spec. nov. with ventrally visible square dorsal plate, sclerotised parts of the vulva visible in transparency through ventral and dorsal plate defining a bright hourglass-like form centrally (Fig. 56). *C. avicula* with rectangular dorsal plate without sclerotised parts visible in transparency through dorsal plate but lateral to it (Fig. 26). Vulva of *C. zamoniensis* spec. nov. without copulatory duct, those of *C. avicula* with. Vulva of *C. zamoniensis* spec. nov. simple with hook-like sclerotised pouch borders, originating anterior and mesal to the receptacula (Figs 57, 58), in *C. avicula* shapes more complex (Figs 27, 28).

**Description. Male** (Holotype, NMBE Ar 6741): Total length 2.18 mm. Cephalothorax: honey brown (138 U); reticulated; broad oval; 0.85 mm long without cephalic lobe (Fig. 54), 1.22 mm long with cephalic lobe (Fig. 54); 0.65 mm wide. Cephalic lobe: honey brown (138 U); shaft with few long hairs (Fig. 52); shaft constantly thick, at thinnest part below the eye-field 0.10 mm wide laterally, 0.11 mm wide dorsally (Figs 52, 54); tip of lobe laterally flattened with many short, stout and few long, slender hairs anterior to the PME (Figs 52, 54); sulcus 0.08 mm below AME (Fig. 53). Eyes: PME topmost on the cephalic lobe; AME projecting forward, lateral eyes besides the AME; one long macroseta projecting forward between AME (Fig. 54). Clypeus: directed obliquely backwards. Sternum: very fine brown (469 U) pigmentation on yellow (124 U) ground, dark brown (469 U) on the margins; 0.47 mm long; 0.51 mm wide; shield-shaped. Chelicerae: yellow (124 U); promargin with 5 teeth; retromargin with 5 denticles; stridulatory striae very dense and fine. Legs: yellow to light brown (120 U); formula 4-1-2-3; tibia I proximally bent and dorsal with glabrous area from proximal to more than half its length (Fig. 55), tibia III–IV with one dorsal proximal macroseta (0-0-1-1); metatarsi I–III with one trichobothrium, Tm I: 0.54 mm, metatarsus IV without trichobothria. Pedipalp: patella two times longer than broad, tibia retrolateral with expansion (round glabrous area, Fig. 51), one retrolateral and one prolateral trichobothrium (Fig. 51); paracymbium a simple clasp; tegulum distal with short and long papillae on protegulum (Fig. 48); suprategular apophysis semi-circular; marginal suprategular apophysis rather small, emerging close to the tip; distal suprategular apophysis robust, highly sclerotised (Figs 49, 50); column broad; embolic membrane slender; radix simple without any processes other than the elongated radial tailpiece and the embolus; embolus strongly sclerotised, twisted; broad at the base; very thin, curved tip (Fig. 50). Abdomen: dark olive green-brown (125 U); booklung covers very light brown (467 U); scaly.

**Female** (Paratype, NMBE Ar 6742): Total length 1.81 mm. Cephalothorax: honey brown (138 U); reticulated; 0.89 mm long; 0.65 mm wide. Eyes: posterior row slightly procurred; anterior row straight. Sternum: very fine brown (469 U) pigmentation on yellow (124 U) ground, dark brown (469 U) on the margins; 0.46 mm long; 0.46 mm wide; shield-shaped. Chelicerae: honey brown (138 U); promargin with 5 large teeth; retromargin with 5 denticles; stridulatory striae very fine and dense. Legs: yellow (122 U); formula 4-1-2-3; tibia I–IV with one dorsal proximal macroseta (0-0-1-1); metatarsi I–III with one trichobothrium, Tm I: 0.54 mm, metatarsus IV without trichobothria. Pedipalp: patella two times longer than broad, tibia retrolateral with expansion (round glabrous area, Fig. 51), one retrolateral and one prolateral trichobothrium (Fig. 51); paracymbium a simple clasp; tegulum distal with short and long papillae on protegulum (Fig. 48); suprategular apophysis semi-circular; marginal suprategular apophysis rather small, emerging close to the tip; distal suprategular apophysis robust, highly sclerotised (Figs 49, 50); column broad; embolic membrane slender; radix simple without any processes other than the elongated radial tailpiece and the embolus; embolus strongly sclerotised, twisted; broad at the base; very thin, curved tip (Fig. 50). Abdomen: dark olive green-brown (119 U), ventral darker (147 U).

**Variation.** The measurements are based on all type material (10♂ 9♀) plus specimens from the NMB (810i: 1♂ 2♀) and the MHNG (Axalp: 1♂; Fionnay: 1♂ 1♀).
FIGURES 48–55. Caracladus zamoniensis spec. nov.. Male: palp retrolateral (48), prolateral (49), embolic division prolateral (50); palpal tibia dorsal (51); cephalothorax dorsal (52), frontal (53) and lateral (54); right leg tibia I retrolateral (55). Scale: 200 μm. Specimens: Paratypes, NMBE Ar6742 (palp), Ar6735 (cephalothorax).

**Males** (n=13, means in brackets): The coloration is variable. Total length 1.91–2.18 mm (2.09 mm). Cephalothorax: 0.73–0.86 mm (0.82 mm) long without cephalic lobe, 1.10–1.23 mm (1.18 mm) long with cephalic lobe; 0.61–0.69 mm (0.65 mm) wide. Cephalic lobe: at thinnest part below the eye-field 0.10–0.13 mm (0.11 mm) wide laterally, 0.09–0.11 mm (0.11 mm) wide dorsally; sulcus 0.07–0.11 mm (0.08 mm) below AME (Fig. 53). Legs: Tm I: 0.50–0.59 mm (0.54 mm).

**Females** (n=12, means in brackets): The colorations are variable. Total length 1.62–2.00 mm (1.82 mm). Cephalothorax: 0.75–0.89 mm (0.82 mm) long; 0.60–0.65 mm (0.62 mm) wide. Legs: Tm I: 0.48–0.60 mm (0.53 mm).

**Distribution.** Endemic to the Alps, occurring in the Western- and Central Alps in France, Switzerland and Austria (Fig. 59). The Eastern distribution border seems to be in Western Austria. Checking of specimens of *C. avicula* collected west of Vorarlberg (Austria) revealed no misidentifications.

**Habitat.** *C. zamoniensis* spec. nov. occurs in the litter layer of Norway spruce (*Picea abies*) forests at the alpine timberline. Most sampling sites were inside the forest with no direct sunlight under branches of Norway spruce. The collection site and its surroundings were sampled intensively in two previous studies (Frick et al. 2006; Frick et al. 2007; Muff et al. 2007). We found no specimens of *C. zamoniensis* spec. nov. around stand alone trees in the dwarf-shrub heath with a similar microclimate as the closed forests. *C. zamoniensis* spec. nov. seems to avoid the open land. We only found two specimens in more open areas in the dwarf-shrub heath close to the subalpine forest. *C. zamoniensis* spec. nov. was never collected together with *C. avicula* in
the same pitfall trap but already in pitfall traps about 20 m away from *C. avicula*. The locus typicus is approximately 50 m away from the alpine timberline in the subalpine deciduous forest. We found the type specimens in litter under snow close to the tree trunk under a Norway spruce (Fig. 47) at 1960 m a.s.l. Other specimens were found between 1400–2000 m in litter and moss of spruce forests (e.g. Schenkel 1939). One record was much lower at app. 800 m in France (Bosmans pers. comm.).

**Phenology.** This species seems to be eurychronous. All records of other authors at altitudes from 1400 m to 1800 m were between July and September. However, at the type locality (1960 m) specimens were exclusively found between September and June. This corresponds with the time between the first snow fall and the beginning of the snow free time.

**Etymology.** The cephalic lobe of the male is morphologically very similar to the noses of the so called dwarf pirates and other imaginary figures from “Zamonia”. Zamonia is a continent inhabited by freaky creatures in the novel “The 13 ½ Lives of Captain Bluebear” by the German writer Walter Moers (2000). Translated, the species name means “*Caracladus* from Zamonia”.

**Remarks.** *C. zamoniensis* spec. nov. lacks a copulatory duct. The insertion of sperm is assumed to take place through a space between the ventral and the dorsal plates which are supposed to be pressed apart during copulation.

The specimens that Lessert (1907, 1910) shows have been evaluated by H.F. The figures of males in Lessert (1907: figs 5, 6) and reprinted in Lessert (1910: figs 98, 99) show *C. zamoniensis* spec. nov. and not *C.
avicula. The female mentioned in Lessert (1907: fig. 7) and Lessert (1910: fig. 100) shows Diplocentria bidentata (Emerton, 1882) (Thaler 1972).

The specimen that was pictured by Pesarini (1996: figs 9–10) was not available to the authors. A definite assignment to either C. avicula or C. zamoniensis spec. nov. is not possible. However, his records are referred to as C. avicula in the distribution map (Fig. 59) and the list of records.

The remaining pictures so far named as C. avicula in Heimer and Nentwig (1991: figs 350.1–350.5), Miliadge (1977: fig. 162), Simon (1884: figs 408, 409 and fig. 8 on plate 27) and Thaler (1969: figs 16–21, 1972: figs 7–11) are correctly assigned to C. avicula.

Erigone pauperula (Bösenberg & Strand, 1906) nov. comb.
(Figs 60–62).

Caracladus pauperulus Bösenberg & Strand, 1906: 161, plate 12, figs 257A–C.


Diagnosis. Female: The specimen was not compared with other Erigone species from Japan so that a sound diagnosis can not be provided. However, the shape of the margin of the ventral plate, seen in dorsal view has been used for species diagnoses in other Erigone species and is assumed to be typical for this species. Additionally, the position and form of the dorsal plate, the spermatheca and the copulatory duct might also provide valuable information to recognise this species.

Males: unknown.

Description. Since the specimen is now bleached white to transparent, the colour description follows Bösenberg and Strand (1906).

Female: Total length: 1.47 mm. Cephalothorax: yellow with narrow dark brown margin and some fine, dark lines; 0.69 mm long, 0.49 mm broad. Eyes: anterior row nearly straight; posterior row slightly procurred; all eyes rather close together (Bösenberg & Strand 1906, Fig 257C). Sternum: dark brown, with small yellow punctuations, black margin below the yellow labium; shield-shaped; 0.43 mm long, 0.34 mm broad. Labium: dark brown. Chelicerae: yellow; promargin with five big teeth; retromargin with four denticles. Legs: yellow with black hairs in rows on all segments; some macrosetae on all femora and tibiae; macrosetae and Tm I not possible to recognise. Palp: yellow. Epigyne: protruding in lateral view (Bösenberg & Strand 1906: Figs 257B, C), transversally striated in ventral view (Fig. 60), margin forming a small protuberance in the middle (Fig. 61). Vulva: ventral plate much larger than dorsal plate; dorsal plate not visible in ventral view; two lobes between the dorsal and ventral plate forming the opening to the copulatory duct (Fig. 62); copulatory duct sclerotised and coiled with unclear entrance to the receptacula, visible as slightly swollen part of the copulatory duct. Abdomen: dorsally brown, with dark brown dense pubescence; ventrally brown with fine yellow stripes and dots. Spinnerets: brown, brighter than the abdomen.

Males: unknown.

Distribution. Japan, no location given in the original description (Bösenberg & Strand 1906).

Habitat and phenology. Unknown.

Remarks. Bösenberg and Strand (1906) note that the eye pattern is atypical for Caracladus but that all other characters argue for Caracladus, especially the long macrosetae on the frontal femora. We do not recognise particularly long macrosetae in neither the holotype of Erigone pauperula nov. comb. nor Caracladus avicula. The genital morphology does not fit the descriptions of the epigyne and vulva of Caracladus given above. It shows some typical characters of Erigone like the rebordered epigyne margin seen in dorsal view (Figs 61, 62) and the transverse striations ventrally on the epigyne. We therefore assign this species to Erig-
However, the conformation of the vulva was very difficult to analyse because it is completely bleached. It was possible to see the form under the compound microscope, but the exact three-dimensional arrangements of the receptacula and the copulatory duct were not recognisable.

Bösenberg and Strand (1906) did not give an etymology for their species epithet “pauperulus”. However, it is assumed that they created a diminutive of “pauper” that can be used as an adjective (pers. comm. Roettig) and must therefore be adjusted to agree with the genus name according to article 31.2 of the international code of zoological nomenclature (International Commission on Zoological Nomenclature 1999).


**Intrageneric relationships**

**Taxa.** Species appearing in the closer relationships of *Caracladus* (according to the analysis of the phylogenetic placement of *Caracladus*) were chosen as outgroup taxa.

**Outgroup taxa:** *Walckenaeria acuminata* Blackwall, 1833 (1♂/1♀ from NMBE), *Gonatium rubens* (Blackwall, 1833) (1♂/1♀ from NMBE), *Parapelecopsis nemoralis* (Blackwall, 1841) (1♀ from NMBE, male according to the figures and plates in Hormiga 2000), *Tapinocyba praecox* (O. P.-Cambridge, 1873) (1♂/1♀ from NMBE).

**Ingroup taxa:** *Caracladus leberti* (1♂/1♀ from NMB), *Caracladus tsurusakii* (1♂/1♀ from NSMT), *Caracladus montanus* (both sexes according to the figures in Sha & Zhu 1994), *Caracladus avicula* (1♂/1♀ from NMBE), *Caracladus zamoniensis* spec. nov. (1♂/1♀ from NMBE).
Characters of males

Ch 1: palpal patella, ratio between length and width. 0: three, 1: about two and a half, 2: two, 3: less than two. Modified character 76 in Miller and Hormiga (2004).

Ch 2: palpal tibia, prolateral trichobothrium. 0: zero, 1: one (Fig. 20). Modified character 73 in Miller and Hormiga (2004).

Ch 3: palpal tibia, retrolateral trichobothrium. 0: one (Fig. 20), 1: two. Modified character 74 in Miller and Hormiga (2004).

Ch 4: prolateral palpal tibia, prolateral glabrous area. 0: absent, 1: present (Fig. 20). This area is usually darker, more sclerotised and somewhat transparent part on the prolateral margin of the tibia.

Ch 5: prolateral palpal tibia, prolateral glabrous area, form. 0: globular (Fig. 20), 1: elongated (Fig. 32).

Ch 6: prolateral tibial apophysis. 0: small tooth-like (Fig. 20), 1: distinct (Fig. 32).

Ch 7: prolateral tibial apophysis, surface. 0: hairy, 1: glabrous (Fig. 32).

Ch 8: retrolateral tibial apophysis. 0: absent (Fig. 32), 1: small tooth-like (Fig. 20), 2: distinct (Fig. 42).

Ch 9: paracymbium, basal hairs. 0: zero, 1: three, 2: five (Fig. 17). Modified character 14 in Miller and Hormiga (2004).

Ch 10: marginal suprategular apophysis. 0: absent, 1: present (Fig. 31). Character 34 in Miller and Hormiga (2004).

Ch 11: marginal suprategular apophysis, form. 0: tooth-like on the STA (Fig. 31), 1: fused to STA (Fig. 19), 2: fused to the embolic membrane (Parapelecopsis nemoralis, Fig. 23A in Hormiga 2000).

Ch 12: distal suprategular apophysis, tip. 0: pointed and sclerotised (Fig. 19), 1: blunt and transparent (Fig. 41).

Ch 13: embolic membrane. 0: absent, 1: present (Fig. 19). Character 40 in Miller and Hormiga (2004).

Ch 14: embolic membrane, papillae. 0: absent (Fig. 19), 1: present (Fig. 41). Character 41 in Miller and Hormiga (2004).

Ch 15: embolus length. 0: short (Fig. 50), 1: long (Fig. 19).

Ch 16: embolus form. 0: robust (Fig. 50), 1: whip-like (Fig. 19).

Ch 17: embolus conformation. 0: straight (Fig. 41), 1: twisted (Fig. 19).

Ch 18: radical tailpiece, form. 0: short (Fig. 30), 1: elongated (Fig. 18).


Ch 20: protegular papillae, short rod-like. 0: absent, 1: present (Fig. 17). Modified character 18 in Miller and Hormiga (2004). Both protegular papillae types are situated distally on the tegulum. The short rod-like papillae look like small peaks or scales. They are about as long as broad, and are situated median to the long rod-like papillae (character 21). The latter are at least three times their diameter but usually much longer and emerge the tegulum retrolateral to the short rod-like papillae. Figure 48 shows both types directly next to each other.

Ch 21: protegular papillae, long rod-like. 0: absent, 1: present (Fig. 17). Modified character 18 in Miller and Hormiga (2004). See character 20 for discussion.

Ch 22: chelicerae, promarginal teeth. 0: five, 1: four.

Ch 23: chelicerae, retrormarginal denticles. 0: five to six, 1: four or less.

Ch 24: chelicerae, stridulatory striae, number. 0: few, 1: many.

Ch 25: chelicerae, stridulatory striae, distance. 0: distant, 1: close.


Ch 27: cephalic lobe. 0: absent (or slightly raised) (Hormiga 2000, plate 64A), 1: PME lobe (Fig. 35), 2: pronounced cephalic lobe (Fig. 23).

Ch 29: thinnest head region lateral. 0: no neck (Fig. 35), 1: broad neck (Fig. 45), 2: narrow neck (Fig. 23).

Ch 30: cephalothorax, reticulation. 0: smooth, 1: reticulated.

Ch 31: thick hairs behind PME on neck. 0: absent (Fig. 45), 1: present (Fig. 23).

Ch 32: thick hairs anterior to PME. 0: absent, 1: present (Fig. 11). The hairs of W. acuminata are alike those of C. avicula. They are both cone-shaped with coiled ridges. However, in W. acuminata they are trident (Hormiga 2000, plate 72F) and in C. avicula single (Fig. 12).

Ch 33: sulcus. 0: absent (Fig. 44), 1: present (Fig. 23). Modified character 108 in Miller and Hormiga (2004).

Ch 34: sulcus position. 0: lateral (Fig. 35), 1: frontal (Fig. 23).

Ch 35: leg, tibia I, glabrous field. 0: absent (Fig. 36), 1: present (Fig. 55).

**Characters of females.**

Ch 36: chelicera, promarginal teeth. 0: six, 1: five, 2: four.

Ch 37: chelicera, retromarginal denticles. 0: five to six, 1: four or less.

Ch 38: eyes, posterior row. 0: straight, 1: procurved.

Ch 39: eyes, anterior row. 0: straight, 1: recurved, 2: procurved.

Ch 40: copulatory pouch. 0: absent, 1: present (Fig. 26).

Ch 41: copulatory pouch, size. 0: small (Fig. 40), 1: big (Fig. 26). These pouches are situated anterior to the visible part of the dorsal plate. The small pouches are much smaller than the receptaculum and together not broader than the narrowest part of the dorsal plate, that is visible in ventral view. The big pouches are about as big as the receptacula and are much broader than the narrowest part of the dorsal plate.

Ch 42: copulatory duct. 0: absent (Fig. 58), 1: present (Fig. 39).

Ch 43: injection opening of receptaculum. 0: dorsal (Fig. 28), 1: frontal (Hormiga 2000, fig. 27G).

Ch 44: fertilization duct orientation. 0: posterior (Hormiga 2000, fig. 23H), 1: mesal (Fig. 28). Modified character 99 in Miller and Hormiga 2004.

Ch 45: fusion of dorsal and ventral plate anteriorly. 0: on “hill” (Fig. 37), 1: below “wave” (Fig. 7, 8), 2: plain (Hormiga 2000, plate 63D). In aboral view, the anterior fusion of the dorsal and ventral plate either build a continuos “hill” or a cavity that looks like a “braking wave”.

Ch 46: dorsal plate, form. 0: anterior narrower than posterior (Fig. 37), 1: anterior as broad as posterior (Fig. 26).

Ch 47: dorsal plate, shape. 0: wider than long (Fig. 37), 1: about as long as wide (Fig. 40), 2: longer than wide (Fig. 26).

Ch 48: receptacula, position. 0: anterior to the dorsal plate (Hormiga 2000, plate 63D), 1: lateral to the dorsal plate (Fig. 26).

Ch 49: leg IV, trichobothrium on metatarsus. 0: absent, 1: present.

**Results and discussion.** The single most parsimonious tree (L= 91, CI=0.62, RI=0.59) is reprinted in figure 63. Eight characters (2, 3, 13, 19, 20, 26, 30 and 41) were phylogenetically uninformative. The characters are optimised using WinClada 1.00.08 (Nixon 1999) with unambiguous changes shown only.

In this analysis Caracladus is monophyletic with Tapinocyba as its sister taxon. The glabrous prolateral tibial apophysis, the slender whip-like embolus (reduced in C. zamoniensis spec. nov.), the copulatory pouch and the dorsal opening to the receptacula are autapomorphies of Caracladus. However, it is important to note, that all these characters could not be assessed for C. montanus which is considered as sister species of C. tsuruskii. Both species lack sulci and cephalic pits.
### TABLE 1. Character matrix concerning the intrageneric relationships.

<table>
<thead>
<tr>
<th>Character State Changes</th>
<th>W. acuminata</th>
<th>G. rubens</th>
<th>P. nemoralis</th>
<th>T. praecox</th>
<th>C. leberti</th>
<th>C. tsurusakii</th>
<th>C. montanus</th>
<th>C. avicula</th>
<th>C. zamoniensis</th>
</tr>
</thead>
<tbody>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>6</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>0</td>
</tr>
</tbody>
</table>

**FIGURE 63.** Single most parsimonious tree (L= 91, CI=0.62, RI=0.59) of *Caradus* with unambiguous optimisation. Synapomorphic character state changes are marked in black.

Walkenaeria acuminata

Gonatium rubens

Parapalecopsis nemoralis

Tapinocyba praecox

Caradus leberti

Caradus avicula

Caradus tsurusakii

Caradus montanus

30 · Zootaxa 1982 © 2009 Magnolia Press

FRICK & MUFF
Five characters support the close relationship between *C. avicula* and *C. zamoniensis* spec. nov.: the pro-
lateral glabrous area, the tooth-like retrolateral tibial apophysis, the twisted embolus, the glabrous field proxim-
al on leg tibia I and the square dorsal plate.

*C. leberti* does not show the typical head lobe and thick hairs anterior to the PME, characters that are sup-
posed to be characteristic for *Caracladus*. However, Thaler (1973) assigned this species to *Caracladus*
according to the genital morphology of both males and females, which is confirmed by our analysis. *C. leberti*
is “basal” with respect to the other *Caracladus* species. It shows ancestral states like the long but not yet thick
hairs on the cephalic lobe. Furthermore, this lobe is only a small narrow bump (Fig. 35) instead of a pro-
nounced structure like in the other *Caracladus* species (e.g. Fig. 23). Additionally, *C. leberti* has a short and
straight embolus instead of a curved one as in other *Caracladus* species and a relatively short radical tailpiece.
All these states are considered to be ancestral.

It is difficult to locate the biogeographic origin of *Caracladus*, even though the current data, with the
alpine endemite *C. leberti* as sister to all other *Caracladus* species, point to Europe with one dispersal event to
Asia (Fig. 63). The distribution of the sister taxon of the close relatives may indicate the biogeographic origin
of *Caracladus*. Unfortunately, these are highly ambiguous as discussed in the following section. *Tapinocyba*
seems to be the closest relative in our analysis with species occurring in Europe and Asia (Platnick 2008). The
exemplar species for the analysis *Tapinocyba praecox* occurs in Europe only. But even the relationships of the
potential close relatives used in this study are not identical in the inter- and intrageneric analysis. This conflict
might be due to the lack of characters that especially account for the relationships between the outgroup taxa
of the intrageneric analysis. The outgroup taxa were chosen to root the cladogram and the character states with
a particular focus on the ingroup relationships rather than the outgroup taxa. The relations of the outgroup taxa
found in the intergeneric analysis might therefore be more reliable.

However, all *Caracladus* species (apart from *C. montanus*) were found in wintertime and on relatively
high altitudes. These habitats are not as frequently sampled as lower altitudes in the snow free time. It is there-
fore assumed that more species of *Caracladus* may be found in the future, which may indicate another than a
European or even alpine origin.

**Phylogenetic placement of *Caracladus***

**Results and Discussion.** The recoding did not influence the results presented in Miller and Hormiga (2004)
apart from one exception: the recoding of *Tapinocyba* resulted in two most parsimonious topologies. *Caracla-
dus avicula* was scored as follows:

0-00001000 0501011100 0001000010 1001100101 0001000001 01000-0000
0-00001101 0013000000 0-00000000 0010000010 1000000111 2010012301
004101100 2210010101 0100000000 0002001111 020111000- ??1100

The inclusion of *Caracladus avicula* in the morphological analysis of 82 taxa used by Miller and Hormiga
(2004) resulted in 3 most parsimonious trees (L= 910, CI=0.23, RI=0.58). Four characters (104, 105, 106 and
155) were phylogenetically uninformative. The topology of the taxa basal to the “distal erigonines” do not dif-
fer from the single most parsimonious tree found by Miller & Hormiga (2004) in all three trees of the current
analysis. Therefore, our figures only show the “distal erigonines”.

The preferred tree is shown in figure 64. The two remaining topologies differ from the preferred tree in the
clades reprinted in figures 65 and 66. *Caracladus* is deeply nested in the “distal erigonines” which are
defined by the reduction of taenidia in the tracheoles, the presence of imbricated instead of ridged stridulatory
striae and the loss of the distal macroseta on tibia IV (Hormiga 2000; Miller & Hormiga 2004). In the current
analysis, the closest relative of *Caracladus* is *Tapinocyba* (Figs 63–68).
Millidge (1977) placed *Caracladus* among the “doubtful genera” because its relations seemed to be obscure. However, he suggested a close relation to *Monocephalus* rather than to *Tapinocyba*. The relation to *Monocephalus* can not be tested here but the following characters support a close relation to *Tapinocyba* and its sister taxa: the presence of rod-like protegular papillae (characters 17 and 18, papillae reduced in *Hybocopus* and scale-like in *Dismodicus*), one retrolateral trichobothrium (character 74, two in *Dismodicus*), cephalic sulci and pits (characters 108, 109) and the lack of a distal macroseta on tibia I and II (characters 137, 139).

The presence of a marginal supratropical appophysis also supports a clade including the taxa between *Diplocentria* and *Parapelecopsis* with two reductions. This character could not be unambiguously coded for *Tapinocyba*. Miller and Hormiga (2004) coded *Tapinocyba* as lacking this apophysis, which is a tooth-like process on the supratropical close to the foramen (Hormiga 2000). However, when coding this character for the intrageneric analysis we found a structure close to the foramen that is not tooth-like (apart from *C. lebertii*) but might be derived from such an apophysis. Because *Tapinocyba* (Hormiga 2000: plate 62A) looks like *C. avicula* (Fig. 19) in this respect, we recoded *Tapinocyba* for this character. Following the original coding of Miller and Hormiga (2004) would lead to 13 most parsimonious topologies instead of three. The differences concern the same variable regions represented in the most parsimonious topologies (Figs 64–66) but without generally new topologies: In some of these trees *Caracladus* emerges basal to *Tapinocyba* and its sister taxa (Fig. 65) or among these taxa.

**FIGURES 64–66.** Preferred most parsimonious tree (L= 910, CI=0.23, RI=0.58) with alternatives marked in bold. Clades basal to the “distal erigonines” are omitted. Preferred tree (64); alternative position of *Lophomma* and *Typhocrestus* (65) and of *Psilocymbium* (66).
FIGURE 67. Strict consensus tree of the eight most parsimonious trees (L= 927, CI=0.23, RI=0.57). Clades basal to the “distal erigonines” are omitted and those shared with the most parsimonious topology in Miller and Hormiga (2004) are marked in bold. Bremer supports (from TNT) below branches.

The strict consensus tree (L= 927, CI=0.23, RI=0.57) (Fig. 67) shows the shared clades with the single most parsimonious topology found by Miller and Hormiga (2004) in bold. The changes concern the position...
of *Psylocymbium*, *Lophomma*, *Walckenaeria* and *Tapinocyba*. The close relation of the latter two with *Caracladus* may have led to these changes. Over all the Bremer supports are relatively low in the clades close to *Caracladus*, its position should therefore be treated with caution and may change with the addition of more closely related taxa and characters that account for those taxa. Most of the characters supporting the relations between these closely related genera are homoplastic (white squares in fig. 68).

**FIGURE 68.** Detail of the preferred most parsimonious tree showing *Caracladus* and its closest relatives (Fig. 64) with AccTran character optimisation. Numbers on the square marks correspond to the characters described in Miller and Horman (2004) and those below to its states. Synapomorphic character state changes are marked in black.

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References

Blackwall, J. (1841) The difference in the number of eyes with which spiders are provided proposed as the basis of their distribution into tribes; with descriptions of newly discovered species and the characters of a new family and three new genera of spiders. Transactions of the Linnean Society of London, 18, 601–670.


