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# Plant bugs with swollen antennae: a morphology-based phylogenetic analysis of *Heterocapillus* Wagner, 1960 and related genera (Hemiptera: Miridae: Phylinae)

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# Abstract

Plant bugs of the genus *Heterocapillus* (Miridae: Phylinae) are predominantly Mediterranean minute black phylines with distinctly swollen antennomeres I and II. The monophyly and relationships of this group has been questioned in several studies. This paper provides a morphology-based phylogeny inferred with Parsimony and Bayesian analyses of the genus and a diverse array of outgroups. Based on these results, *Heterocapillus* is here redefined as monotypic. A new monotypic genus *Abietocapsus* **gen. nov**. is erected to accommodate *Phoenicocoris dissimilis* (Reuter, 1878) and updated diagnoses are provided for the genera *Lobicris* Putshkov, 1977 **gen. dist.**, *Mesopsallus* Wagner, 1970 **gen. dist.**, and *Salicarus* Kerzhner, 1962. The following new combinations are established: *Campylomma atlanticum* (Wagner, 1963) **comb. nov.**, *Campylomma pusillum* (Reuter, 1878) **comb. nov.**, *Mesopsallus amygdali* (Wagner, 1960) **comb. nov.**, *Mesopsallus fagi* (Drapolyuk, 1990) **comb. nov.**, *Mesopsallus mali* (Meyer-Dür, 1843) **comb. nov.**, *Mesopsallus pici* (Reuter, 1899) **comb. nov.**, *Mesopsallus rhodani* (Fieber, 1861) **comb. nov.**, *Mesopsallus validus* (Reuter, 1901) **comb. nov.**, *Psallus* (*Phylidea*) *validicornis* (Reuter, 1876) **comb. nov.**, *salicarus cavinotum* (Wagner, 1973) **comb. nov.**, *Salicarus nitidus* (Horváth, 1905) **comb. nov.**, and *Salicarus perpusillus* (Wagner, 1960) **comb. nov.**, *Salicarus nitidus* (Horváth, 1905) **comb. nov.**, and *Salicarus perpusillus* (Wagner, 1960) **comb. nov.**, *Salicarus nitidus* (Horváth, 1905) **comb. nov.**, and *Salicarus perpusillus* (Wagner, 1960) **comb. nov.**, *Salicarus nitidus* (Horváth, 1905) **comb. nov.**, and *Salicarus perpusillus* (Wagner, 1960) **comb. nov.**, *Atractotomus schmiedeknechti* Reuter, 1899 is synonymized with *Atractotomus parvulus* Reuter, 1878. *Heterocapillus niger* Wagner, 1966 is synonymized with *Psallus* (*Phylidea*) *validicornis* (Reuter, 1876). The highly homoplastic nature of the antennal shape in phylines is demonstrated, suggesti

# Key words

Taxonomy; phylogeny; Palearctic; new combinations; new synonyms

# 1. Introduction

The Miridae or plant bugs are an exceptionally species-rich group containing more than 11,000 described species, which makes it the second-largest insect family with incomplete metamorphosis (Cassis and Schuh 2012). Plant bugs exhibit great morphological diversity in terms of size, coloration, body shape, and structure. Greatly exaggerated (Cassis et al. 2013: fig. 1), swollen (Fig. 5G–N) or otherwise modified (Taszakowski et al.:

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fig. 1A–C) antennal segments have evolved independently in many mirid lineages. The driving forces behind the evolution of exaggerated antennae, which may or may not be sexually dimorphic, are poorly understood. Proposed mechanisms for this structural diversity have focused on the increase of the surface area available for antennal sensilla (Schneider 1964; Chinta et al. 1997), sexual signaling (Gourevitch and Shuker 2021), grasping female during copulation (Stork 1981; Konstantinov and Simov 2018) or a combination of these processes.

Heterocapillus Wagner, 1960 was originally described as a subgenus of Atractotomus Fieber, 1858, and belongs to the worldwide distributed and the second largest subfamily Phylinae, containing close to 40% of total family diversity. Atractotomus has had a checkered taxonomic history and for more than a century since the original description it was recognized by the distinctly swollen, spindle-shaped antennomere II, the presence of silvery scales on dorsum, and the vertical head with barely visible clypeus in dorsal view (Wagner 1952; Carvalho 1955; Wagner and Weber 1964). Wagner (1960) established the subgenus Heterocapillus to accommodate three species united by dorsum vestiture composed of three types of setae and the male genitalia structure, specifically the secondary gonopore located far from the apex of the vesica. Kerzhner (1962) recognized Heterocapillus as a separate genus but did not augment its diagnosis. Two years later he (Kerzhner 1964) described the monotypic subgenus Phaeochiton within Heterocapillus, which in turn was upgraded to generic rank by Putshkov (1977).

Stonedahl (1990) provided a monographic treatment of *Atractotomus*, and an updated diagnosis of this genus mainly based on the male genitalia structure. While discussing the diagnostic features and the taxonomy of related genera, he correctly pointed out that *Heterocapillus* is apparently non-monophyletic and at least two distinct groups may be recognized within this genus. Finally, Stonedahl examined the shape of antennal segments as a potential diagnostic character and indicated low utility at the generic level.

Male genitalia have been extensively applied over the last decades to diagnose genera and higher taxa. For instance, Rhinacloa (Schuh and Schwartz 1985), Megalopsallus (Schuh 2000), Plagiognathus (Schuh 2001), Europiella (Schuh 2004), Phoenicocoris (Schwartz and Stonedahl 2004), Chlamydatus (Schuh and Schwartz 2005), Plesiodema (Schwartz 2006), Camptotylus (Konstantinov 2008a), Solenoxyphus (Konstantinov 2008b), Tytthus (Henry 2012), Leucodellus (Konstantinov 2012), Semium (Henry 2018), Hypseloecus (Yasunaga and Duwal 2019) and many other genera were mainly diagnosed by the vesica, an intromittent organ of male genitalia. In contrast, the genus Heterocapillus demonstrates a high diversity in the male genitalic structure and is currently diagnosed by two non-unique features viz., the three types of setae on dorsum combined with fusiform antennae.

Thus, the current study seeks to reveal monophyletic lineages within taxa related to *Heterocapillus* based on a morphology-based phylogenetic analysis and to provide updated diagnoses for groups under consideration. The paper also discusses the phylogenetic utility of the exaggerated antennal segments, long used in mirid taxonomy, and assesses their correlation with other somatic characters.

## 2. Materials and Methods

#### 2.1. Specimens and collections

More than 2,000 specimens were examined for this study. Institutions, their acronyms, and names of curators are as follows: **AMNH** – American Museum of Natural History, New York (R.T. Schuh and R. Salas); **BMNH** – Natural History Museum, London (M. Webb); **ISNB** – Institut Royal des Sciences Naturelles de Belgique, Brussels (W. Dekoninck); **MNHN** – Muséum national d'Histoire naturelle, Paris (E. Guilbert, A. Matocq); **MZH** – Finnish Museum of Natural History (H. Viljanen); **NMPC** – National Museum of Natural History, Prague (P. Kment); **NMWC** – National Museum of Wales (M. Wilson); **ZISP** – Zoological Institute, Russian Academy of Sciences, St. Petersburg; **ZMUH** – Zoological Museum, University of Hamburg (F. Wieland, M. Husemann).

Bar code labels or unique specimen identifiers (USIs) were attached to all examined specimens. Further information such as additional photographs of habitus and genitalic structures, georeferenced coordinates of each locality, specimens dissected, notes, collecting method can be obtained from the Heteroptera Species Pages (http://research. amnh.org/pbi/heteropteraspeciespage/), which assembles available data from a specimen database (Konstantinov and Namyatova 2019). Refer to Supplementary Material (File S1) for USI numbers of illustrated specimens. Species in the Taxonomy section are listed alphabetically.

#### 2.2. Microscopy and illustrations

Observations and measurements were made with a Nikon SMZ 1500 stereomicroscope. Images of the dorsal habitus and male genitalic structures were taken with a Keyence VHX-500F digital microscope (University of Hamburg). Genitalia were macerated in potassium hydroxide, cleared in distilled water, and then transferred to glycerin jelly for proper orientation. Scanning electron micrographs of selected structures were taken using a Quanta 250 scanning electron microscope.

Unless otherwise stated, all measurements are in millimeters. Measurements shown in Table 1 include body length, clypeus to apex of cuneus length, width of head, interocular distance, length of antennomere II and hind tibia, and pronotum length and width.

#### 2.3. Terminology

The morphological terminology follows Schuh and Weirauch (2020) except for genitalia, which follows Konstantinov (2003, 2019) for males, Pluot-Sigwalt and Matocq (2006) and Schuh and Schwartz (2016) for females. Terms used for structures of vesica were provided in Konstantinov (2008c: figs 13, 15).

#### 2.4. Character and taxa sampling

A morphological matrix (File S2) of 62 characters coded for 46 terminals was prepared using Mesquite, version 3.70 (Maddison and Maddison 2018). Of the total characters, 33 are binary and 29 multistate; four taxon-state entries are polymorphic. Seven characters were selected from the vestiture, 12 from the coloration, five from the structure of antennomeres, five from the structure of the head including labium, seven from the thorax including legs and wings, 22 from the male and four from the female genitalia. At the initial stage of the work, all ten species currently assigned to the genus Heterocapillus were included as terminals in the matrix. However, several species were found to be identical to each other with respect to all coded traits and were excluded from the subsequent analysis. The excluded species were Heterocapillus cavinotum Wagner, 1973 (identical to H. genistae (Lindberg, 1948)), Heterocapillus niger Wagner, 1966 (identical to Heterocapillus validicornis (Reuter, 1876)), Heterocapillus perpusillus (Wagner, 1960) (identical to Heterocapillus nitidus (Horváth, 1905)), and Heterocapillus validus (Reuter, 1901), an obscure species known from a single female syntype which appears to be identical to females of H. pici (Reuter, 1899). The monophyly of the genus has been questioned in several studies (Stonedahl 1990; Konstantinov 2008c) and a broad, comprehensive set of outgroup taxa were added into the analysis. In total, 40 terminals were chosen as outgroup taxa to reflect the diversity of potentially related genera viz., Atractotomus Fieber, 1858, Campylomma Reuter, 1878, Europiella Reuter, 1909, Phaeochiton Kerzhner, 1964, Phoenicocoris Reuter, 1875, Psallus Fieber, 1858, Plagiognathus Fieber, 1858, Rhinacloa Reuter, 1876, Salicarus Kerzhner, 1962, Sthenarus Fieber, 1858, and Zophocnemis Kerzhner, 1962. Additionally, four apparently unrelated genera having swollen antennomere II, Criocoris Fieber, 1858, Bergmiris Carvalho, 1984, Dacota Uhler, 1872, and Excentricoris Carvalho, 1955 were added to reflect the morphological diversity. Trees (Figs 1, 2) were rooted with Compsidolon pumilum (Jakovlev, 1876).

# 2.5. Software and tree searching strategies

Data were analyzed using Maximum Parsimony and Bayesian frameworks. The parsimony analysis (MP) was performed using PAUP 4.0 (Swofford 2000) and independently verified using TNT 1.5 (Goloboff et al. 2000) with all characters treated as unordered and equally weighted. Analyses were performed in two ways: (1) any polymorphic taxon-state entry was set as missing data i.e., equivalent to '?' (called MI) (Pimentel and Rig-

gins 1987) and (2) computed without any changes e.g., 0+2 (called PL) (Campbell and Frost 1993). A heuristic search of 1,000 replicates, using tree-bisection-reconnection branch-swapping algorithm with reconnection limit = 8 and retaining 100 trees per replicate was performed. Branches were collapsed if minimum length was zero. To assess the impact of homoplasy in the data, PL trees were used as starting topologies for successive approximations weighting (SAW) using rescaled consistency index (Farris 1969; Carpenter 1988) in PAUP 4.0. The reliability of each branch was assessed using the Jackknife and Bremer supports. Jackknife supports were calculated in PAUP with 1,000 permutations, independent character removal and removal probability of 36% (as suggested by Farris et al. (1996). Bremer supports or Decay indices for each node were estimated in PAUP using batch file generated in PRAP2 (Müller 2004). Character-state optimization and editing of the resulting trees was performed by Winclada version 1.00.08 (Nixon 2002).

Bayesian tree (BI) was inferred using MrBayes 3.2.7 (Ronquist et al. 2012) under the Mk model with a gamma distribution (Lewis 2001). Two simultaneous runs of 2,000,000 generations with four chains each were performed, starting with a random tree and with uninformative priors. Parameters and trees were sampled at intervals of 1,000 generations, with the first 25% discarded as burn-in prior to assembling a majority rule consensus tree. Convergence and mixing of parameters were evaluated through the average standard deviation of split frequencies (0.01) and the potential scale reduction factor. The resulting topology and posterior probabilities were visualized using FigTree 1.4.4 (Rambaut 2018).

#### 2.6. Characters

- Scalelike setae on dorsum: (0) absent (Fig. 5 D, E); (1) present (Fig. 5G–N). — Types of setae on the dorsum has long been used as a potentially phylogenetically informative character in Miridae and within Phylinae more specifically (e.g., Schuh and Schwartz 1985, Stonedahl 1990).
- Scalelike setae on thoracic pleura: (0) absent; (1) present (Figs 6G, H, 7). The position of scale-like setae has been found to be informative in *Atractotomus* (Stonedahl 1990) and in the phyline tribe Pilophorini (Schuh and Schwartz 1985).
- **3.** Type of scalelike setae: (0) type I, narrow, apically acuminate (Fig. 6A–D); (1) type II, broad, apically serrate (Fig. 6E, H). These two types of scalelike setae were first characterized by Schuh & Schwartz (1985), while Stonedahl (1990) referred to the apically acuminate and apically broad scales as types 1 and 2, respectively.
- 4. Metafemoral spicules: (0) absent (Schuh and Schwartz 1985: fig. 35); (1) a few spicules present, forming short irregular row on apex of femur (Schwartz and Stonedahl 2004: figs 9C, 11B, 13B, 15D); (2) present, arranged into regular uninterrupted row on distal one half of femur (Schuh and Schwartz

1985: fig. 36). — Schuh & Schwartz (1985) documented a long row of minute spicules on the dorsal surface of metafemur as a synapomorphy uniting genera *Campylomma* and *Rhinacloa*. Stonedahl (1990) used the term "spinules" for the same structure and found that the presence of a short, irregular row of spicules on the distal one-third of the metafemur is typical for *Atractotomus* spp. Schwartz & Stonedahl (2004) documented this feature for additional related phyline genera.

- 5. Tibial spines: (0) dark (Fig. 3); (1) whitish (Konstantinov 2006: figs 34–36).
- Dark spots at bases of tibial spines: (0) absent (Fig. 3M, N); (1) present (Fig. 3G–L).
- Simple setae on dorsum: (0) short, adpressed to semiadpressed, pale or predominantly pale, with a few darker setae on apical part of forewing (Fig. 3M, N); (1) short, adpressed to semiadpressed, dark (Fig. 4A, B, D, F–J); (2) distinctly long, erect to semierect, pale (Konstantinov 2006: figs 34–36); (3) absent (Fig. 4C).
- Robust spinelike setae on dorsum: (0) absent (Fig. 4I–L); (1) present at sides of pronotum and hemelytra (Fig. 4A–B); (2) entire dorsum clothed with spinelike setae (Fig. 4C).
- **9.** Coloration of antennomere II, male: (0) same color as dorsum (Fig. 5B,E,F,H); (1) dirty whitish, paler than dorsum (Fig. 5A); (2) whitish to yellow with darkened base (Konstantinov et al. 2015: fig. 10); (3) darker than dorsum (Schuh 2001: fig. 15).
- Coloration of antennomere II, female: (0) same color as dorsum (Fig. 5G,I,K); (1) whitish, paler than dorsum (Fig. 4B); (2) whitish to yellow with darkened base (Konstantinov et al. 2015: fig. 11); (3) darker than dorsum.
- Coloration of antennomeres III & IV, male: (0) same color as segment II (Fig. 3I); (1) paler than segment II (Fig. 3A–C, E, G, K).
- **12.** Coloration of antennomeres III & IV, female: (0) same color as segment II (Fig. 3J); (1) paler than segment II (Fig. 3D, H, L).
- **13.** Coloration of head: (0) entirely dark (Fig. 5M–P); (1) uniformly dark with pale vertex (Fig. 5H, I, L); (2) pale with defined dark pattern (Konstantinov 2008c: figs 1–4); (3) without dark pattern (Fig. 5B).
- **14.** Metathoracic scent gland evaporatory area: (0) of same color with thoracic pleurite; (1) distinctly paler than reminder of thoracic pleurite (Fig. 6G).
- **15.** Coloration of pronotum and scutellum: (0) uniformly or largely dark, without pale pattern (Fig. 5I–K); (1) whitish to yellowish, sometimes with dark markings (Fig. 5B, L).
- **16.** Coloration of hemelytron: (0) uniformly or largely dark, without pale pattern (Fig. 4A–E); (1) whitish to yellowish, sometimes with dark markings (Fig. 4H).
- Ground color of femur: (0) same color as pronotum (Fig. 4A–E); (1) whitish yellow, paler than dorsum (Fig. 4F, G).

- 18. Color pattern on hind femur: (0) absent (Fig. 4A–E);(1) round spots on fore and hind surfaces (Fig. 4F, G, K, L).
- 19. Coloration of tibiae: (0) uniformly dark (Fig. 4D, H); (1) yellowish or whitish (Fig. 4A, B); (2) basally dark, apically pale (Fig. 4E); (3) yellowish or whitish with dorsal dark spot at base (on a "knee") (Fig. 4F, G); (4) yellowish, with entire ventral surface dark (Figs 3I, J, 4C).
- **20.** Shape of antennomere I, male: (0) distinctly swollen (Fig. 5G, H, J); (1) not swollen (Fig. 5A, B, E, O).
- Shape of antennomere I, female: (0) distinctly swollen (Fig. 5I, K, L); (1) not swollen, almost parallel-sided, slightly wider than segment II (Fig. 5C, D, P).
- 22. Shape of antennomere II, male: (0) not swollen, parallel-sided (Fig. 5A, B, E, O); (1) swollen along entire length, parallel-sided, almost as wide as segment I (Fig. 5F, O); (2) fusiform (Fig. 5H, M).
- 23. Shape of antennomere II, female: (0) not swollen (Fig. 5C, D); (1) swollen along entire length; (2) apically clavate (Fig. 5P); (3) fusiform (Fig. 5I, L, N).
- 24. Antennomere II, length, male: (0) distinctly shorter than basal width of pronotum (Fig. 5A, B, E); (1) longer than or equal to basal width of pronotum (Fig. 5F, O).
- **25.** Head, orientation: (0) vertical, slightly produced anterior to eyes (Fig. 4A, B, D–L); (1) strongly extended forward (Fig. 4C).
- 26. Shape of head in frontal view: (0) head weakly protruded beyond inferior margin of eyes, almost triangular (Wagner 1975: fig. 630i); (1) head with clypeus visibly protruded below inferior margin of eyes (Wagner 1975: fig. 630q); (2) head rounded, slightly protruded beyond inferior margin of eyes (Wagner 1975: fig. 630h).
- 27. Antennal fossa location in frontal view: (0) above inferior margin of eye (Wagner 1975: fig. 630h); (1) near inferior margin of eye (Wagner 1975: fig. 630l); (2) below inferior margin of eye (Wagner 1975: fig. 630k).
- Posterior margin of vertex: (0) rounded (Fig. 5G–L);
   (1) with transverse carina especially well developed in females (Fig. 5D, E); (2) pointed and posteriorly attenuated, covering extreme apex of pronotum (Fig. 5A, B, J, K).
- **29.** Labium, length: (0) barely reaching middle coxae; (1) surpassing hind coxae.
- **30.** Hemelytron, female: (0) shorter than in male, almost not protruded beyond apex of abdomen; (1) not sexually dimorphic, well protruded beyond apex of abdomen in both sexes, or barely protruding in both sexes.
- 31. Subapical spines on hind femur: (0) absent (Fig. 4C);(1) present, arranged in a pair of two large and a pair of smaller ones just at apex (Fig. 4F–L).
- **32.** Claw, shape: (0) elongate, slender, gradually broadened basally (Fig. 7H); (1) wide at base, abruptly narrowing towards midpoint (Fig. 7G). — Schuh (1975) found several characters of the pretarsus that are phylogenetically important.

- **33.** Claw, curvature: (0) smoothly curving towards apex (Fig. 7H); (1) sharply bent in apical part; (2) sharply bent close to base; (3) bent at midpoint (Fig. 7I).
- **34.** Pulvilli, length: (0) covering less than one half of ventral claw surface (Fig. 7I); (1) covering about two thirds of ventral claw surface (Fig. 7L); (2) small, barely recognizable; (3) absent (Schwartz and Stonedahl 2004: fig. 21B–D).
- **35.** Pulvilli, apex: (0) attached to claw along entire length (Fig. 7G); (1) apically free (Fig. 7L); (2) absent (Schwartz and Stonedahl 2004: fig. 21B–D).
- **36.** Parempodium: (0) gradually tapering, acute (Fig. 7G); (1) apically spatulate (Fig. 7K); (2) flattened along entire length (Schwartz and Stonedahl 2004: fig. 21B–D).
- **37.** Genital capsule: (0) large, about 0.5 of abdomen length; (1) about 0.3 of abdomen length.
- **38.** Ventroapical keel of genital capsule: (0) absent; (1) present.
- **39.** Right paramere: (0) elongate-oval, lanceolate, more than twice as long as wide (Fig. 8P); (1) broadly oval, short and tiny, less than 1.5 × as long as wide (Fig. 8F).
- **40.** Apex of right paramere: (0) more or less gradually attenuated (Fig. 10O); (1) twin-coned (Fig. 10C–F).
- **41.** Apical process of left paramere: (0) long, slightly gradually curved (Fig. 10P); (1) short and straight (Fig. 8B, G, Q).
- **42.** Body of left paramere, shape: (0) boat-shaped, of typical phyline shape (Fig. 8B, G, Q); (1) distinctly extended backwards (Wagner 1975: fig. 705a, c); (2) thin, deeply excavated, with unusually long processes (Wagner 1975: fig 689d).
- 43. Apex of phallotheca: (0) without dorsal subapical tooth and without dorsal cleft (Fig. 8H); (1) with dorsal subapical tooth and without dorsal cleft (Fig. 9P); (2) with large dorsal cleft and without dorsal subapical tooth.
- **44.** Shape of vesica: (0) C-shaped (Wagner 1975: fig. 705); (1) S-shaped (Fig. 9Q–T); (2) J-shaped (Fig. 9F, G).
- **45.** Shape of vesica body: (0) gradually curving (Fig. 9F–N); (1) strongly bent at middle (Fig. 9Q–T).
- **46.** Sclerotization of vesica body: (0) vesica formed of single gutter-like strap (Wagner 1975: fig. 705); (1) body formed of two straps separated by membrane (Fig. 9I–M); (2) body composed of three differently shaped straps (Fig. 10G–N).
- 47. Lateral strap of vesica at middle: (0) with several longitudinal sclerotized ridges (Fig. 10G–N, S); (1) without longitudinal sclerotized ridges (Fig. 9F–N, Q–T).
- Portion of one strap terminating near secondary gonopore: (0) present (Fig. 8S, T); (1) absent (Fig. 8D, E, I, J, L–N).
- 49. Apical part of vesica: (0) deeply divided into two variously shaped and widely spaced branches (Fig. 8S–U); (1) with single apical blade (Fig. 9A–N); (2) with two apical blades tightly adjoining along entire length (Fig. 9Q–T).

- Single apical blade of vesica: (0) straight (Fig. 9F– N); (1) curved at base, directed laterally (Fig. 9A–E).
- **51.** Apical process of vesica: (0) immovably connected with straps of vesica body (Fig. 9); (1) separated from straps of vesica by membranous area (Konstantinov et al. 2015: figs 15–24).
- **52.** Series of minute teeth at base of apical process of vesica: (0) absent (Fig. 9F–N, Q–T); (1) present (Fig. 9A–E).
- **53.** Position of secondary gonopore relative to vesica body: (0) subapical, located at base of apical blade (Fig. 9A–N); (1) far removed basally from apex of vesica (Fig. 9Q–T); (2) subapical, located laterad of apical blades (Fig. 10G, I, M).
- 54. Position of secondary gonopore relative to vesica sclerotizations: (0) located on membrane (Fig. 10G, I, M); (1) located on a sclerotized strap of the vesica (Fig. 9A–N).
- 55. Shape of secondary gonopore: (0) round (Fig. 9G–J);
  (1) elongate-oval (Fig. 9Q–T); (2) distinctly elongate and twisted at base (Fig. 9A–E).
- **56.** Sculpture of secondary gonopore: (0) well-developed; (1) absent.
- 57. Gonopore sclerite: (0) absent (Fig. 9A–N); (1) present, straight, serrate (Stonedahl 1990: figs 146–160);
  (2) present, straight not serrate (Schwartz and Stonedahl 2004: fig. 24). The gonopore sclerite located on membrane proximally of the secondary gonopore was first described by Stonedahl (1990) as a diagnostic feature for *Atractotomus* and was subsequently documented for several related genera (Schwartz and Stonedahl 2004).
- 58. C-shaped sclerotized band adjacent to secondary gonopore: (0) absent (Fig. 9); (1) present (Konstantinov 2008c: figs 13, 15). — The C-shaped sclerotized band near secondary gonopore was discussed by Konstantinov (2008c) as one of the diagnostic features of the genus *Phaeochiton* and here documented for a few other phyline genera.
- **59.** Size of sclerotized rings of the dorsal labiate plate: (0) small (Fig. 12A, B); (1) large, occupying large part of dorsal labiate plate so the distance between them is less than diameter of a ring (Fig. 12D–F).
- **60.** Shape of the sclerotized ring: (0) oval (Fig. 11A); (1) elongate, apically attenuated (Fig. 11G); (2) distinctly elongate, but apically rounded (Fig. 12A).
- **61.** Vestibulum: (0) S-shaped, thick (Fig. 11F); (1) S-shaped, very thin and long (Fig. 12C, F); (2) C-shaped, thin and long (Fig. 11C); (3) very short, not twisted, slightly curved and directed straight towards seminal depository (Fig. 12A).
- 62. Apex of second valvula: (0) only slightly dilated sub-apically, sword-shaped (Yasunaga 2022: fig. 15F);
  (1) harpoon-shaped (Konstantinov and Korzeev 2014: fig. 39); (2) arrow-shaped (Yasunaga 2022: fig. 3D).

**Table 1.** Measurements (mm). Abbreviations and explanations: Cun–Clyp distance between apex of clypeus and apex of cuneus in dorsal view, Tibia3 – length of the metatibia, AntSeg2 –length of antennomere II, InterOcDi – minimal width of vertex between inner margins of compound eyes in dorsal view.

	Length						Width				
Species		Body	Cun-Clyp	Pronotum	Tibia3	AntSeg2	Head	Pronotum	InterOcDi		
				Abietocapsu	ıs dissimilis						
්් (n=3)	Mean	3.00	2.55	0.49	1.53	0.71	0.71	1.09	0.34		
	SD	0.17	0.14	0.02	0.07	0.01	0.01	0.02	0.01		
	Range	0.34	0.26	0.04	0.14	0.02	0.02	0.04	0.01		
	Min	2.82	2.40	0.48	1.46	0.70	0.70	1.06	0.34		
	Max	3.16	2.66	0.52	1.60	0.72	0.72	1.10	0.35		
♀♀ (n=3)	Mean	3.53	2.95	0.49	1.45	0.84	0.73	1.07	0.33		
	SD	0.13	0.11	0.03	0.01	0.02	0.01	0.06	0.01		
	Range	0.24	0.22	0.06	0.02	0.04	0.02	0.12	0.02		
	Min	3.44	2.84	0.46	1.44	0.82	0.72	1.02	0.32		
	Max	3.68	3.06	0.52	1.46	0.86	0.74	1.14	0.34		
Atractotomus parvulus											
් ් (n=5)	Mean	2.71	2.25	0.36	1.10	0.65	0.64	0.89	0.27		
	SD	0.37	0.21	0.02	0.07	0.05	0.03	0.04	0.01		
	Range	0.92	0.52	0.06	0.16	0.11	0.07	0.10	0.02		
	Min	2.10	1.90	0.32	0.98	0.59	0.59	0.82	0.26		
	Max	3.02	2.42	0.38	1.14	0.70	0.66	0.92	0.28		
♀♀ (n=3)	Mean	2.38	2.11	0.33	1.09	0.61	0.66	0.89	0.30		
	SD	0.02	0.03	0.02	0.05	0.04	0.01	0.03	0.02		
	Range	0.04	0.06	0.04	0.08	0.08	0.02	0.06	0.04		
	Min	2.36	2.08	0.32	1.06	0.58	0.65	0.86	0.28		
	Max	2.40	2.14	0.36	1.14	0.66	0.67	0.92	0.32		
			"He	eterocapillus s	chmiedeknech	ti"					
් ර (n=1)		2.44	2.0	0.34	1.08	0.62	0.59	0.80	0.28		
				Campylomm	a atlanticum						
් ර (n=5)	Mean	2.42	2.19	0.45	1.08	0.55	0.63	0.98	0.34		
	SD	0.10	0.11	0.01	0.06	0.01	0.01	0.03	0.01		
	Range	0.26	0.28	0.03	0.14	0.04	0.03	0.06	0.01		
	Min	2.28	2.10	0.44	1.00	0.53	0.61	0.94	0.33		
	Max	2.54	2.38	0.47	1.14	0.57	0.64	1.00	0.34		
♀♀ (n=2)	Min	2.36	2.14	0.48	1.12	0.58	0.62	1.07	0.36		
	Max	2.40	2.18	0.50	1.12	0.60	0.63	1.08	0.37		
				Campylomm	ıa pusillum						
්් (n=4)	Mean	2.05	1.83	0.40	0.98	0.50	0.58	0.88	0.32		
	SD	0.19	0.19	0.02	0.04	0.04	0.04	0.05	0.01		
	Range	0.42	0.42	0.03	0.08	0.08	0.09	0.10	0.02		
	Min	1.78	1.58	0.39	0.95	0.46	0.53	0.83	0.32		
	Max	2.20	2.00	0.42	1.03	0.54	0.62	0.93	0.34		
♀♀ (n=3)	Mean	2.19	1.95	0.39	1.00	0.45	0.60	0.89	0.34		
	SD	0.19	0.13	0.01	0.06	0.01	0.00	0.01	0.01		
	Range	0.34	0.26	0.02	0.11	0.02	0.01	0.01	0.01		
	Min	2.06	1.84	0.38	0.95	0.44	0.59	0.89	0.34		
	Max	2.40	2.10	0.40	1.06	0.46	0.60	0.90	0.35		
				Heterocapil	lus tigripes						
∂∂ (n=5)	Mean	3.25	2.84	0.63	1.68	0.84	0.84	1.29	0.47		
	SD	0.10	0.08	0.04	0.03	0.01	0.03	0.05	0.01		
	Range	0.26	0.20	0.10	0.06	0.02	0.07	0.14	0.03		
	Min	3.10	2.70	0.58	1.64	0.82	0.81	1.22	0.45		

	Length							Width		
Species		Body	Cun-Clyp	Pronotum	Tibia3	AntSeg2	Head	Pronotum	InterOcDi	
	Max	3.36	2.90	0.68	1.70	0.84	0.88	1.36	0.48	
♀♀ (n=5)	Mean	3.28	2.85	0.61	1.68	0.83	0.85	1.26	0.48	
	SD	0.24	0.12	0.02	0.05	0.01	0.03	0.07	0.01	
	Range	0.62	0.28	0.04	0.12	0.03	0.07	0.14	0.02	
	Min	2.88	2.64	0.60	1.64	0.81	0.81	1.20	0.47	
	Max	3.50	2.92	0.64	1.76	0.84	0.88	1.34	0.49	
Lobicris basalis										
්∂ (n=5)	Mean	3.46	2.97	0.58		1.00	0.86	1.25	0.43	
	SD	0.12	0.04	0.03		0.04	0.02	0.05	0.02	
	Range	0.25	0.07	0.07		0.11	0.04	0.14	0.05	
	Min	3.36	2.94	0.53		0.96	0.85	1.17	0.41	
	Max	3.61	3.01	0.60		1.06	0.88	1.31	0.46	
♀♀ (n=5)	Mean	3.62	3.19	0.62		0.95	0.88	1.34	0.45	
	SD	0.17	0.12	0.02		0.05	0.02	0.04	0.02	
	Range	0.42	0.28	0.04		0.11	0.04	0.07	0.04	
	Min	3.47	3.01	0.60		0.88	0.87	1.31	0.42	
	Max	3.89	3.29	0.64		0.99	0.90	1.38	0.46	
Psallus validicornis										
්් (n=4)	Mean	3.73	3.05	0.55	1.80	1.08	0.75	1.13	0.32	
	SD	0.13	0.11	0.01	0.07	0.03	0.02	0.02	0.00	
	Range	0.30	0.24	0.02	0.18	0.07	0.06	0.05	0.01	
	Min	3.60	2.96	0.54	1.72	1.05	0.72	1.10	0.32	
	Max	3.90	3.20	0.56	1.90	1.12	0.78	1.15	0.33	
♀♀ (n=3)	Mean	3.25	2.81	0.57	0.54	1.11	0.74	1.14	0.37	
	SD	0.31	0.23	0.04	0.94	0.07	0.02	0.06	0.01	
	Range	0.60	0.46	0.08	1.62	0.13	0.04	0.11	0.02	
	Min	3.00	2.60	0.53	0.00	1.05	0.73	1.08	0.36	
	Max	3.60	3.06	0.60	1.62	1.18	0.76	1.18	0.38	

## 3. Phylogenetic results

The MP analysis with polymorphic character states treated as missing data (MI) resulted in 24 equally parsimonious trees with 297 steps (CI = 0.32, RI = 0.68). Analysis with polymorphic characters treated as such (PL-MP) also rendered 24 trees of 310 steps (CI = 0.35, RI = 0.68). The strict consensus trees derived from the MI-MP and PL-MP analyses are topologically identical (Fig. 1). The successive approximation weighting resulted in three equally parsimonious topologies the strict consensus of which is shown in Fig. 2. All MP analyses rendered generally well resolved relationships of Heterocapillus spp. and allied genera, although relations between major clades are weakly supported. BI tree (File S3) recovered six major clades with a large basal polytomy among them. The discussion below is focused on the clades A-F recovered in all analyses. BI posterior probabilities, Jackknife and Bremer supports are shown in the strict consensus MP analysis with equal weights (Fig. 1) and character data are plotted on the SAW strict consensus tree using fast optimization (ACCTRAN) (Fig. 2).

**Clade A** (PP 100, JK 89, BS 3) is supported by a single apomorphy, short and straight apical process of the left paramere (41-2). Homoplastic characters supporting this node include the absence of scalelike setae on thoracic pleura (2-0), hind femur with distinct round spots on fore and hind surfaces (18-1), and curved at base, laterally directed single apical blade of the vesica (50-1). This clade unites three *Campylomma* spp. with *Salicarus atlanticus* and *S. pusillus*.

**Clade B** (PP 96, BS 2) comprises *Dacota* + *Bergmiris* + *Excentricoris* spp. and is corroborated by four apomorphies, including the presence of robust spinelike setae on dorsum (8-2, reversed in *Bergmiris egregius*), head strongly produced forward (25-1), and the absence of subapical spines on hind femur (31-1). The clade is further corroborated by nine homoplastic changes viz., whitish coloration of antennomeres III and IV in females (12-1), distinctly swollen antennomere I in females (21-0), fusiform antennomere II in females (23-3), hemelytron in female not protruded beyond apex of abdomen (30-0), apically free pulvilli (35-1), distinctly extended body of the left paramere (42-1), and elongate,



**Figure 1.** Strict consensus of 24 equally parsimonious trees with Bremer support values indicated above branches and posterior probabilities / Jackknife values > 50 indicated below branches. Highlighted clades A–I are discussed in the text. The species names are displayed in the taxonomic combinations used prior to the present work.

apically attenuated sclerotized rings of bursa copulatrix (60-1).

**Clade C** (PP 92, JK 70, BS 3) is defined by eight homoplasies, including whitish antennomeres III and IV in males (11-1) and females (12-1), segment II in males

swollen along entire length, rod-shaped (22-1), subapically bent claw (33-1), pulvilli covering two thirds of ventral claw surface (34-1), and sword-shaped apex of second valvula (62-0). This clade comprises *Rhinacloa forticornis*, *Phoenicocoris dissimilis*, *Heterocapillus schmiedeknechti*, *Atractotomus parvulus*, and *A. magni*-



**Figure 2.** Strict consensus of the three equally parsimonious trees received under successive approximation weighting. Characters are plotted showing fast optimization. Filled squares indicate non-homoplastic characters mapped by state (discontinuous characters are mapped as homoplasy), open squares indicate homoplastic characters. Highlighted clades A–I are discussed in the text. The species names are provided according to the new classification established in the present work.

*cornis*. The last three species form a well-supported clade (PP 97, JK 93) united by a single apomorphy, the serrate gonopore sclerite (57-1) and five homoplastic characters viz., the presence of spinelike setae at sides of pronotum and on hemelytron (8-1), fusiform antennomere II in females (23-3), and secondary gonopore located at base of the apical blade (53-0).

**Clades D+E+F** form a monophyletic group (PP 64, BS 3) supported by five homoplastic character changes, the absence of spots at bases of tibial spines (6-0), the presence of robust simple setae at sides of pronotum and hemelytron (8-1), and location of the secondary gonopore at base of the apical blade (53-0) and on the sclerotized strap (54-1). The following three groups were recognized within this clade:

**Clade D** (PP 100, JK 100, BS 7) unites two *Criocoris* spp. based on 10 character changes including one apomorphy, C-shaped structure of the vesica (44-0).

**Clade E** (PP 100, JK 94, BS 6) comprises two *Psallus* species from the subgenus *Phylidea* + *Heterocapillus validicornis* and is defined by a single apomorphy viz., distinctly elongate and basally twisted secondary gonopore (55-2). The clade is further corroborated by nine homoplasies, including the large genital capsule (37-0) with ventroapical keel (38-1), apex of phallotheca with dorsal subapical tooth (43-1), vesica composed of three sclerotized straps (46-2), lateral strap of vesica equipped with several longitudinal sclerotized ridges (47-0), apical blade of vesica curved at base and laterally oriented (50-1), with a series of minute teeth at base (52-1), and arrow-shaped apex of the second valvula (62-2).

**Clade F** (PP 95, JK 57, BS 2) unites four *Psallus* species from the subgenus *Mesopsallus* with *Atractotomus mali* and *Heterocapillus pici*. The clade is united by two uncontradicted apomorphies, J-shaped shape of the vesica (44-2) and elongate, apically attenuated sclerotized rings of the bursa copulatrix (60-2).

Clades G+H form a well-supported group (PP 95, JK 65, BS 3) supported by three non-unique character changes, including the apically spatulate parempodia (36-1), the presence of the not serrate gonopore sclerite (57-2), and elongate, apically attenuated sclerotized rings of bursa copulatrix (60-1). This clade unites the genus Phoenicocoris (clade G, PP 98, JK 95, BS 4) with three Salicarus spp. + Heterocapillus genistae and H. nitidus (clade H, PP 87, JK 63, BS 2). The latter clade is united by two uncontradicted apomorphies, posterior margin of vertex with transverse carina (28-1) and two apical blades of the vesica tightly adjoining to each other along the entire length (49-2). It is further defined by two homoplasies, labium barely reaching middle coxa (29-0) and S-shaped, very thin and long vestibulum of bursa copulatrix (61-1).

**Clade I** (PP 93, BS 2) comprise three clades, *Heterocapillus tigripes* + *Phaeochiton* spp. + the clade uniting *Salicarus basalis, Europiella* spp., *Plagiognathus* spp., and *Zophocnemis bicolor*. It is supported by two uncontradicted apomorphies, the presence of additional sclerotized strap of the vesica terminating near secondary gonopore (48-0) and the presence of C-shaped sclerotized band adjacent to secondary gonopore (58-1). Homoplasies supporting the clade include the presence of the vetroapical keel of the genital capsule (38-1) and structure of the vesica composed by three differently shaped sclerotized straps (46-2).

The clade comprising *Salicarus basalis* with *Europiel-la-Plagiognathus* complex of genera is supported by a single apomorphy, the secondary gonopore located laterad of apical blades of the vesica (53-2) and four homoplasies, including the absence of scalelike setae on thoracic pleura (2-1), the large genital capsule occupying

half of abdomen (37-0), and the absence of ventroapical keel of the genital capsule (38-0).

The *Europiella-Plagiognathus* complex of genera share a single apomorphy, the presence of a dark spot at the base tibiae (19-3), and three homoplasies including long labium surpassing hind coxae (29-1) and the absence of C-shaped sclerotized band near secondary gonopore (58-1). Relationships between four genera comprising this group were not resolved on the EW strict consensus tree, but two clades, *Europiella* and *Zophocnemis* + *Plagiognathus* were recovered on the SAW tree.

## 4. Discussion

#### 4.1. Phylogenetic analyses

All phylogenetic analyses (Figs 1, 2) demonstrate nonmonophyly of *Heterocapillus* in the currently accepted sense. This is not surprising given that the concept of this genus (Wagner 1960, 1975) was based on two non-unique features, the vestiture having three distinct types of setae and the fusiform antennal segment II. Major clades revealed in this study warrant significant taxonomic changes not only in the placement of *Heterocapillus* spp. but also in the position of species from related genera.

The clade A corresponds to *Campylomma*, one of the largest phyline genera, which can be distinguished by a combination of characters outlined by Konstantinov et al. (2015). Two little-studied species of *Salicarus* also rendered within this clade, *S. atlanticus* and *S. pusillus*, thus clearly belong to this genus. Examination of the available material shows that both species share essential features of *Campylomma* including the shape of head (Fig. 5A, B), vestiture (Fig. 4K, L), the presence of an incomplete row of spicules on the dorsoapical surface of hind femur, and characteristic apical blades of the vesica (Fig. 8H–J, L–N). Based on the above features, the following two new combinations are established: *Campylomma atlanticum* (Wagner, 1963) **comb. nov.** and *Campylomma pusillum* (Reuter, 1878) **comb. nov.** 

Clade C unites two subclades, Heterocapillus schmiedeknechti + Atractotomus spp. and Phoenicocoris dissimilis + Rhinacloa forticornis. Members of the first clade share all essential diagnostic features of Atractotomus sensu Stonedahl (1990), necessitating the transfer of H. schmiedeknechti to this genus (refer to the discussion of Atractotomus parvulus in the Taxonomy section for more details). Phoenicocoris dissimilis possesses a combination of unique features including the lamellate and uniformly wide parempodia (Schwartz and Stonedahl 2004: fig. 21 B, C) and strongly coiled, single-bladed vesica (Fig. 8D, E). Schwartz & Stonedahl (2004) removed dissimilis from Phoenicocoris and treated this species as incertae sedis. I concur with their findings and consider this taxon as a new monotypic genus Abietocapsus gen. nov. Based on available data, neither Phoenicocoris, nor any other phyline genus can adequately accommodate P. dissimilis.



**Figure 3.** Dorsal habitus of species included in the phylogenetic analysis. A Atractotomus amygdali; **B** A. rhodani 3; **C** A. magnicornis 3; **D** A. magnicornis 3; **E** Mesopsallus mali 3; **F** M. mali 2; **G** Salicarus genistae 3; **H** S. genistae 2; **I** Heterocapillus tigripes 3; **J** H. tigripes 2; **K** Salicarus cavinotum 3; **L** S. cavinotum 2; **M** Mesopsallus pici 2; **N** Mesopsallius ambiguus 3; **O** Atractotomus parvulus, holotype 2; **P** Atractotomus parvulus 3, a specimen described as a male of Heterocapillus schmiedeknechti (Wagner 1973a). Scale bar in A valid for all pictures.



**Figure 4.** Dorsal habitus of species included in the phylogenetic analysis. A *Criocoris crassicornis*  $\Im$ ; **B** *C. crassicornis*  $\Im$ ; **C** *Excentricoris pictipes*  $\Im$ ; **D** *Abietocapsus dissimilis*  $\Im$ ; **E** *Psallus (Phylidea) validicornis*  $\Im$ ; **F** *Lobicris basalis*  $\Im$ ; **G** *L. basalis*  $\Im$ ; **H** *Zophocnemis bicolor*  $\Im$ ; **I** *Salicarus fulvicornis*  $\Im$ ; **J** *S. fulvicornis*  $\Im$ ; **K** *Campylomma atlanticum*  $\Im$ , holotype; **L** *Campylomma pusillum*  $\Im$ .

Clade E unites *Heterocapillus validicornis* with two *Psallus* spp. from the subgenus *Phylidea*. Although females of *H. validicornis* have distinctly fusiform antennae, a feature previously not documented in *Psallus* spp., this species agrees with the current concept of *Phylidea* (Kerzhner 1993) in all other respects, especially in the characteristic structure of the vesica. Therefore, a new combination *Psallus (Phylidea) validicornis* (Reuter, 1876) **comb. nov.**, is proposed.

Clade F includes three *Psallus* species from the subgenus *Mesopsallus*, *Psallus* (*Apocremnus*) fagi Drapolyuk, 1990 and *Atractotomus mali* + *Heterocapillus pici*. In the



**Figure 5.** Head and pronotum in dorsal view. A *Campylomma pusillum*  $\mathcal{F}$ ; **B** *Campylomma atlanticum*  $\mathcal{F}$ ; **C** *Lobicris basalis*  $\mathcal{G}$ ; **D** *Salicarus roseri*  $\mathcal{G}$ ; **E** *S. roseri*  $\mathcal{F}$ ; **F** *Psallus (Phylidea) validicornis*  $\mathcal{F}$ ; **G** *P. (P.) validicornis*  $\mathcal{G}$ ; **H** *Heterocapillus tigripes*  $\mathcal{F}$ ; **I** *H. tigripes*  $\mathcal{G}$ ; **J** *Mesopsallus amygdali*  $\mathcal{F}$ ; **K** *M. amygdali*  $\mathcal{G}$ ; **L** *Mesopsallus pici*  $\mathcal{G}$ ; **M** *Salicarus nitidus*  $\mathcal{F}$ ; **N** *S. nitidus*  $\mathcal{G}$ ; **O** *Abietocapsus dissimilis*  $\mathcal{F}$ ; **P** *A. dissimilis*  $\mathcal{G}$ .

monographic revision of *Atractotomus*, Stonedahl (1990) correctly pointed out that *A. mali*, *A. vireti*, *A. amygdali*, and *A. rhodani* (referred to as *mali*-group) do not belong

to this genus and appear to form a monophyletic group together with *Heterocapillus pici* based on the vesica structure. Pending further investigation, species of the



**Figure 6.** Vestiture. A–F Hemelytron in dorsal view: A Salicarus halimodendri  $\mathcal{E}$ ; B Abietocapsus dissimilis  $\mathcal{E}$ ; C Heterocapillus genistae  $\mathcal{P}$ ; D Mesopsallus ambiguus  $\mathcal{E}$ ; E Mesopsallus mali  $\mathcal{E}$ ; F Mesopsallus pici  $\mathcal{P}$ . G–H Head and pronotum in lateral view: G Heterocapillus tigripes  $\mathcal{E}$ ; H Salicarus perpusillus  $\mathcal{E}$ .

*mali*-group were treated by him as *incertae sedis*, and *A. vireti* was subsequently synonymized with *A. mali* by Kerzhner and Matocq (1994).

Mesopsallus Wagner, 1970 was originally described as a subgenus of *Psallus* to accommodate the type species,

*P. ambiguus* and *P. pseudoambiguus* Wagner, 1970 based on the male genitalia structure viz., straight and thin vesica, and genital capsule with a ventral keel. Four species are currently recognized within *Mesopsallus*, as *Psallus pseudoambiguus* was synonymized with *P. ambiguus* 



**Figure. 7.** SEM images of selected structures. A *Mesopsallus ambiguus*, head and pronotum in lateral view  $\Im$ ; **B** *Salicarus roseri*, head and pronotum in lateral view  $\Im$ ; **C** *Mesopsallus ambiguus*, head in lateral view  $\Im$ ; **D** *Mesopsallus ambiguus*, abdomen in lateral view  $\Im$ ; **E** *Mesopsallus ambiguus*, vestiture of hemelytron  $\Im$ ; **F** *Salicarus fulvicornis*, vestiture of hemelytron  $\Im$ ; **G** *Mesopsallus ambiguus*, metathoracic pretarsus in lateral view  $\Im$ ; **H** *Salicarus fulvicornis*, metathoracic claw in lateral view  $\Im$ ; **I** *Mesopsallus mali*, metathoracic pretarsus in lateral view  $\Im$ ; **L** *Lobicris basalis*, metathoracic pretarsus in lateral view  $\Im$ ; **L** *Heterocapillus tigripes*, metathoracic pretarsus in ventral view  $\Im$ .

(Rizzotti Vlach 2000) and three more species were transferred to this subgenus by Kerzhner and Josifov (1999). Drapolyuk (1990) placed *Psallus fagi* in the subgenus *Apocremnus* without comment, mentioning that the species is similar to *Psallus (Apocremnus) variabilis* (Fallén, 1807) in the overall coloration and to *Psallus (Mesopsallus) ambiguus* (Fallén, 1807) in the vesica structure. Based on the Central European taxa, Wyniger (2004) suggested that all subgenera of *Psallus* be synonymized, but *Mesopsallus* (represented in her analysis only by *P. ambiguus*) be treated as a distinct genus. Pagola-Carte et al. (2006) noted striking resemblance in the vesica structure between *Atractotomus amygdali* and *Psallus (Meso-* *psallus*) *ambiguus* but refrained from taxonomic amendments.

Phylogenetic analyses and morphology of allied taxa support monophyly of the group containing *A. mali* group of species, *Mesopsallus* spp., and *Psallus (Apocremnus) fagi*. All members of this clade share the characteristic J-shaped vesica formed of two straps separated by a membrane, equipped with a large, round and distinctly sculptured secondary gonopore located almost at the apex of the vesica, and straight apical blade (Fig. 9F–N). The dorsal labiate plate of the bursa copulatrix in these species have distinctly elongate but apically rounded sclerotized rings (Fig. 12A, B). Therefore, *Mesopsallus* 



Figure 8. Male genitalia. A–E *Abietocapsus dissimilis*: A right paramere in lateral view; B left paramere in lateral view; C apex of phallotheca in lateral view; D vesica in lateral view; E magnified apex of vesica in ventral view. F–K *Campylomma atlanticum*: F right paramere in lateral view; G left paramere in lateral view; H apex of phallotheca in lateral view; I, J vesica in left and right lateral views; K genital capsule in dorsal view. L–N *Campylomma pusillum*, vesica in ventral, left and right lateral views. O–U *Heterocapillus tigripes*: O apex of phallotheca; P right paramere; Q left paramere; R genital capsule in dorsal view; S–U vesica in right and left lateral, and ventral views.

Wagner, 1970 is here recognized as a distinct genus to accommodate the following ten species: *Mesopsallus ambiguus* (Fallén, 1807), *M. amygdali* (Wagner, 1960) **comb. nov.**, *M. fagi* (Drapolyuk, 1990) **comb. nov.**, *M. holomelas* (Reuter, 1906), *M. mali* (Meyer-Dür, 1843) **comb. nov.**, *M. pici* (Reuter, 1899) **comb. nov.**, *M. rhodani* (Fieber, 1861) **comb. nov.**, *M. samdzijonicus* (Josifov, 1983), *M. tibialis* (Reuter, 1894), and *M. validus* (Reuter, 1901) **comb. nov.** A detailed revision of this genus is beyond the scope of the present paper and will be addressed elsewhere.

Clade H form a strongly supported sister group to *Phoenicocoris* spp. (Clade G) and unites *Salicarus* spp.

with *Heterocapillus genistae* and *H. nitidus*. Stonedahl (1990) indicated that four principally Mediterranean and Fabaceae-feeding *Heterocapillus* species (*H. cavinotum*, *H. genistae*, *H. nitidus*, and *H. perpusillus*) form a group similar to *Phoenicocoris* in the vesica structure but differing from that genus in the shape of the head, vestiture, and other characters of the male genitalia. Schwartz and Stonedahl (2004) emphasized great similarity of *Salicarus* and *Phoenicocoris* in several features including the apically spatulate parempodia and structure of the vesica. Both genera have tightly coiled, apically bifd vesica with distinct gonopore sclerite and characteristic secondary gonopore located on membrane, but apical blades in

*Salicarus* are fused along almost entire length (distinctly divergent in *Phoenicocoris*).

Available data suggest that Heterocapillus genistae and three related species feeding on Fabaceae belong to Salicarus despite comparatively small size and distinctly fusiform antennomere II. These species share with Salicarus the same structure of vesica with almost entirely fused apical blades (Fig. 9Q-T), S-shaped, characteristically long and thin vestibulum of bursa copulatrix (Figs 11C, 12C), and posteriorly carinate or attenuated vertex. They also possess apically spatulate parempodia typical for the Phoenicocoris + Salicarus clade, although this feature sporadically occurs in otherwise unrelated taxa e.g., Campylomma verbasci, Atractotomus mali, and Heterocapillus pici. Consequently, the following new combinations are proposed: Salicarus cavinotum (Wagner, 1973) comb. nov., Salicarus genistae (Lindberg, 1948) comb. nov., Salicarus nitidus (Horváth, 1905) comb. nov., and Salicarus perpusillus (Wagner, 1960) comb. nov. It is intended that a full taxonomic treatment of Salicarus will be published later.

Salicarus basalis did not cluster with congeners and forms the sister group to the Europiella-Plagiognathus complex of genera within the Clade I. This species has a checkered history of taxonomic placement being originally described in the genus Neocoris (Reuter 1878) and subsequently placed within Monosynamma (Reuter 1910), Plagiognathus (Kerzhner 1964), and Salicarus (Putshkov 1977). Recognizing the distinctive nature of S. basalis, Putshkov (1977) erected the monotypic subgenus Lobicris to accommodate this species. Its placement within Salicarus was based on the characters of external morphology viz., coloration, slightly carinate vertex, moderately protruded clypeus, short antennae, and tarsal structure. However, combination of other characters including the coloration of tibia with darkened bases and spots at bases of tibial spines (Fig. 4F, G), the non-spatulate parempodia (Fig. 7J), the thick and short vestibulum of bursa copulatrix (Fig. 11I), and it's peculiar vesica (Fig. 10Q-S) clearly contradicts with the current generic placement of S. basalis. Vesica of this species have several features common for Clade I: the body of vesica is strongly bent at middle and composed of three straps, the lateral strap is equipped with several longitudinal ridges, the portion of one strap is terminating near secondary gonopore (missing in Plagiognathus), the membrane around the secondary gonopore is equipped with the C-shaped sclerotized band (missing in Europiella-Plagiognathus complex). Still, S. basalis readily differs from all members of the Clade I in having eversible membranous lobe at the apex of the vesica and by the shape of its apical blades. A combination of characters not found in other phylines warrant treatment of Lobicris stat. nov. as a separate monotypic genus.

*Heterocapillus tigripes*, the type species of the genus, also holds an isolated position within the clade I and may be distinguished by a unique combination of features including the structure of the male and female genitalia (refer to the respective differential diagnosis in the taxonomic section). Therefore, the genus *Heterocapillus* is here redefined as monotypic.

Both EW and SAW analyses yielded the Europiella + Plagiognathus subclade within the Clade I. The modern concept of Europiella was established by Schuh (2004) who recognized the characteristically twin-coned apex of the right paramere as the main distinctive feature of the genus. Noting great similarity in the vesica structure between E. lividella (Kerzhner, 1979) and other Europiella spp., he transferred this species to *Plagiognathus* due to the absence of this feature. Duwal et al. (2014) erected the monotypic genus Europiellomorpha Duwal, 2014 to accommodate P. lividellus mainly based on the characteristic additional sawtooth edge at the apex of the vesica. Yasunaga (2022) synonymized this genus with Europiella due to the absence of the unique characters and I fully concur with this action. Europiella lividella clearly belongs to the group of closely related pale-yellow species also containing E. alpina (Reuter, 1875), E. gilva (Kulik, 1965), E. kiritshenkoi (Kulik, 1965), E. livida (Reuter, 1906), E. leucopus (Kerzhner, 1979), and E. miyamotoi (Kerzhner, 1988). All these species possess similar structure of the vesica with more or less developed sawtooth edge at the apex (Fig. 10G-N), while the right paramere is ranging from distinctly twin-coned (E. alpina., E. livida, E. leucopus) to single-coned (E. lividella, E. kiritshenkoi) with an intermediate state observed in E. gilva and E. mivamotoi (Fig. 10A-F).

The genus Zophocnemis Kerzhner, 1962, originally described as a subgenus of *Plagiognathus* for the single species *P. bicolor* (Jakovlev, 1880), was upgraded to generic status by Schuh (2001). Both EW and SAW analyses rendered Zophocnemis within *Plagiognathus* clade. Aedeagal structure, the main diagnostic feature of *Plagiognathus* as diagnosed by Schuh (2001) also suggest inclusion of *Z. bicolor* in *Plagiognathus* (Fig. 10U) given the diversity observed in the Palaearctic fauna. However, a broader study of related taxa is not in the context of this manuscript, and I refrain from offering a formal taxonomic conclusion at this point.

#### 4.2. Character informativeness

Despite significant progress in quantifying morphological homoplasy (Klingenberg and Gidaszewski 2010; Speed and Arbuckle 2017), in case of discrete characters it can be assessed only with traditionally used parsimony metrics such as consistency (CI), retention (RI) indices or their combinations e.g., rescaled consistency (RC) or homoplasy (HI) indices. These indices were calculated in PAUP for each character individually (Supplementary Material, File S4) and as mean values for five categories of characters: genitalia (26), structure (11), vestiture (8), coloration (11), and shape of antennomeres (5) (Table 2). The last two types of characters appear to be the most homoplastic both in terms of the mean and individual metrics. The mean CI is highest for genitalic characters (0.49), followed by the structural somatic characters (0.43), vestiture (0.40), coloration (0.24), and characters describing the shape of antennomeres (0.23). This pattern is generally supported by the distribution of

Character source	Number of characters	Tree steps	CI	RI	RC	HI
Genitalia	26	3.38	0.49	0.75	0.39	0.51
Structure	11	4.55	0.43	0.61	0.30	0.57
Vestiture	8	4.88	0.40	0.62	0.27	0.60
Coloration	11	7.27	0.24	0.43	0.09	0.76
Antennal shape	5	6.20	0.23	0.58	0.13	0.78

Table 2. Mean values of tree steps, consistency (CI), retention (RI), rescaled consistency (RC) and homoplasy (HI) indices calculated for five sources of characters and sorted by CI value.

mean RI, with the characters of antennomeres (0.58) and coloration (0.43) being the least informative. CI and RI values scored for individual characters also demonstrate high amount of homoplasy for each of the five structural antennal characters included in the analysis (Supplementary Material, File S4).

Moderate phylogenetic signal may indicate higher rates of evolution of the antennal shape in comparison with genitalia and somatic characters. The driving forces behind the fast evolution of antennae in true bugs remain largely unknown and it is premature to speculate on the role of the sexual selection and other potentially involved evolutionary mechanisms (Menard 2015). However, low informativeness of the antennal characters strongly suggest against using these features as diagnostic at the generic level. This result is consistent with earlier taxonomic works on the subfamily Phylinae (Schuh 1984; Stonedahl 1990). Species with swollen antennomeres sporadically occur in large genera otherwise possessing non-modified antennae e.g., Campylomma atripes (Linnavuori 1993: fig. 70f). Interestingly, mean CI values shows that antennal traits are more homoplastic than coloration, a classic example of generally unreliable taxonomic character.

## 5. Taxonomy

#### 5.1. Abietocapsus gen. nov.

http://zoobank.org/66CFB326-6CB6-412F-AA51-B27527E994A0

Figs 4D, 5O, P, 6B, 8A-E, 11A, B

Type species. Sthenarus dissimilis Reuter, 1878

**Diagnosis.** Recognized among other phylines by the following combination of characters: uniformly dark brown, with antennomeres III and IV, apices of femora, and tarsi yellowish brown (Fig. 4D); dorsum clothed with narrow, apically pointed scalelike setae and pale yellow simple setae (Fig. 6B); dorsoapical surface of hind femur with a row of minute spicules (Schwartz and Stonedahl 2004: fig. 21A); parempodia parallel, short and wide, distinctly flattened along entire length; claw bent at midpoint, pulvillum absent (Schwartz and Stonedahl 2004: fig. 21B– D); vesica strongly twisted at middle, with single clawshaped apical blade (Fig. 8D, E); secondary gonopore located on membrane, subapical, elongate-oval; gonopore sclerite absent; bursa copulatrix with elongate-oval, broadly rounded sclerotized rings and S-shaped, large and wide vestibulum (Fig. 11A, B).

Remarks. The taxonomic position of Sthenarus dissimilis Reuter, 1878 has been controversial despite much effort. In the revision of the genus Sthenarus, Wagner (1958) treated this species within the subgenus Phoenicocoris based on the head shape and the pattern of vestiture. Kerzhner (1962) raised Phoenicocoris to the rank of a separate genus but noted that the position of "Sthenarus" dissimilis remains uncertain. He mentioned that despite some resemblance in the male genitalia structure between S. dissimilis and the genera Atractotomus, Phoenicocoris, and Salicarus, this species could not be attributed to any of these taxa. Wagner (1975) retained this species within Phoenicocoris. Schwartz & Stonedahl (2004) provided a detailed and perfectly illustrated redescription of P. dissimilis, treated this species as incertae sedis, and refrained from taxonomic actions. Based on a preponderance of the morphological evidence, I must conclude that neither Phoenicocoris, nor any other phyline genus, can adequately accommodate dissimilis and the new monotypic genus Abietocapsus gen. nov. is erected to place it.

The characteristically flattened and uniformly wide through entire length parempodia of A. dissimilis are highly untypical for the Phylini. A more or less similar flashy parempodia were documented within a handful of otherwise not related genera viz., Semium (Schuh 1976: fig. 27; Schwartz and Stonedahl 2004: fig. 21D), Moissonia (Schuh 1976: figs 30-32; Schuh 1984: fig. 1412; 1993: fig. 1b), Opuna (Schuh 1984: figs 1364, 1365), the Melaleucoides group of genera (Schuh and Weirauch 2010: figs 10D, 12C, 17C, 24C, 33D; Schwartz et al. 2018: fig. 18B), Chinacapsus (Wagner 1975: fig. 629a, b), and Lindbergopsallus (Wagner 1975: fig. 781f-i). The small North American genus Semium is clearly not related to A. dissimilis due to - among other characters - the structure of head and pronotum, vestiture, shape of the scentgland evaporative area, and the male genitalia (Schuh and Menard 2013; Schuh 2017). Moissonia (under the subsequently synonymized names *Ellenia* and *Ragmus*) and *Opuna* were rendered as a monophyletic predominantly oriental clade (Schuh 1984) differing from other phylines in the general appearance and characteristic male genitalia structure. The recently described Australian Melaleucoides group of genera share several unique features



**Figure 9.** Male genitalia. **A**–**E** *Psallus (Phylidea) validicornis*, vesica: **A** apex of vesica in lateral view, magnified, **B**–**C**: vesica in ventral and lateral views. **D**, **E**: holotype of *P* (*P*.) *niger*, vesica in ventral and lateral views. **F**–**N**: vesica of *Mesopsallus* spp: **F** *M. ambiguus*; **G**–**H** *M. mali* in lateral and ventral views; **I**, **J** *M. rhodani* in left and right lateral views; **K**, **L** *M. pici* in lateral and ventral views; **M**, **N** *M. amygdali* in lateral and ventral views. **O**, **P** *Psallus (Phylidea) validicornis*, holotype of *P. niger*: **O** right paramere, **P** apex of phallotheca. **Q**–**T** *Salicarus* spp., vesica in lateral view: **Q** *S. cavinotum*; **R** *S. nitidus*; **S** *S. genistae*; **T** *S. perpusillus*.



Figure 10. Male genitalia. A–F *Europiella* spp., right paramere: A, B *E. gilva*; C *E. leucopus*; D *E. kiritshenkoi*; E *E. miyamotoi*; F *E. lividella*. G–N *Europiella* spp., vesica: G *E. leucopus*; H–I *E. gilva*; J *E. kiritshenkoi*; K *E. miyamotoi*; L–N *E. lividella*. O–T *Lobicris basalis*: O right paramere; P left paramere; Q–S vesica in lateral and ventral views; T apex of phallotheca. U *Zophocnemis bicolor*, vesica in lateral view. V *Sthenarus rothermundi*, vesica in ventral view.



Figure 11. Female genitalia. A, B *Abietocapsus dissimilis*: A dorsal labiate plate; B vestibulum. C *Campylomma pusillum*, vestibulum. D–F *Heterocapillus tigripes*: D dorsal labiate plate; E posterior wall; F vestibulum. G–I *Lobicris basalis*: G dorsal labiate plate; H posterior wall; I vestibulum.

in the male and female genitalia, as well as host associations with Myrtaceae (see Schuh & Weirauch 2010 for more details). *Lindbergopsallus* and *Chinacapsus*, island endemic genera restricted to Canary Islands and Madeira, respectively, clearly differ from *Abietocapsus* in the coloration, body proportions, structure of the male genitalia and the presence of pulvilli reaching at least midpoint of the claw. *Chinacapsus* is somewhat similar to *Phoenicocoris* in having strongly twisted, apically twin-bladed vesica, but both blades are larger and clearly separated along the entire length (Wagner 1975: figs 783a, 784i, 785i).

The structure of the vesica, being tightly twisted, with rounded secondary gonopore located on membrane, and single, claw-shaped apical blade, clearly differs from that of the habitually similar genera. All members of the genera *Atractotomus*, *Phoenicocoris*, and *Salicarus* possess gonopore sclerites missing in *A. dissimilis*. In addition, these genera have different apical structure of the vesica, with characteristically short single blade in *Atractotomus* and two long and thin blades in *Phoenicocoris* and *Salicarus*. *Rhinacloa*, a New World genus rendered as a sister group to *Abietocapsus* in the present phylogenetic analysis, also differs from the latter genus in having slender, weakly curved at middle vesica with poorly ornamented secondary gonopore (Schuh and Schwartz 1985). *Rhinacloa* further differs from *Abietocapsus* in the large eyes occupying almost entire sides of the head, the basally broad claws with large flaplike pulvilli, and the distinctly wide, apically serrate scales on dorsum. The structure of the female genitalia of *Abietocapsus* is also distinctive as compared to *Atractotomus*, *Phoenicocoris*, *Salicarus*, and *Rhinacloa* in having small, oval sclerotized rings of the dorsal labiate plate and S-shaped, very long and thin vestibulum.

Detailed descriptions, illustrations, and host information for *A. dissimilis* were provided by Henry and Wheeler (1974) and Schwartz and Stonedahl (2004), and not repeated here.

Material examined. Lectotype of Sthenarus dissimilis Reuter: FRANCE: Lorraine: Vosges Co.: Vosges Mts, 48.038°N 6.95°E, coll. A. Puton, Abies alba Mill. (Pinaceae),  $\mathcal{J}$ , designated by Kerzhner & Matocq, 1994 (AMNH\_PBI 00345054) (MNHN). — Paralectotypes of Sthenarus dissimilis Reuter: FRANCE: Lorraine: Vosges Co.: Vosges Mts, 48.038°N 6.95°E, V. Jakovlev coll., 1 $\mathcal{J}$  (AMNH\_PBI 00237480) (ZISP); coll. A. Puton, Abies alba Mill.,  $\mathcal{Q}$  (AMNH\_PBI 00237481) (MNHN). Gallia, V. Jakovlev coll.,  $\mathcal{J}$  (AMNH\_PBI 00237481) (ZISP). — Other specimens: DENMARK: Thorso, Stoholm Jylland, 56.51787°N 9.1524°E, 27 Jun 1964, Gaun, 1 $\mathcal{Q}$  (AMNH\_PBI



Figure 12. Female genitalia. A *Mesopsallus ambiguus*, vestibulum. B *Psallus (Phylidea) validicornis*, dorsal labiate plate. C *Salicarus genistae*, vestibulum. D-F *Salicarus roseri*: D dorsal labiate plate; E sclerotized ring, magnified; F vestibulum.

00338321) (NMWC),  $43^{\circ}$  (AMNH\_PBI 00340519–AMNH\_PBI 00340522),  $49^{\circ}$  (AMNH\_PBI 00340527, AMNH\_PBI 00340528, AMNH\_PBI 00340527, AMNH\_PBI 00340528) (ZMUH). **FRANCE**: Occitanie: Pyrenees orientales, Aude, Col de Jau, 42.688°N 2.688°E, 26 Jun 2005, J.-C. Streito,  $13^{\circ}$  (ZISP\_ENT 00011726) (ZISP). **MONTE-NEGRO**: Between Zabljak and Podgorica, 42°N 19.1°E, 02 Jul 1958, L. Hoberlandt,  $63^{\circ}$  (ZISP\_ENT 00011743–ZISP\_ENT 00011748),  $39^{\circ}$  (ZISP\_ENT 00011749–ZISP\_ENT 00011751) (NMPC). **ROMA-NIA**: Bucarest, 44.43668°N 26.08902°E, 76 m, A. L. Montandon,  $73^{\circ}$ (AMNH). **UKRAINE**: Kvasovsk Menculi, Rakhov Distr., Zakarpatska, 48.4167°N 23.6833°E, 21 Jul 1972, Putshkov,  $19^{\circ}$  (AMNH\_PBI 00237484) (ZISP). Uzhgorod, Zakarpatska, 48.61666°N 22.3°E, 26 May 1958, Roshko, *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr. (Pinaceae),  $63^{\circ}$  (AMNH\_PBI 00237479, AMNH\_PBI 00237478) (ZISP).

#### 5.2. Atractotomus parvulus Reuter, 1878

Fig. 30, P

Atractotomus parvulus Reuter, 1878: 95.

- Atractotomus brevicornis Reuter, 1899: 140 (synonymized by Aukema 1998: 153).
- Atractotomus (Heterocapillus) mirificus Woodroffe, 1971: 265 (synonymized by Stonedahl 1990: 43).

Atractotomus schmiedeknechti Reuter, 1899: 141 syn. nov.

**Remarks.** Atractotomus schmiedeknechti and A. brevicornis were originally described by Reuter (1899) from females collected in northwestern Algeria. He noted similarity of both species with A. parvulus and distinguished A. schmiedeknechti by the moderately fusiform antennomere II and strongly depressed cuneal fracture. Atractotomus brevicornis was subsequently synonymized with A. parvu*lus* (Stonedahl 1990; Aukema 1998). Wagner (1973a) provided description of a male of *A. schmiedeknechti* based on the single male from Morocco and transferred this species to the genus *Heterocapillus*. No new data on this species have been published since 1973 and its taxonomic status has remained questionable. I examined the male specimen of *A. schmiedeknechti* described by Wagner but failed to locate its vesica. Still, based on the measurements (Table 1), vestiture, shape of the antennomeret II of both sexes I consider *A. schmiedeknechti* Reuter, 1899 to be conspecific with *Atractotomus parvulus* Reuter: 1878, the only *Atractotomus* species known from North Africa, and having relatively long apical blade of vesica which resembles the drawing provided by Wagner (1973a).

Material examined. Atractotomus parvulus: Holotype: FRANCE: Lorraine: Vosges Co.: Remiremont, 48.02°N 6.58°E, ♀ (AMNH\_PBI 00345055) (MNHN). - Other Specimens: CROATIA: Split, Dalmatia, 43.5°N 16.43333°E, 18 Jul 1943, Novak, Pinus halepensis Mill. (Pinaceae), 23 (AMNH PBI 00336935, AMNH PBI 00337040), 3♀ (AMNH PBI 00336931, AMNH PBI 00336933, AMNH PBI 00337043) (ZMUH). FRANCE: Ile-de-France: Essonne Co.: Umg. Paris, Saclas, 48.3667°N 2.1167°E, 88 m, 16 Jul 1960, J. Pericart, Pinus sp. (Pinaceae), 1∂ (AMNH\_PBI 00337038) (ZMUH). GERMANY: Bavaria: Aschaffenburg, 49.96666°N 9.15°E, 17 Jul 1935, K. Singer, 1∂ (AMNH\_PBI 00337039) (ZMUH); 23 Jul 1935, K. Singer, 1♀ (AMNH\_PBI 00337046) (ZMUH). Lower Saxony (Niedersachsen): Lüneburg, Dieksbeck, 53.2525°N 10.41444°E, 27 Jun 1948, Rabeler, 1º (AMNH PBI 00337044) (ZMUH). Neu-Darchau, Hannover Distr., 53.227°N 10.884°E, 24 Jul 1937, 1 (AMNH PBI 00337042) (ZMUH); 29 Jul 1937, 1<sup>o</sup> (AMNH PBI 00337047) (ZMUH). Rheinland-Pfalz: Wöllstein, Höllberg, 49.81444°N 7.96083°E, 18 Jul 1938, E. Wagner, 1♂ (AMNH PBI 00337041), 1♀ (AMNH PBI 00337045) (ZMUH). Atractotomus schmiedeknechti: MOROCCO: Ketama, 34.86°N 4.61°W, Jul 1972, A. Pardo, 13 (AMNH\_PBI 00336932) (ZMUH).

### 5.3. Campylomma atlanticum (Wagner, 1963) comb. nov.

Figs 4K, 5B, 8F-K

Sthenarus atlanticus Wagner, 1963: 11 Sthenarus (Salicarius (sic!)) atlanticus: Wagner, 1975: 101

**Diagnosis.** Recognized by the following combination of characters: dorsum uniformly yellow, rarely cuneus with reddish tinge; head and antenna without dark color-pattern (Fig. 4K); posterior margin of vertex slightly attenuate and covering extreme apex of pronotum (Fig. 5B); dorsum with dense, short and thin goldish simple setae; hind femur with a series of oval brown spots along anterior margin ventrally and a few additional subapical spots; vesica with two large claw-shaped apical blades directly continued into lateral straps (Fig. 8I, J).

*Campylomma atlanticum* belongs to a group of species with lateral straps of the vesica directly continued into large apical blades viz., *C. acaciae*, *C. attilioi*, *C. leptadeniae*, *C. lindbergi*, *C. nigrifemur*, and *C. pusillum* (Konstantinov 2016: figs 6, 7). Somewhat similar to *C. acaciae* in the uniformly pale yellow antenna and dorsum, as well as in the relatively large, claw shaped apical blades of the vesica (Fig. 8I, J). However, this species easily differs from *C. atlanticum* in the smaller sizes and the shape of the vesica, with one blade being significantly shorter than the other. Most similar to *C. pusillum* in the body proportions, slightly attenuated posterior margin of the vertex, and by the shape of the vesica but differs in the larger sizes, coloration and interposition of the vesical blades.

Redescription. Male. Coloration: Dorsum uniformly olive yellow, head without color-pattern, antenna immaculate, uniformly whitish yellow, segment II sometimes dirty yellow (Fig. 4K); labium pale, with darkened apex; cuneus with more or less darkened, pale brown apex, sometimes apex of corium and entire cuneus or apex of cuneus with reddish orange tinge; membrane pale brown to brown, slightly darker at apex, veins sometimes with reddish tinge; legs whitish yellow, thoracic pleurites dirty yellow to pale brown; hind femur with a series of oval brown spots along anterior margin ventrally and a few subapical spots dorsally and ventrally; fore and middle femora immaculate or with confluent dark spots at base of subapical spines; all tibiae without spots at bases of tibial spines; abdomen pale yellow. Surface and vestiture: Body very finely rugose, shining, dorsum with dense, short and very thin, adpressed pale (goldish?) simple setae; scales absent; venter and appendages with pale simple setae; antennomere I with two pale mesial setae; subapical spines on femora and tibial spines black. Structure: Body 2.4-2.5 × as long as width of pronotum, elongate oval, total length 2.4-2.5. Head strongly flattened anteroposteriorly, clypeus not visible from above; eye occupying nearly entire side of head in lateral view; vertex  $2.3-2.4 \times$  as wide as eye, with posterior margin finely carinate, smoothly curving between inner angles of eyes; antennomere I short;

segment II cylindrical, slightly thinner than segment I,  $0.5-0.6 \times$  as long as basal width of pronotum,  $0.8-0.9 \times$ as long as width of head; segments III and IV filiform; labium reaching hind coxa; pronotum  $2.1-2.3 \times$  as wide as long, with distinctly rounded anterior angles and weakly convex lateral margins; scent gland evaporatory area broadly triangular, with large oval peritreme; hind femur swollen; second and third tarsal segments nearly equal in length; claw short, with comparatively wide base, bent at midpoint, pulvillum broad, reaching midpoint of claw, attached to claw along entire length. Genitalia: Genital capsule relatively small, about  $0.3 \times \text{length of abdomen}$ , without distinctive ornamentation, trapezoidal, shorter than width at base; right paramere short, broadly oval, with gradually tapering apex (Fig. 8F); left paramere with comparatively short sensory lobe and apical process (Fig. 8G); sclerotized apex of phallotheca narrow, with distinct subapical constriction (Fig. 8H); vesica strongly coiled at middle, with distinctly sculptured subapical gonopore located on membrane and two large claw-shaped apical blades directly continued into lateral straps (Fig. 8I, J). -Female. Coloration, surface and vestiture: As in male. Structure: Similar to male in sizes and body proportions, body 2.3-2.4 × as long as width of pronotum, total length 2.2-2.3. Vertex 2.4-2.8 × as wide as eye; antennomere II distinctly thinner than segment I, slightly incrassate at apex,  $0.5-0.6 \times$  as long as basal width of pronotum,  $0.9 \times$ as long as width of head; pronotum  $2.1-2.2 \times as$  wide as long. Genitalia: Not examined.

**Distribution.** This species was described from Tabarka, northwestern Tunisia and subsequently found in Sardinia (Carapezza 1984).

Host. Quercus suber L. (Fagaceae) (Wagner 1963; Carapezza 1984).

Material examined. Holotype: TUNISIA: Jendouba: Tabarka, 36.95444°N 8.75806°E, 10 May 1961 – 11 May 1961, Eckerlein, *Quercus suber* L. (Fagaceae), ♂ (AMNH\_PBI 00184008) (ZMUH). — Paratypes: TUNISIA: Jendouba: Tabarka, 36.95444°N 8.75806°E, 10 May 1961 – 11 May 1961, Eckerlein, *Quercus suber* L. (Fagaceae), 5♂ (AMNH\_PBI 00337051–AMNH\_PBI 00337055), 2♀ (AMNH\_PBI 00337056, AMNH PBI 00337058) (ZMUH).

# 5.4. Campylomma pusillum (Reuter, 1878) comb. nov.

Figs 4L, 5A, 8L, N

Sthenarus pusillus Reuter, 1878: 44. Sthenarus pusillus Carvalho 1958: 147. Sthenarus (Phoenicocoris) pusillus Wagner 1958: 413. Sthenarus (Salicarius (sic!)) pusillus Wagner 1975: 101.

**Diagnosis.** Recognized by the following combination of characters: dorsum uniformly chestnut brown (Fig. 4L); antenna without dark color-pattern, segment I and base of segment II sometimes slightly darkened; posterior margin

of vertex slightly attenuate and covering extreme apex of pronotum (Fig. 5A); dorsum with dense, short and thin whitish simple setae; hind femur with a series of oval brown spots along anterior margin ventrally and a few additional subapical spots; vesica with two large clawshaped apical blades directly continued into lateral straps. Most similar in the vesica structure to *Campylomma atlanticum* but differs from that species in the dark dorsum, smaller size, and the apical blades of the vesica tightly adjoining to each other (Fig. 8L, N).

Redescription. Male. Coloration: Dorsum and venter uniformly chestnut brown, base of vertex somewhat paler (Fig. 4L); antenna uniformly whitish yellow or segment I and extreme base of segment II slightly darkened; labial segments I and IV dark, reminder segments pale; legs whitish yellow, all femora with conspicuous round black subapical spots on anterior and posterior margins, hind femur in addition with a series of brown spots along entire anterior margin; spots at bases of tibial spines very minute to almost absent on hind tibia; always absent on fore and middle tibia; membrane uniformly pale smoky brown in specimens from Sicily, uniformly dark brown, almost of same color as rest of body in specimens from Greece, veins dark brown or brown with reddish tinge. Surface and vestiture: Body very finely rugose, shining, dorsum with dense, short and very thin, adpressed goldish simple setae; scales absent; venter and appendages with pale simple setae; antennomere I with two pale mesial setae; subapical spines on femora and tibial spines black. Structure: Body distinctly ovoid, broad and short,  $2.2-2.4 \times$ as long as width of pronotum, total length 1.8-2.2. Head strongly flattened anteroposteriorly, clypeus not visible from above, eye occupying nearly entire side of head in lateral view (Fig. 5A); vertex  $2.4-2.9 \times$  as wide as eye, posterior margin of vertex finely carinate, smoothly curving between inner angles of eyes; antennomere I short, segment II cylindrical,  $0.5-0.6 \times$  as long as basal width of pronotum,  $0.8-0.9 \times$  as long as head width, slightly thinner than segment I; segments III and IV filiform; labium slightly surpassing middle coxa; pronotum with distinctly rounded anterior angles and weakly convex lateral margins,  $1.5-1.6 \times$  as wide as long; scent gland evaporatory area broadly triangular, with large oval peritreme; hind femur swollen; second and third tarsal segments nearly equal in length; claw short, with comparatively wide base, bent close to midpoint, pulvillum slightly not reaching midpoint of claw, attached to claw along entire length. Genitalia: Genital segment trapezoidal, short and wide; parameres and apex of phallotheca similar to those of C. atlanticum; vesica strongly bent at middle, terminating with two large claw-shaped and tightly adjoining apical blades directly continued into lateral straps; secondary gonopore subapical, distinctly sculptured, located on membrane (Fig. 8L, N). - Female. Coloration: Similar to male but vertex uniformly chestnut brown, fore and middle tibiae with minute spots at bases of tibial spines. Surface, vestiture and genitalia: As in male. Structure: Body 2.3–2.4 × as long as width of pronotum; total body length 2.1–2.4. Vertex 2.6–2.8  $\times$  as wide as eye; antennomere II  $0.5-0.7 \times as$  long as basal width of pronotum,  $0.7-0.8 \times as$  long as head width, distinctly thinner than segment I, slightly incrassate at apex; pronotum  $2.3-2.4 \times as$  wide as long. **Genitalia**. Dorsal labiate plate small, strongly excavated at sides, sclerotized rings weakly sclerotized, rather small, oval; vestibulum S-shaped, relatively thin, laterally extending to middle of one ring and slightly surpassing the curvature of rami (Fig. 11C) Apex of second valvula distinctly arrow-shaped.

**Distribution.** Originally described from southern Italy mainland (Naples), this species was subsequently reported from Sicily (Wagner 1975), Greece (Linnavuori 1999), and Monaco (Ponel et al. 2013).

Host. Quercus sp. (Linnavuori 1999).

Material examined. GREECE: Peloponnese: Laconia (Lakonias) Co.: nr Vrodamas, 36.9667°N 22.65°E, 127 m, 03 Jun 1989 – 04 Jun 1989, Linnavuori, 2♂ (AMNH\_PBI 00338315, AMNH\_PBI 00338314), 1♀ (AMNH\_PBI 00338317) (NMWC). Messinia (Messenia, Messinias) Co.: Kalamata, 37.0389°N 22.1142°E, 06 Jun 1989, R. Linnavuori, 1♂ (AMNH\_PBI 00338314) (NMWC). Tripi – Artemissia Road, 37.1°N 22.2333°E, 06 Jun 1989, R. Linnavuori, 1♀ (AMNH\_PBI 00338318) (NMWC). ITALY: Sicily: Mt. Etna dint. Pedara, 600 m, 25 Jul 1948, Hartig, 1♀ (AMNH\_PBI 00337050) (ZMUH). Genova, 37.95°N 12.7°E, Martini coll., 1♂ (AMNH\_PBI 00337049) (ZMUH).

#### 5.5. Heterocapillus Wagner, 1960

#### Figs 3I, J, 5H, I, 6C, G, 7L, 8O-U, 11D-F

*Heterocapillus* Wagner, 1960: 83 (as subgenus of *Atractotomus*; upgraded by Kerzhner 1962: 379).

**Type species.** By original designation: *Capsus tigripes* Mulsant and Rey, 1852.

**Diagnosis.** Recognized among other Phylini by the following combination of characters: dorsum uniformly dark brown, usually with whitish basal margin of vertex (Fig. 3I, J); tibiae dirty yellow, with dark brown ventral surfaces, bases, apices, and large spots at bases of tibial spines; antenna uniformly dark brown, two first segments swollen in both sexes, segment I obconic, segment II fusiform (Fig. 5H, I); dorsum and thoracic pleura clothed with moderately flattened silver scales and robust dark simple setae (Fig. 6G); dorsal labiate plate with large, broadly oval sclerotized rings; vestibulum short and wide, C-shaped; vesica with a series of rectangular notches on a strap terminating near secondary gonopore and with two very long, characteristically shaped apical blades.

*Heterocapillus tigripes* forms a sister group to all other representatives of the clade I (Figs 1, 2) which contains *Europiella* spp., *Phaeochiton* spp., *Plagiognathus* spp., and *Lobicris basalis*. Members of this group share many common traits in the structure of the complex vesica including the presence of longitudinal sclerotized ridges on the lateral strap, additional strap terminating near secondary gonopore, and apical half deeply subdivided into two variously shaped branches. Heterocapillus also possesses a C-shaped sclerotized band located on membrane and associated with secondary gonopore, a feature documented only for Phaeochiton and Lobicris. Phaeochiton differs from H. tigripes in the absence of robust dark setae on dorsum, fusiform antennomere II in both sexes, small pulvillus (Konstantinov 2008c: figs 19, 20), vesica with differently shaped apical blades (Konstantinov 2008c: figs 13, 15, 21), dorsal labiate plate with small sclerotized rings (Konstantinov 2008c: figs 32-34), and S-shaped vestibulum (Konstantinov 2008c: fig. 37). Lobicris may be easily distinguished by the not uniformly dark coloration of dorsum, thin antennomeres, apically tapering sclerotized rings of the dorsal labiate plate, S-shaped vestibulum, and by the presence of inflatable, finely serrate membranous lobe at the apex of vesica. Representatives of several otherwise unrelated genera e.g., Chrysochnoodes (Carapezza 1994: fig. 4f), Josifovius Konstantinov 2008d: figs 18, 20), Megalodactylus (Carapezza 1997: fig. 75), Moissonia (Linnavuori and Al-Safadi 1993: fig. 1a), Pachyxyphus (Pagola-Carte 2015: figs 10c, 11c), and Tinicephalus (Matocq 1993: fig. 23) also possesses a series of rectangular notches on vesica, but not in a form of a separate strap terminating near secondary gonopore. Pachyxyphus linneellus (Mulsant and Rey, 1852) forms an exception (Pagola-Carte 2015: fig. 11c) in having a separate strap with a series of rectangular notches similar to that of *H. tigripes*. However, this species readily differs in all other respects including body proportions, coloration, vestiture, and vesica structure.

Redescription. Male. Macropterous, with rather robust oval body. Coloration: Dark brown (Fig. 3I), head, pronotum, and scutellum darker than hemelyron; base of vertex and posterior margin of eye dirty whitish (Fig. 4H); all antennomeres and labium uniformly dark brown; thoracic pleura dark brown, with more or less developed pale edging, scent gland evaporatory area whitish; femora uniformly dark brown with pale edgings at apices, tibiae dirty yellow, with darkened ventral surfaces, bases, apices, and large dark spots at bases of tibial spines; tarsi dark brown; membrane uniformly brown, veins usually entirely or apically pale, rarely brown; abdomen uniformly dark brown. Surface and vestiture: Smooth, moderately shining; dorsum, thoracic pleura, and abdomen with dense, moderately flattened, apically acuminate scalelike silver setae (Fig. 6G); in addition clypeus, area between antennal fossa and eye, vertex, sides of pronotum and hemelytron with robust dark simple setae, contrastingly long, erect to semierect on pronotum and at base of forewing, almost twice shorter, adpressed elsewhere; venter of head with long, pale and thin simple setae; appendages with simple, adpressed to semierect, setae, contrastingly dense and long on antennomeres I and II; each femur with a few dark spines apically, tibial spines dark brown to black. Structure: Head moderately produced anteriorly in dorsal view, strongly declivent; eyes occupying 3/4 of height of head in lateral view, posterolateral margins of eyes contiguous with anterolateral margins of pronotum;

vertex weakly convex, with posterior margin slightly attenuate at middle, frons vertical, clypeus weakly produced, usually not visible in dorsal view; antenna inserted near ventral margin of eye; segment I short, obconic, strongly swollen apically, slightly longer than width at apex; segment II swollen along entire length, somewhat fusiform, wider at apical 2/3, about  $5 \times$  as long as width, segments III and IV filiform; labium reaching metacoxa. Pronotum trapezoidal, about twice as broad as long, disk distinctly convex, calli indistinct; mesonotum moderately exposed; metathoracic scent-gland evaporatory area broadly triangular. Legs comparatively short, hind femur swollen, broader medially, tibia cylindrical, second and third tarsal segments of nearly equal length, claw (Fig. 7L) with relatively wide base, strongly bent in apical 2/3, pulvillus large, far surpassing midpoint of claw, attached to the claw along whole length. Genitalia: Genital capsule (Fig. 8R) large, almost 0.6 of abdomen length, slightly shorter than basal width, without keels and distinctive ornamentation, dorsal wall basally with a pair of small tubercles at sides. Parameres of typical phyline shape, right paramere lanceolate (Fig. 8P), left paramere (Fig. 8Q) with comparatively thin, flattened and gradually curving processes. Apex of phallotheca as in Fig. 8O. Vesica S-shaped, robust, body of vesica of distinctive curvature and form, with a portion of one strap terminating near secondary gonopore and bearing a series of square dentations (Fig. 8S–U), apical portion of vesica with two large, smoothly curved and gradually tapering blades of equal length, apex of left blade more or less straight, right blade apically lanceolate and strongly upcurved; secondary gonopore large, with well-developed sculpture, far removed from apex and located on membrane at base of apical blades. — Female. Macropterous. Coloration, surface and vestiture: Similar to male (Fig. 3H), but eves slightly smaller, with correspondingly broader vertex (Table 1); antennomere I with two dark mesial spines usually somewhat adpressed and similar to dark simple setae in male, segment II more distinctly fusiform, widened towards middle, about 5  $\times$  as long as wide (Fig. 5I). Genitalia: As in Fig. 11D-F, dorsal labial plate with large, broadly oval sclerotized rings; posterior wall simple, with a pair of very slightly sclerotized, elongate sclerites at sides; vestibulum wide and comparatively short, C-shaped, irregularly sclerotized.

**Remarks.** As justified in the relevant part of the discussion section, the genus *Heterocapillus* is here redefined as monotypic to accommodate its type species, *H. tigripes* (Mulsant & Rey, 1852).

# 5.6. Heterocapillus tigripes (Mulsant & Rey, 1852)

Capsus magnicornis (non Fallén, 1807) Hahn, 1833: 130. Misidentification (see Fieber 1861: 295).

Capsus tigripes Mulsant & Rey, 1852: 129.

*Atractotomus tigripes*: Fieber 1861: 295; Reuter 1879: 302, 1883: 457, 1909: 73; Wagner 1952: 189, 1961: 68.

- Atractotomus (Heterocapillus) tigripes: Wagner 1960: 4; Wagner and Weber 1964: 450; Ribes 1965: 78.
- Heterocapillus tigripes: Kerzhner 1962: 379; Wagner 1975: 122; Tamanini 1981: 68; Ribes 1981: 83; Stonedahl 1990: 6.

**Diagnosis.** Recognized by the characters given in the generic diagnosis.

**Redescription. Male. Coloration, surface, vestiture and genitalia**: As in generic description. **Structure**: Body 2.5–2.7 × as long as width of pronotum; total body length 3.1–3.4. Vertex 2.4–2.6 × as wide as eye; antennomere II 0.6–0.7 × as long as basal width of pronotum, subequal to width of head; pronotum 2.0–2.1 × as wide as long. — **Female. Coloration, surface, vestiture and genitalia**: As in generic description. **Structure**: Body 2.4–2.7 × as long as width of pronotum; total body length 3.3–3.5. Vertex 2.5–2.7 × as wide as eye; antennomere II 0.6–0.7 × as long as basal width of pronotum, subequal to width of head; pronotum 2.0–2.2 × as wide as long.

**Distribution.** North Mediterranean species, spanning from Spain in the West to Turkey in the East, and extending to Carpathian Mountains of Czech Republic, Poland, and Ukraine in the North, mostly inhabiting open xero-thermic grasslands on calcium-rich soils (Ribes 1981; Kment and Baňař 2012).

Hosts. Lotus dorycnium L. (Fabaceae) (Kerzhner 1962; Wagner 1975; Ribes 1981), Lotus hirsutus L. (Fabaceae) (Tamanini 1981).

Material examined. AUSTRIA: Leithagebirge, Winden, 1900, H. Franz, 1d (AMNH PBI 00336949) (ZMUH). BOSNIA HERCE-GOVINA: Vaganj, 43.78611°N 16.79555°E, 08 Jun 1946, Novak, 2♀ (AMNH\_PBI 00336951, AMNH\_PBI 00336952) (ZMUH). BULGAR-IA: Blagoevgrad: Slavyanka (Alibotush Mt), 41.48938°N 23.5756°E, 07 Jun 2014, Simov N., 2 (AMNH\_PBI 00341026, AMNH\_PBI 00342998) (ZISP). CROATIA: Dalmatia: Svilaja Mts, 22 Jun 1947, Novak, 1 (AMNH\_PBI 00336948) (ZMUH). CZECH REPUBLIC: Moravia: Mohelno (step), 30 Jun 1946, J. L. Stehlik, 1º (AMNH PBI 00336953) (ZMUH). FRANCE: Corsica: Corse-du-Sud Co.: 13 km E Puerta Veccio, Rt D71, Corsica, 41.6°N 9.3°E, 23 May 1990 - 30 May 1990, G.M. Stonedahl, Genista sp. (Fabaceae), 13 (AMNH PBI 00095773) (AMNH). Midi-Pyrenees: Tarn Co.: Albi (Tarn), Cote de Jussens, 43.93°N 2.15°E, 14 Jun 1954 – 16 Jun 1954, E. Wagner, 4ð (AMNH\_PBI 00336944–AMNH\_PBI 00336947), 3♀ (AMNH\_PBI 00336954-AMNH PBI 00336956) (ZMUH). Gallia, V. Jakovlev coll., 1♂ (AMNH\_PBI 00240938), 3♀ (AMNH\_PBI 00240939–AMNH\_ PBI 00240941) (ZISP). GREECE: Peloponnese: Kollines, 37.28389°N 22.35167°E, 17 Jun 1990, R. Linnavuori, 4<sup>o</sup>/<sub>+</sub> (AMNH PBI 00340917, ZISP ENT 00011722), 83 (AMNH PBI 00340917, ZISP ENT 00011724, ZISP ENT 00011723) (NMWC). MONTENEGRO: Between Zabljak and Podgorica, 42°N 19.1°E, 02 Jul 1958, L. Hoberlandt, 13 (ZISP ENT 00011717) (NMPC). SLOVAKIA: Kovacovske kopce, 47.83333°N 18.76667°E, 09 Jun 1960, Exc. M. N. Pragae, 10♂ (ZISP\_ENT 00011730–ZISP\_ENT 00011739), 5♀ (ZISP\_ENT 00011727-ZISP\_ENT 00011729, ZISP\_ENT 00011715, ZISP\_ENT 00011716) (NMPC). **SPAIN**: ES Almeria, Huercal-Overa, 37.3833°N 1.93°W, 16 Mar 2001, J. M. Bruers, 1 $^{\circ}$  (ZISP\_ENT 00011855), 1 $^{\circ}$  (ZISP\_ENT 00011856) (ISNB). Valldoreix (Valles Ocid.), 41.45°N 2.03°W, 13 May 1956, *Dorycnium suffruticosum* Vill. (Fabaceae), 1 $^{\circ}$  (AMNH\_PBI 00095774) (AMNH). **UKRAINE**: Glubokoe, Zakarpatska prov., 48.55°N 22.415°E, 03 Jul 1957, Roshko, 4 $^{\circ}$  (AMNH\_PBI 00233309, AMNH\_PBI 00240944, AMNH\_PBI 00151728, AMNH\_PBI 00252541), 3 $^{\circ}$  (AMNH\_PBI 00238411, AMNH\_PBI 00240943, AMNH PBI 00231370) (ZISP).

#### 5.7. Lobicris Putshkov, 1977 stat. nov.

Figs 4F, G, 5C, 7J, 100-T, 11G-I

Lobicris Putshkov, 1977: 368 (as a subgenus of Salicarus).

**Type species.** By original designation: *Neocoris basalis* Reuter, 1878.

Diagnosis. Recognized by the following combination of characters: head strongly declivent, with slightly attenuate posterior margin of vertex (Fig. 5C); antenna short, segment II distinctly shorter than basal width of pronotum in both sexes; dorsum dark brown, hemelytron with narrowly whitish claval suture and wide whitish stripe at base of cuneus (Fig. 4F, G); hind tibia with darkened base; dorsum clothed with moderately flattened, apically acuminate silver scalelike setae; claw with relatively wide base, strongly bent apicad midpoint, pulvillus large, surpassing midpoint of claw, apically free (Fig.7J); vesica strongly bent at middle, composed of three straps (Fig.10Q-S); lateral strap with several longitudinal ridges; portion of one strap abruptly terminating at middle of vesica; secondary gonopore large and distinctly sculptured, with large C-shaped sclerotized band at base; apex of vesica with two thin sclerotized blades and partly inflatable, finely serrate membranous lobe.

*Lobicris* is related to the genera *Heterocapillus*, *Phaeochiton*, *Europiella*, and *Plagiognathus* (see Discussion) but may be distinguished by the inflatable, finely serrate membranous lobe at the apex of vesica. This feature is highly unusual for Palaearctic phylines and to my knowledge is known only in otherwise unrelated *Sthenarus* spp. (Fig. 10V).

**Redescription. Male**. Macropterous, oval, total length 3.4–3.6. **Coloration**: Dorsum dark brown, with wide whitish stripe at base of cuneus (Fig. 4F); head dark brown, usually with dirty whitish posterior margin of vertex, rarely uniformly dark brown; antennomere I dirty yellow, with darkened base and large dark brown spot on mesial surface, rarely almost uniformly brown, segment II dark brown, rarely pale brown with darkened basal part, segments III and IV somewhat paler than segment II; pronotum, scutellum, thoracic pleura, and coxae uniformly dark brown; femora dirty yellow, with a few dark brown round spots at bases of subapical spines, hind femur sometimes with more or less darkened apical third;

tibiae with dark brown spot at base and round brown spots at bases of tibial spines; tarsi dirty yellow, sometimes apically darkened; hemelytron dark brown, claval suture usually narrowly whitish, base of cuneus with wide transverse whitish band and usually with narrowly whitish apex, membrane uniformly brown to pale brown, with apically whitish veins; abdomen uniformly dark brown. Surface and vestiture: Smooth, shining; dorsum clothed with a mixture of dense, moderately flattened, apically acuminate silver scalelike setae and long, scarce, adpressed, goldish simple setae; appendages with short, adpressed, whitish simple setae; thoracic pleura and pregenital abdomen segments with long, adpressed, simple setae, genital segment with short adpressed simple setae; each femur with a few dark spines apically, tibial spines dark brown. Structure: Head moderately produced anteriorly in dorsal view, strongly declivent; clypeus weakly produced, barely visible in dorsal view; eyes occupying 3/4 of height of head in lateral view, posterolateral margins of eyes contiguous with anterolateral margins of pronotum; antennal fossa located slightly above ventral margin of eye; segment I short, cylindrical, about 1.5 times as wide as segment II; segment II slender, linear, slightly wider than segments III and IV; labium reaching or surpassing mesocoxa. Thorax: Trapezoidal, about twice as broad as long, with indistinct calli; mesonotum moderately exposed; metathoracic scent-gland evaporatory area narrowly triangular. Tarsal segment I twice shorter than II, segments II and III subequal in length; claw with relatively wide base, strongly bent apicad midpoint, pulvillus large, surpassing midpoint of claw, apically free (Fig. 7I). Genitalia: Genital capsule large and wide, more than half of abdomen, strongly sclerotized, without distinct ornamentation. Right paramere short, broadly oval, gradually tapering apically (Fig. 10O). Left paramere with long and narrow sensory lobe and long, straight, basally upturned apical process (Fig. 10P). Apex of phallotheca as in Fig. 10T, with subapical step-shaped projection ventrally. Vesica large and strongly sclerotized, strongly bent at middle, with portion of one strap abruptly terminating at middle of vesica, lateral strap of vesica equipped with several longitudinal sclerotized ridges (Fig. 10Q-S); secondary gonopore subapical, large, oval, distinctly sculptured, with large C-shaped sclerotized band at base; apex of vesica with partly inflatable, finely serrate membranous lobe and with two thin apical blades, smaller one nearly straight, larger blade curved at middle, apically twin-coned. -Female. Coloration, surface and vestiture, structure: As in male, with almost no sexual dimorphism. Body

As in male, with almost no sexual dimorphism. Body somewhat bigger in average (see Table 1), antennomere II usually slightly thinner than in male, brown with darkened base, rarely uniformly dark to pale brown. **Genitalia**: Sclerotized rings of dorsal labiate plate very large, elongate, apically tapering; dorsal labiate plate with two symmetric slightly sclerotized oval areas at sides of midline; vestibulum S-shaped, thick, slightly sclerotized; posterior wall of bursa copulatrix with two distinct and symmetrical blade-shaped sclerites at sides.

#### 5.8. Lobicris basalis (Reuter, 1878)

Neocoris basalis Reuter, 1878: 59. Monosynamma basalis: Oshanin 1910: 93; Carvalho 1958: 75. Microsynamma basalis: Wagner 1947: 480. Monosynamma basale: Popov 1965: 193. Plagiognathus basalis: Kerzhner 1970: 645. Salicarus (Lobicris) basalis Putshkov 1977: 368.

**Diagnosis.** Recognized by the characters given in the generic diagnosis.

**Redescription.** Male. Coloration, surface, vestiture and genitalia: As in generic description. Structure: Body 2.7–2.9 × as long as width of pronotum; total body length 3.4–3.6. Vertex  $1.8-2.0 \times$  as wide as eye; antennomere II 0.7–0.8 × as long as basal width of pronotum and  $1.1-1.2 \times$  as long as width of head; pronotum  $2.1-2.2 \times$ as wide as long. — Female. Coloration, surface, vestiture and genitalia: As in generic description. Structure: Body 2.6–2.8 × as long as width of pronotum; total body length 3.5–3.9. Vertex 2.0–2.2 × as wide as eye; antennomere II 0.7–0.8 × as long as basal width of pronotum,  $1.0-1.1 \times$  as long as width of head; pronotum  $2.1-2.3 \times$ as wide as long.

**Distribution.** Western Tian Shan Mountains of Central Asia (Kyrgyzstan, Tajikistan, and Uzbekistan). Recorded from mountain steppes and mixed forests along rivers of Qurama, Chatqol, Alai, Turkestan, Zarafshon Mts ridges and Fergana Valley (Putshkov 1977).

Hosts. Salvia scrophulariifolia (Bunge) B.T. Drew (Lamiaceae), Spiraea hypericifolia L. (Rosaceae) (Popov 1965).

Material examined. KYRGYZSTAN: 15 km S Osh, Fergana Valley, 40.4°N 74.46666°E, 09 Jun 1958, Gorodkov, 4∂ (AMNH\_PBI 00332194-AMNH PBI 00332197), 2<sup>+</sup> (AMNH PBI 00332192, AMNH\_PBI 00332193) (ZISP). Jordan, 39.63°N 70.95°E, 02 Jun 1908, A. N. Kiritshenko, 1<sup>♀</sup> (AMNH\_PBI 00332223) (ZISP). Katta-Taldyk, Osh Distr., 40.51222°N 72.96583°E, 14 May 1962, Putshkov, 1♀ (AMNH PBI 00332202), 3♂ (AMNH PBI 00332202, AMNH PBI 00332203) (ZISP). Taka Pass, Alay Mts Range, 39.48333°N 72.41666°E, 7390 m, 1 larva (AMNH PBI 00332172) (ZISP). Yangryk no Gul'cha River, 40.33°N 73.43°E, 23 Jun 1928, Reichardt, 4ð (AMNH PBI 00332164–AMNH PBI 00332167), 7♀ (AMNH PBI 00332185-AMNH\_PBI 00332191) (ZISP). TAJIKISTAN: Muynak Mt. nr Vorukh, 39.85°N 70.55°E, 14 Jun 1908, Zarudny, 26 (AMNH\_ PBI 00332236, AMNH PBI 00332237), 5<sup>Q</sup> (AMNH PBI 00332253-AMNH\_PBI 00332257) (ZISP). Vorukh, 39.85°N 70.55°E, 08 Jun 1908, Zarudny, 48 (AMNH\_PBI 00332232-AMNH\_PBI 00332235), 5♀ (AMNH PBI 00332247–AMNH PBI 00332251) (ZISP). UZ-BEKISTAN: Fergana Valley: Chatkalsky tract, Quqon [Kokand], 40.51666°N 70.93333°E, 28 Jun 1908, Zarudny, 4 (AMNH PBI 00332159-AMNH PBI 00332162), 5<sup>o</sup> (AMNH PBI 00332173-AMNH PBI 00332177) (ZISP). Aman-Kutan river, Kyrk-Tau Mt. [Kyr-Tau], 39.33333°N 67.16667°E, 12 Jun 1932, Gussakovskiy, 3 (AMNH\_PBI 00332238-AMNH\_PBI 00332240), 2♀ (AMNH\_PBI 00332258, AMNH\_PBI 00332259) (ZISP); 13 Jun 1932, Gussakovskiy, 2♂ (AMNH PBI 00332241, AMNH PBI 00332242), 1♀ (AMNH PBI 00332260) (ZISP). Fergana [Skobelev], 40.38333°N 71.76666°E, 13 May 1908, A. N. Kiritshenko, 43 (AMNH PBI 00332198-AMNH PBI 00332201), 12<sup>o</sup> (AMNH\_PBI 00332211–AMNH\_PBI 00332222) (ZISP). Kempir-tyube [Kempyrg-tepe], 37.78°N 66.68°E, 20 May 1910, Zarudny, 1<sup>Q</sup> (AMNH PBI 00332228) (ZISP). Kyshtut, 38.83333°N 67.9°E, 30 May 1908, A. Hohlbeck, 3∂ (AMNH\_PBI 00332243-AMNH\_PBI 00332245), 4♀ (AMNH\_PBI 00332263–AMNH\_PBI 00332266) (ZISP); 31 May 1908, A. Hohlbeck, 1 (AMNH PBI 00332246) (ZISP). Padshaata, 41°N 71.666666°E, 29 May 1908, B. Grigoriev, 2<sup>(1)</sup> (AMNH PBI 00332168, AMNH PBI 00332171) (ZISP); 04 Jun 1908, B. Grigoriev, 28 (AMNH PBI 00332169, AMNH PBI 00332170) (ZISP). Shakhimardan, Alayskiy Mts. Range, 39.96666°N 71.78333°E, 05 Jun 1900, Germs, 7♀ (AMNH\_PBI 00332178-AMNH\_PBI 00332184), 1 (AMNH\_PBI 00332163) (ZISP). Skalyat-Zarkent-Nanay, 41.46666°N 71.66666°E, 02 Jun 1909, Zarudny, 43 (AMNH PBI 00332207-AMNH PBI 00332210), 3♀ (AMNH PBI 00332229-AMNH\_PBI 00332231) (ZISP). Takhtakaracha Pass, Zeravshan Mts. Range, 39.26°N 66.9°E, 27 May 1909, A. Hohlbeck, 2♀ (AMNH PBI 00332261, AMNH PBI 00332262) (ZISP). Urgut, foothills of Zeravshan ridge, 39.4022°N 67.2431°E, 01 Jun 1945 - 08 Jun 1945, Fursov, 38 (AMNH PBI 00332204-AMNH PBI 00332206), 4<sup>Q</sup> (AMNH PBI 00332224-AMNH PBI 00332227) (ZISP).

# 5.9. *Mesopsallus* Wagner, 1970 stat. nov.

Figs 3E, F, 5J–M, 6D–F, 7A, D, E, G, I, 9 F–N, 12A

Mesopsallus Wagner, 1970: 302 (as a subgenus of Psallus)

Type species. Lygaeus ambiguus (Fallén, 1807)

**Diagnosis.** Recognized by the following combination of characters: dorsum with apically serrate or acuminate silver scales and simple setae (Fig. 6D–F); vesica J-shaped, formed by two straps separated by membrane (Fig. 9F–N); secondary gonopore large, round, and distinctly sculptured, located almost at the apex of the vesica; apical blade of vesica short and straight; dorsal labiate plate with distinctly elongate, apically rounded sclerotized rings (Fig. 12A).

Most similar to many *Psallus* spp. in the general appearance, body proportions, and vestiture composed of a mixture of whitish scalelike setae and simple setae but differing from that genus in the vesica structure.

**Species composition.** *Mesopsallus ambiguus* (Fallén, 1807) – broadly distributed in Europe, East to Komi and Bashkortostan republics of Russia, South to Turkey, Transcaucasia, and Northern Iran.

Mesopsallus amygdali (Wagner, 1960) comb. nov. – Iran. Mesopsallus fagi (Drapolyuk, 1990) comb. nov. – Azer-

baijan.

Mesopsallus holomelas (Reuter, 1906) – Sichuan, China. Mesopsallus mali (Meyer-Dür, 1843) comb. nov. – Eu-

rope, East to Nizhegorod Prov. and Bashkortostan Rep. of Russia, South to Israel, Turkey, Transcaucasia, and Northern Iran.

- Mesopsallus pici (Reuter, 1899) comb. nov. Morocco, Algeria, Tunisia.
- *Mesopsallus rhodani* (Fieber, 1861) **comb. nov.** From Germany, France and Italy in the West to Ukraine, Romania and Turkey in the East.
- Mesopsallus samdzijonicus (Josifov, 1983) North Korea.

Mesopsallus tibialis (Reuter, 1894) - Spain.

Mesopsallus validus (Reuter, 1901) comb. nov. – Algeria.

### 5.10. *Psallus (Phylidea) validicornis* (Reuter, 1876) comb. nov.

Figs 4E, 5F, G, 9A-E, 12B

Atractotomus validicornis Reuter, 1876: 21.

Atractotomus putoni Reuter, 1878: 175 (syn. by Reuter 1881: 183; Wagner 1973b: 105).

Heterocapillus validicornis: Wagner 1975: 123.

Heterocapillus niger Wagner, 1966: 217 syn. n.

**Diagnosis.** Recognized by the structure of antenna in both sexes (Fig. 5F, G), the uniformly dark coloration, the distribution of flattened silver setae, whitish and dark simple setae on dorsum and venter, the narrow genital segment with ventral finely dentate keel, the phallotheca with subapical teeth, and the apex of twin-bladed vesica (Fig. 9A–E).

Most similar to several species from the subgenus *Phylidea* viz. *P. cyprius* Wagner, 1968, *P. halidi* Drapolyuk, 1991, *P. henschii* Reuter, 1888, *P. transcaucasicus* Zaitseva, 1966, *P. samedovi* Drapolyuk, 1991, *P. ussuriensis* Kerzhner, 1979, and *P. cinnabarinus* Kerzhner, 1979 in the color-pattern of dorsum, vestiture, shape of the genital segment, subapically dentate phallotheca and the structure of the vesica, but clearly differing in the shape and coloration of antennomeres in both sexes as well as in the shape of inflated portion and blades at the apex of the vesica.

Redescription. Male. Macropterous, almost parallel-sided (Fig. 4E), total length 3.6-3.9. Coloration: Dorsum uniformly brown to dark brown, without any pale areas; labium, antennomeres I and II dark brown, segment III pale yellow, slightly darkened at base, segment IV uniformly pale yellow; all femora dark brown, tibiae pale yellow, with small diffuse spots at bases of tibial spines, basal half of hind tibia more or less darkened, in the darkest specimens fore and middle tibiae with darkened bases while hind tibia almost entirely brown; tarsi pale, apically darkened; thoracic pleurites and abdomen uniformly dark brown; membrane uniformly brown, sometimes with indistinct pale area near apex of cuneus, veins brown. Surface and vestiture: Smooth, shining; dorsum, thoracic pleura, and abdomen with dense, apically acuminate scalelike silver setae; dorsum also clothed with simple setae, predominantly whitish on head, pronotum, base and inner margin of hemelytron, dark brown in latero-apical

part of hemelytron, semierect on vertex and apex of pronotum, adpressed elsewhere; sides of pronotum with contrastingly long semierect bristlelike dark setae; appendages with simple pale adpressed setae, contrastingly dense, long, dark and semierect on antennomeres I and II; tibial spines dark brown. Structure: Body  $3.2-3.4 \times as$  long as width of pronotum. Head moderately produced anteriorly in dorsal view, clypeus not visible or barely visible from above, vertex  $1.4-1.6 \times$  as wide as eye; antennomere I short and thick, about twice longer than width, segment II somewhat thickened, cylindrical,  $0.8 \times$  as wide as segment I, almost twice as wide as segments III and IV,  $0.9-1.0 \times$  as long as basal width of pronotum,  $1.4-1.5 \times$ as long as width of head, labium reaching to metacoxa. Pronotum 2.0–2.1 × as wide as long, 1.5-1.6 × as wide as head; second and third tarsal segments of nearly equal length, claw with relatively wide base, gradually and rather strongly bent in apical 2/3, pulvillus reaching midpoint of claw, attached to the claw along whole length. Genitalia: Genital capsule about 0.4 of abdomen length, rather narrow, slightly longer than basal width, ventral wall humped, with median finely dentate keel running towards apex. Right paramere lanceolate, left paramere subquadrate in lateral view, with comparatively short, almost straight processes. Apex of phallotheca with small subapical tooth. Vesica S-shaped, gracile, twin-bladed, apically with inflated portion bearing small teeth on outer margin and ending with thin, almost straight tapering blade (Fig. 9A-E); second blade shorter and wider, distinctly sclerotized, sickle-shaped; secondary gonopore subapical, oblong-oval. - Female. Macropterous, elongate-oval, somewhat smaller than male, total length 3.0-3.6. Coloration, surface and vestiture: As in male. **Structure**: Body  $2.6-3.0 \times$  as long as width of pronotum. Head distinctly produced anteriorly, almost triangular in dorsal view, clypeus visible from above, vertex 1.5–1.6  $\times$ as wide as eye (Fig. 5G); antennomere I short and thick, obconic, apically wider than in male,  $1.6-1.7 \times \text{times}$  as long as width, segment II distinctly swollen, fusiform, about twice as wide as segment I, somewhat wider than eye width,  $0.9-1.0 \times$  as long as basal width of pronotum,  $1.4-1.5 \times$  as long as width of head, labium reaching to metacoxa. Genitalia: Dorsal labiate plate with rather small, elongate oval, apically rounded sclerotized rings; common oviduct basally widened (Fig. 12B); posterior wall with a pair of very finely sclerotized areas at sides.

**Distribution.** *Psallus validicornis* is currently known from southern France, Spain, and Morocco, while *P. ni-ger* was described from Crete.

**Hosts.** *Quercus coccifera* (Ribes 1978; Linnavuori 1994), *Quercus ilex* (Wagner 1973b). According to Wagner (1975), several specimens collected by H. Lindberg in Sierra de Cordoba (see material examined) were sampled from *Genista hirsuta*, but this single occurrence probably represents a sitting record.

**Remarks.** Reuter (1876) described *Atractotomus validicornis* from females sampled in Avignon and provided by Puton for investigation. Subsequently he (Reuter 1878) described *A. putoni* known only from males from the same locality and collection. Three years later Reuter (1881) synonymized the latter species with the former, referring to Puton's personal communication and additional observations. Wagner & Weber (1964), apparently unaware of above-mentioned synonymy, treated both species as distinct until Wagner (1973b) again synonymized *A. putoni* with *A. validicornis*. Since 1960 the species has been treated within *Heterocapillus*, originally erected by Wagner (1960) as a subgenus of *Atractotomus* and raised to generic rank by Kerzhner (1962). Stonedahl (1990) in the monographic treatment of *Atractotomus* correctly pointed out that *H. validicornis* appears to have affinities with "*Psallus* complex."

Careful investigation of the male and female genitalic characters allowed me to conclude that the species undoubtedly belong to the subgenus *Phylidea* of the genus *Psallus*. This is mainly confirmed by the structure of the apical portion of the vesica and features of the genital capsule, phallotheca, and vestiture mentioned in the diagnosis, although females of *Psallus validicornis* strikingly differ from congeners in having unusually dilated and swollen antennomere II. Host plant associations are also congruent with the accepted generic assignment of the species.

Wagner (1966) described Heterocapillus niger from two males collected in Cyprus. According to the original description and subsequently published key (Wagner 1975), males of the species differ from those of H. va*lidicornis* in having thinner antennomere II  $(12-15 \times as)$ long as wide in *H. niger* and  $11-12 \times as$  long as wide in H. validicornis) and some unnamed distinctions in the vesica structure. Comparison of the holotype of H. niger with the available material and lectotype of H. validicornis allows for conclusion that they are conspecific. No distinctions were found in the sizes and measurements (see Table 1), color-pattern, vestiture, structure of antenna and vesica (Fig. 9A-E). On the grounds of the above discussion, I am treating Heterocapillus niger Wagner, 1966 as a synonym of Psallus validicornis (Reuter, 1876).

Material examined. Lectotype of Atractotomus validicornis: FRANCE: Provence-Alpes-Côte d'Azur: Avignon, 43.953°N 4.812°E, ♀ (AMNH PBI 00337990) (MNHN). — Lectotype of Atractotomus putoni: Avignon, 43.953°N 4.812°E, 1906, coll. A. Puton, ♂ (AMNH\_PBI 00337989) (MNHN). Holotype of Heterocapillus niger: CYPRUS: Yermasoyia River, 35.11337°N 32.53349°E, Jan 1965, G. Mavromoustakis, d (AMNH\_PBI 00184016) (ZMUH). - Other specimens : France: Provence-Alpes-'ôte d'Azur: La Ciotat, 43.17694°N 5.60861°E, Jun 1900, Payan, 1<sup>o</sup> (AMNH PBI 00336833) (ZMUH). SPAIN: N avarra: Yesa Reservoir, 42.6167°N 1.2°W, 26 Jun 1967, Eckerlein, Quercus ilex L. (Fagaceae), 1∂ (AMNH\_PBI 00336828), 1♀ (AMNH PBI 00336830) (ZMUH). Sierra de Cordoba, 10 Apr 1926 -11 Apr 1926, Lindberg, 1∂ (AMNH PBI 00336829), 1♀ (AMNH PBI 00336831) (ZMUH). Valldoreix (Valles Ocid.), 41.45°N 2.03°W, 23 May 1992, J. Ribes, Quercus ilex (Fagaceae), 13 (AMNH\_PBI 00240966) (ZISP).

#### 5.11. Salicarus Kerzhner, 1962

Figs 3G, H, K, L, 4I, J, 5D, E, M, N, 6A, H, 7F, H, K, 9Q–T, 11C, 12C–F

Salicarus Kerzhner, 1962: 381. Sthenarus (Salicarius [sic!]): Wagner 1975: 99. Salicarus: Putshkov 1977: 370.

**Type species.** By original designation: *Capsus roseri* Herrich-Schaeffer, 1838.

**Diagnosis.** Body broadly oval, with short appendages (Fig. 3G, H, K, L, 4I, J); head vertical, clypeus barely visible in dorsal view, posterior margin of vertex carinate (Fig. 5D, E) or posteriorly attenuate (Fig. 5M, N); dorsum and/or thoracic pleura clothed with scalelike setae and simple setae (Fig. 6A, 7B, F); parempodium apically spatulate; pulvillum small, not reaching midpoint of claw (Fig. 7H); vesica large, strongly coiled at middle, apically with two long and thin, gradually tapering blades tightly fused along almost entire length (Fig. 9Q–T); secondary gonopore large, located close to middle of vesica, equipped with gonopore sclerite; vestibulum of bursa copulatrix S-shaped, contrastingly long and thin (Fig. 12C–F).

Despite some habitual distinctions, the genus Salicarus in its present concept contains ten species united by the pretarsal structure, male and female genitalia. Most species of the group utilize different Fabaceae (Genista, Caragana, Halimodendron, Calicotome spp.) as hosts, although Salix spp. were documented for S. concinnus, S. roseri, and S. urnammu. The genus appears to be most closely related to Phoenicocoris due to the similar pattern of vestiture, the presence of minute spicules on dorsoapical surface of the hind femur, the apically spatulate parempodia, and the tightly coiled, apically bifid vesica with gonopore sclerite. However, Phoenicocoris spp. differ from Salicarus in having rounded posterior margin of vertex, larger pulvillum reaching half-length of claw, smaller and more tightly coiled vesica with apically bifurcating blades (Schwartz and Stonedahl 2004: figs 23, 24), and S-shaped, but thick and short vestibulum of the bursa copulatrix. Refer to Schwartz and Stonedahl (2004) for additional discussion.

Species composition. *Salicarus cavinotum* (Wagner, 1973) comb. nov. – Rhodes, Greece.

- Salicarus concinnus Putshkov, 1977 Mountains of Central Asia, Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan.
- Salicarus fulvicornis (Jakovlev, 1889) Mongolia, Altai, Buryatia, Zabaikalsky Terr. (South Siberia, Russia), Inner Mongolia (China).
- Salicarus genistae (Lindberg, 1948) comb. nov. Cyprus, Turkey.
- Salicarus halimodendri Putshkov, 1977 Kazakhstan, Uzbekistan, Mongolia.
- Salicarus nitidus (Horváth, 1905) comb. nov. Spain, Corsica, Sardinia.

- Salicarus perpusillus (Wagner, 1960) comb. nov. Spain, Corsica, Italy, Greece, Crete.
- Salicarus qiliananus (Zheng, 1996) Gansu (NW China).
- Salicarus roseri (Herrich-Schaeffer, 1838) Transeurasian species, widely distributed from Western Europe to Kamchatka except high north but absent in North Africa and Middle East, spanning south to Northern Turkey, Transcaucasia, Iran, Kazakhstan, and Mongolia.
- Salicarus urnammu Linnavuori, 1984 Iraq, Armenia, Iran.

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# **Supplementary Material 1**

#### File S1

Author: Konstantinov FV (2023) Data type: .pdf

Explanation note: USI numbers of figured specimens.

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Link: https://doi.org/asp.81.e104396.suppl1

# Supplementary Material 2

#### File S2

Author: Konstantinov FV (2023) Data type: .nex Explanation note: Morphological matrix in .nex format.

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# **Supplementary Material 3**

#### File S3

Author: Konstantinov FV (2023)

Data type: .pdf

Explanation note: Bayesian tree in .pdf format.

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Link: https://doi.org/asp.81.e104396.suppl3

# **Supplementary Material 4**

## File S4

Author: Konstantinov FV (2023)

Data type: .xlsx

Explanation note: CI and RI values scored for individual characters.

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