

Taxonomy and phylogeny of the genera *Gymnocnemia* Schneider, 1845, and *Megistopus* Rambur, 1842, with remarks on the systematization of the tribe Nemoleontini (Neuroptera, Myrmeleontidae)

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Abstract

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The delineation of antlion genera has often been based on morphological characters not tested in a phylogenetic context, thus seriously impairing the study of systematics of the family Myrmeleontidae. Nebulous generic limits also impede the taxonomy and study of the affinities of closely related species. As a case study, the generic placement of *Megistopus mirabilis* Hölzel, 1980, was based on a single leg character. To test the position of this species, the reciprocal relationships of the members of the genera *Gymnocnemia* Schneider, 1845, and *Megistopus* Rambur, 1842 were investigated, using a morphology-based phylogenetic analysis. This approach demonstrated that *M. mirabilis* should actually be assigned to the genus *Gymnocnemia*, as *G. mirabilis* **comb. n.** This analysis also supports the subdivision of the tribe Nemoleontini in two subclades based on morphology of male and female genitalia. A new characterisation of these genera is provided, as well as a redescription of the very rare *G. mirabilis* and the poorly investigated *Megistopus lucasi* (Navás, 1912). An updated identification key to the members of the genera *Gymnocnemia* and *Megistopus* is presented.

Introduction

Myrmeleontidae, commonly known as antlions, are the most species-rich family of the order Neuroptera, including 1657 described species (Oswald 2016) that are distributed in all tropical and temperate regions of the world. The Western Palearctic, including the Arabian peninsula (following the boundaries of H. Aspöck et al. 2001), harbours a relatively rich fauna with at least 285 known species (H. Aspöck et al. 2001, Oswald 2016). Despite the notable diversity and wide distribution of this family, the phylogeny of antlions has been poorly investigated and few studies have dealt with this subject in a modern quantitative approach (Badano et al. 2017, Michel et al. 2017). Moreover, one of the main problems afflicting the systematics of Myrmeleontidae is the

poor characterisation of supraspecific taxa, thus making it difficult to trace the relationships among genera and to determine the placement of certain species. In fact, most genera are based on morphological characters that have not been tested in a phylogenetic context and have doubtful systematic value, as in the case of the commonly used wing markings and wing shape. An interesting case study is represented by two closely related genera, both restricted to the Western Palearctic: *Gymnocnemia* Schneider and *Megistopus* Rambur. As the name itself implies, *Gymnocnemia* (from Greek, “naked legs”) was distinguished from *Megistopus* by Schneider (1845) due to the absence of tibial spurs. In the beginning of the 20th century, during a period of intense taxonomic activity, the genus *Gymnocnemia* became an assemblage for a number of unrelated, usually long-legged, antlions from all

the main biogeographic regions that were only grouped together due to the lack of tibial spurs. In the following years, the exotic taxa were eventually excluded and assigned to other genera. Therefore, *Gymnocnemia* was long considered monotypic, including only *G. variegata*, a widespread but uncommon Holomediterranean species, until the description of a second species from the Moroccan Atlas Mountains, *G. editaerevayae* Michel, 2013. The diagnostic character proposed by Schneider (1845) remained the main criterion to distinguish *Gymnocnemia* from *Megistopus*, whose type species is the Holomediterranean *M. flavicornis* (Rossi, 1790). Hölzel (1980) placed a new species, *Megistopus mirabilis*, from the Sinai Peninsula in the latter genus due to the presence of spurs, following an almost one and a half century-old convention. Lastly, Güsten (2003) transferred *M. lucasi*, which was originally described by Navás (1912) as a member of the genus *Nelees* Navás, 1912 (now a synonym of *Neuroleon* Navás, 1909), to *Megistopus*, although its real affinities had already been hinted at by Banks (1913). Since the specimens from Italy, which were originally identified as *M. mirabilis*, actually belong to *M. lucasi* (Letardi and Pantaleoni 1996, Badano and Pantaleoni 2014), *M. mirabilis* was only known from the holotype. Based on a study of the collection of the late Herbert Hölzel, a foremost figure in the study of Palaearctic antlions, a series of undetermined specimens from Oman belonging to this taxon was brought to the attention of the authors. After careful examination of the morphology of this species, its generic placement was questioned, and the species was considered to have closer ties to *Gymnocnemia* thus challenging the value of certain morphological characters commonly used by specialists as diagnostic at the genus level. Therefore, we performed a morphology based quantitative phylogenetic analysis to test the affinities of the members of *Gymnocnemia* and *Megistopus* and to provide a solid phylogenetic argumentation for their delimitation. The aim of the present study is to re-describe these genera, discuss their affinities and detail the morphology of the inadequately known species.

Materials and methods

Examined specimens are deposited in the following collections: collection of Davide Badano, Taggia, Italy (DB); collection of Horst and Ulrike Aspöck, Vienna, Austria (HUAC); collection of Herbert Hölzel, Natural History Museum Vienna, Austria (NHMW) (Suppl. material 1).

Specimens were examined and measured with a Leica® MZ 9.5 stereomicroscope equipped with an optical micrometre and photographed with a Canon® EOS 600D digital camera with Canon® lens MP-E 65 mm; obtained images were stacked with the software Zerene® STACKER. Specimens were measured following the protocol of Pantaleoni and Badano (2012): body length was taken from vertex to abdomen tip; wing length was

measured longitudinally from base to apex, and wingwidth was taken as the maximum width perpendicular to the length measurement line. Genitalia were macerated in 10% KOH (potassium hydroxide) at room temperature, later rinsed in acetic acid and water and finally preserved in glycerol. Terminology mainly follows Stange (1970a) for body and wing morphology and U. Aspöck and H. Aspöck (2008) for genitalia.

The distribution map was made with Natural Earth, free vector and raster map data, available at www.naturalearthdata.com.

Abbreviations used in the text: Biogeogr, biogeography; Biol, biology; Cat, catalogue; Com, comment; Distr, distribution; Key, identification key; List, checklist; ODescr, original description; Syn, synonymy.

Phylogenetic analysis

Characters and states were coded for a set of antlion taxa illustrative of morphological variability across the family. *Palpares libelluloides* Linnaeus (Palparinae) was selected as the outgroup. A data matrix including 56 characters and 121 states was prepared in MESQUITE version 3.03 (Maddison and Maddison 2015) (Suppl. material 2). Inapplicable and unknown states were coded as ‘-’ and ‘?’ respectively. Cladistic parsimony analyses were conducted with TNT version 1.5 (Goloboff and Catalano 2016). The analyses were run under equal weights, selecting the ‘traditional search’ option with the following parameters: general RAM of 1000 Mbytes, memory set to hold 1,000,000 trees, setting 1000 replicates with tree bisection-reconnection (TBR) branch swapping and saving 1000 trees per replicate. Multistate characters were treated as unordered and zero-length branches were collapsed. Unambiguous character state changes were mapped on the most parsimonious trees using WINCLADA version 1.00.08 (Nixon 2002). Bremer support values were calculated in TNT from 10,000 trees up to 10 steps longer than the shortest trees obtained from a ‘traditional search’, using the ‘trees from RAM’ setting. Consistency and retention indices were calculated in MESQUITE version 3.03 (Maddison and Maddison 2015).

List of characters and character states used in the phylogenetic analysis

1. Labial palpus: (0) short and stout; (1) extremely long and thin. The labial palpus is extremely elongated, much longer than the head width in *Palpares Rambur*.
2. Labial palpus, sensory area (palpimacula): (0) rounded; (1) slit-like. The sensory area of the apical palpomere is slit-like in *Palpares libelluloides* (see also Stange 1994).
3. Pronotum: (0) wider than long; (1) as long as wide, (2) noticeably longer than wide. The proportions of pronotum widely vary across the family. In *Palpares* it is much wider than long, while in most antlions it is subquadrate and as long as wide. In

- Dendroleontini (*Dendroleon* Brauer, *Tricholeon* Esben-Petersen) and in *G. mirabilis* the pronotum is characteristically much longer than wide (see also Stange 1994) (Fig. 2E).
4. Thorax, outstanding setae: (0) absent; (1) present. In members of the genus *Gymnocnemia*, the thorax is covered with large and robust setae (Fig. 1B).
 5. Legs: (0) short and stout; (1) long and slender. Most myrmeleontids have relatively short and robust legs. Several species of Dendroleontini, such as *Dendroleon* and *Tricholeon*, and Nemoleontini, such as *Gymnocnemia*, *Megistopus* and *Nedroledon* Navás, have very long and slender legs, with the femur at least 7 times longer than wide (Fig. 1).
 6. Legs, colour pattern: (0) similar in all legs; (1) differing in each leg pair. In members of the genus *Gymnocnemia*, pro-, meso- and metathoracic legs have a strikingly different colour pattern.
 7. Tarsus, segments 1-4: (0) T1-T4 short, of the same size; (1) T1 much longer than the others, T2-T4 short; (2) T1-T3 elongated, of the same size. In *Palpares*, tarsomeres 1-4 are of similar length and equally short. In most genera of myrmeleontids, the basal tarsomere (T1) is much longer than tarsomeres 2-4, which are short; the basal tarsomere is usually as long as tarsomeres 2 and 3 together (T2+T3). In *Megistopus*, tarsomeres 1-3 are subequal in size, equally elongated while T4 is short (Fig. 1A).
 8. Tibial spurs: (0) absent; (1) present. Tibial spurs are absent in *G. variegata* and *G. editaerevayae*.
 9. Tibial spurs (if present), length: (0) long, at least 1/3 of tarsus length; (1) short, 1/4-1/5 of tarsus length; (2) minute, 1/6 of tarsus length. Tibial spurs are relatively long (at least one third of tarsus length) in most analysed taxa; however, they are relatively short, less than one fourth of tarsus length in *Cueta lineosa* (Rambur) and *Megistopus* (Fig. 1A). In *G. mirabilis*, tibial spurs are very small, much shorter than one sixth of tarsus length (Fig. 1C).
 10. Tarsal claws: (0) not opposable; (1) opposable. In some antlions, the tarsal claws can be folded against a brush of thickened setae on the distal tarsomere. Of the analysed species, this condition is found in members of the genera *Megistopus*, *Gymnocnemia* and *Nedroledon* (Fig. 1D).
 11. Prothoracic leg: (0) similar in length to meso- and metathoracic legs; (1) longer than meso- and metathoracic legs. In *Gymnocnemia* the prothoracic leg is much longer and thinner than the following pairs (Fig. 1B).
 12. Prothoracic leg femur, hair-like sensillum (femoral sense hair *sensu* Stange 1994): (0) absent; (1) present. The hair like sensillum is a synapomorphy of subfamily Myrmeleontinae (Stange 1994).
 13. Forewing, origin of Rs: (0) 1/4 of wing length or less; (1) 1/3 of wing length; (2) 1/2 of wing length. Rs arises near wing base (1/4 of wing length) in Dendroleontini (*Dendroleon* and *Tricholeon*), while it originates distally (around 1/3 of wing length) in all the other analysed taxa. In *G. mirabilis*, Rs arises at half wing length (Fig. 4A).
 14. Forewing, vein CuP: (0) long vein, running independently from 1A for its entire length; (1) short vein, parallel to 1A for a short distance and then merging with it, (2) crossvein-like. In *Palpares* and other Palparini, CuP is not fused with 1A, rather it is a distinct vein. In most other myrmeleontids, CuP is a very short vein fusing with 1A (Fig. 5A). In *Macronemurus* Costa, CuP is further reduced and is similar to a crossvein.
 15. Forewing, vein CuP+1A: (0) convergent with wing margin; (1) parallel to wing margin. The vein CuP+1A runs toward wing margin in almost all the analysed taxa, while it is parallel to wing margin in *Dendroleon*, *Tricholeon* and *Creoleon* Tillyard.
 16. Forewing, vein 2A: (0) gently curved; (1) close to 1A, then strongly bent toward to 3A. In *Palpares*, *Dendroleon*, *Tricholeon* and *Solter* Navás, vein 2A runs as a smooth curve. In *Cueta* Navás, *Myrmeleon* Linnaeus and in the members of Nemoleontini 2A is characteristically angled (Fig. 5A) (Stange 2004).
 17. Hind wing, presectoral area: (0) 1 crossvein; (1) more than 4 crossveins. The hind wing presectoral area is crossed by one crossvein in Dendroleontini (*Dendroleon*, *Tricholeon*) and Nemoleontini (*Nemoleon* Navás, *Distoleon* Banks, *Neuroleon*, *Macronemurus*, *Creoleon*) (Fig. 5B). In the other analysed taxa (*Palpares*, *Cueta*, *Solter*, *Myrmeleon*), the presectoral area is filled by numerous crossveins.
 18. *Pilula axillaris*: (0) absent; (1) present. Among the analysed taxa, the *pilula axillaris* is absent in *Cueta* and Nemoleontini (see Discussion).
 19. Male, abdomen length: (0) as long as the wings; (1) noticeably longer than the wings. The males of several antlion genera, such as *Cueta*, *Distoleon*, *Macronemurus*, *Creoleon* and *Nedroledon*, are characterized by elongated abdomens, much longer than wings.
 20. Male gonocoxites 9 and 11: (0) not fused; (1) fused into a tube-like structure. In *Palpares* and *Cueta* gonocoxites 9 and 11 are amalgamated into a tube-like structure.
 21. Male, gonocoxites 9, relative position to gonocoxites 11 (if not fused): (0) ventro-caudal to gonocoxites 11; (1) partly encircling gonocoxites 11. In *G. variegata* and *G. editaerevayae*, the proximal part of gonocoxites 9 characteristically curves upward, partly surrounding gonocoxites 11 in lateral view (Fig. 8B).
 22. Male, gonocoxites 9, shape: (0) plate-like; (1) fused in a Y-shaped structure; (2) fused in an upward hook-shaped structure. In ventro-caudal view, the apex of gonocoxites 9 appears as paired sclerotized plate-like structures in most myrmeleontid

- taxa. In several genera of Nemoleontini, including *Nemoleon*, *Distoleon*, *Neuroleon*, *Macronemurus*, *Creoleon*, gonocoxites 9 are fused into a structure resembling a “Y”, with a ventral projection and two processes curved upward (Fig. 8H). In *Cueta*, gonocoxites 9 are merged into a hook-like structure.
23. Male, gonocoxites 9 (if plate-like), relative position: (0) parallel; (1) oblique, converging apically. In ventro-caudal view, the plate-like apices of gonocoxites 9 are parallel to each other in *Palpares*, *Solter* and *Gymnocnemia* (Fig. 8A). In contrast, in *Dendroleon*, *Tricholeon*, *Megistopus* and *Nedroledon* they converge apically (Fig. 8C, E, G). This character is not applicable to taxa with fused gonocoxites 9.
24. Male, ectoproct, ventrocaudal projections: (0) absent; (1) present. In the males of several antlion genera, including *Palpares*, *Cueta*, *Macronemurus*, *Nedroledon*, and *Nemoleon*, the ectoproct is equipped with a posterior “clasper-like” processus (Fig. 8G, H).
25. Male ectoproct, length of ventrocaudal projection (if present): (0) short, as long or slightly longer than ectoproct; (1) extremely long, much longer than ectoproct. The posterior projections of ectoproct are short in *Cueta*, while they are extremely long in *Palpares*, *Macronemurus* and *Nemoleon* (Fig. 8H). In *Nedroledon* both conditions are present: *N. anaticus* Navás and *N. iranensis* Hölzel have short processes (Fig. 8G), while *N. striatus* Hölzel is characterized by a long and narrow processes.
26. Female, process on segment 8: (0) absent; (1) present. In the female of several myrmeleontid genera, on the segment 8, proximal to gonocoxites 8 or at their base a pair of setiferous processes is present, usually termed “anterior gonapophyses” (e.g. Stange 1994). However, these processes are not homologous with the actual gonapophyses 8, and they are not as sclerotized as gonocoxites 8 (see also U. Aspöck and H. Aspöck 2008). Therefore, we presently term these structures as processes of segment 8 to distinguish them from the genital sclerites, gonocoxites or gonapophyses. Of the analysed taxa, they are present in *Dendroleon*, *Tricholeon* and *Myrmeleon*.
27. Female, gonocoxite 7: (0) absent; (1) present. The gonocoxite 7 (praegenitale of authors, see Stange 1994) is absent in *Palpares libelluloides*, *Cueta lineosa* and the nemoleontine genera *Nemoleon*, *Distoleon*, *Neuroleon*, *Macronemurus* and *Creoleon*. This structure is present as a roughly triangular sclerite in *Myrmeleon*, *Dendroleon*, *Tricholeon*, *Gymnocnemia*, *Megistopus* and *Nedroledon* (Fig. 9).
28. Female, gonocoxites 8: (0) not prominent; (1) short, 3–4 times longer than wide; (2) long, digitiform, over 5 times longer than wide. The gonocoxites 8 (posterior gonapophyses *sensu* Stange 1970a, 1994) are not prominent in *Palpares*, while they are longer than wide in all other analysed genera. Gonocoxites 8 are relatively short in *Cueta*, *Solter*, *Myrmeleon*, *Nemoleon*, *Distoleon*, *Neuroleon*, *Macronemurus* and *Creoleon*. In contrast, they are much longer than wide in *Dendroleon*, *Tricholeon*, *Gymnocnemia*, *Megistopus* and *Nedroledon* (Figs 7B, 9).
29. Female, processes on segment 9: (0) absent; (1) present. Setiferous processes at base of gonocoxites 9 are present in the analysed species of *Cueta*, *Dendroleon* and *Tricholeon*.
30. Female, gonocoxites 9, chaetotaxy: (0) only thin setae; (1) stout setae present. Gonocoxites 9 are only covered with thin setae in *Dendroleon* and *Tricholeon*, while the remaining analysed genera are characterised by the presence of stout digging setae. (Figs 7B, 9).
31. Female, ectoproct, chaetotaxy: (0) only thin setae; (1) stout setae present. The female ectoprocts are only covered with thin setae in *Cueta*, *Solter*, *Dendroleon* and *Tricholeon*, while all other analysed genera are provided with stout digging setae.
32. Larva, chaetotaxy of the dorsal side of the head capsule: (0) sensilla mainly bristle-like; (1) sensilla mainly dolichasters; (2) sensilla scale-like. See Badano et al. (2017).
33. Larva, ocular tubercle, size: (0) large; (1) small. See Badano et al. (2017).
34. Larva, upward bending of mandible: (0) not bent, i.e. straight; (1) bent upward. See Badano et al. (2017).
35. Larva, fringe of extremely long setae on lateral side of the mandible: (0) absent; (1) present. See Badano et al. (2017).
36. Larva, mesothoracic spiracle: (0) not raised; (1) raised. See Badano et al. (2017).
37. Larva, metanotum tuft of setae: (0) absent; (1) present. See Badano et al. (2017).
38. Larva, anterior mesothoracic setiferous process, type: (0) scoli-like; (1) small protuberance. See Badano et al. (2017).
39. Larva, posterior mesothoracic setiferous process: (0) scoli-like; (1) tubercle-like. See Badano et al. (2017).
40. Larva, anterior metathoracic setiferous process, type: (0) scoli-like; (1) tubercle-like; (2) small protuberance. See Badano et al. (2017).
41. Larva, fringe of elongated setae on meso- and metathoracic legs: (0) absent; (1) present. See Badano et al. (2017).
42. Larva, abdominal segment 9, shape: (0) longer than wide; (1) wider than long. See Badano et al. (2017).
43. Larva, abdominal sternite 9, specialized digging setae on ventral surface: (0) absent; (1) present. See Badano et al. (2017).
44. Larva, abdominal sternite 9, specialized digging setae (if present), number and pattern: (0) one line of 2–4 narrow digging setae at the base of rastra;

- (1) six stout digging setae arranged into a X-shaped pattern; (2) one or two transversal rows of stout digging setae. See Badano et al. (2017).
45. Larva, rastra: (0) absent; (1) present. See Badano et al. (2017).
 46. Larva, rastra (if present), size: (0) very small, not prominent; (1) prominent and sclerotized.
 47. Larva, rastra (if present), digging setae: (0) fused; (1) unfused. See Badano et al. (2017).
 48. Larva, rastra (if present), relative dimensions of digging setae: (0) subequal in size; (1) medial pair distinctly smaller than lateral ones. See Badano et al. (2017).

Results

Phylogenetic analysis

The cladistic analysis yielded two most parsimonious trees with a tree length of 83 steps, a consistency index (CI) of 0.687 and a retention index (RI) of 0.752. One of the two most parsimonious trees was selected to map inferred character changes and is shown in Fig. 10. The two obtained trees uniquely differ in the reciprocal relationships among the species of *Gymnocnemia*. The strict consensus cladogram with Bremer support values is shown in Fig. 11. Two main clades, A and D, emerged from the analysis. Clade A was based on two nonhomoplasious apomorphies (31:0, chaetotaxy of female ectoproct as thin setae; 36:0, larva with mesothoracic spiracle not raised), obtaining a Bremer support value of 1. Within this clade, *Dendroleontini* (clade B), including *Dendroleon* and *Tricholeon*, were strongly supported as monophyletic based on six nonhomoplasious apomorphies (13:0, origin of forewing Rs at ¼ of wing length; 30:0, chaetotaxy of female ectoproct as thin setae; 37:1, larva with a tuft of setae on metanotum; 42:0, larva with abdominal segment 9 longer than wide; 43:0, larva with abdominal segment 9 devoid of specialized digging setae; 45:0, larva without rastra) and seven homoplasious apomorphies (3:2; 5:1; 15:1; 23:1; 26:1; 29:1; 34:1) and garnered a Bremer support value of 9. *Solter* (Myrmecaelurini *sensu* Stange 2004), *Cueta* (Nesoleontini) and *Myrmeleon* (Myrmeleontini) grouped in clade C, which relied on two nonhomoplasious apomorphies (33:1, larva with small ocular tubercles; 41:1, larva with a fringe of elongated setae on meso- and metathoracic legs) and received a Bremer support value of 1. Within the latter group, a sister relationship between *Cueta lineosa* and *Myrmeleon inconspicuus* Rambur was based on five nonhomoplasious apomorphies (32:0, larva with dorsal side of the head capsule covered with bristle-like sensilla; 35:1, larva with a fringe of very long setae on the lateral side of the mandible; 38:1, larva with the anterior mesothoracic setiferous process as a small protuberance; 40:2, larva with the anterior metathoracic setiferous process as a small protuberance; 48:0, larva with digging setae of ra-

stra subequal in size) and one homoplasious apomorphy (16:1) and obtained a Bremer support value of 1. Clade D, corresponding to the tribe Nemoleontini *sensu* Stange (2004) was reconstructed as monophyletic based on two homoplasious apomorphies (16:1; 18:0) and garnered a Bremer support value of 1. Nemoleontini were divided in two subclades E and G. Clade E was supported by one nonhomoplasious apomorphy (22:1, male gonocoxites 9 fused in a Y-shaped structure) and retrieved a Bremer support value of 1. The relationships within the latter group remained poorly resolved with a polytomy including *Distoleon tetragrammicus* (Fabricius), *Neuroleon arenarius* Navás and a group (clade F) formed by *Creoleon lugdunensis* (Villers) + (*Nemoleon notatus* (Rambur) + *Macronemurus appendiculatus* (Latreille)). The latter clade was corroborated by just one homoplasious apomorphy (19:1), and the sister relationship between *Nemoleon* and *Macronemurus* likewise relied on one homoplasious apomorphy (24:1).

Clade G was supported by one nonhomoplasious apomorphy (10:1, tarsal claws opposable) and one homoplasious apomorphy (5:1) with a Bremer support value of 1. Within the latter group, the genus *Megistopus* broke up as polyphyletic with “*Megistopus*” *mirabilis* forming a clade (clade H) with the members of the genus *Gymnocnemia*. The monophyly of this genus (“*M.*” *mirabilis* + (*G. variegata* + *G. editaerevayae*)), relied on three nonhomoplasious apomorphies (4:1, thorax with outstanding setae; 6:1, leg colour pattern differing in each leg pair; 11:1, prothoracic leg longer than meso- and metathoracic legs) and obtained a Bremer support value of 3. A sister relationship between *G. variegata* and *G. editaerevayae* was retrieved based on one nonhomoplasious apomorphy (8:0, tibial spurs absent). Clade I, composed by the species of *Megistopus* (exclusive of “*M.*” *mirabilis*) and *Nedroledon* was supported by just one homoplasious apomorphy (23:1) with a Bremer support value of 1. A clade composed by *M. flavicornis* and *M. lucasi* (clade J) was reconstructed as monophyletic based on one nonhomoplasious apomorphy (7:2, tarsomeres T1–T4 elongated, of the same size) and one homoplasious apomorphy (9:1) and garnered a Bremer support value of 2. The genus *Nedroledon* (clade K), whose monophyly was supported by one homoplasious apomorphy (24:1), received a Bremer support value of 1. *N. anatolicus* and *N. iranensis* were recovered as sister taxa based on one homoplasious apomorphy (25:0).

Systematics

The genus *Gymnocnemia* was recently revised by Michel (2013) on the occasion of the description of *G. editaerevayae*, while Badano and Pantaleoni (2014) detailed the larval morphology of *Gymnocnemia*, as well as *Megistopus* highlighting the importance of larval characters in systematics. Therefore, we focused on the species that are least known and on how they influence the delimitation of genera and recognition of species.

Gymnocnemia Schneider, 1845

Gymnocnemia Schneider, 1845: 343.

Type species *Megistopus variegatus* Schneider, 1845.

Aplectrocnemus Costa, 1855: 18.

Type species *Aplectrocnemus multipunctatus* Costa, 1855 (Syn).

Comprised species. *G. variegata*, *G. editaerevayae*, and *G. mirabilis*.

Recognition. Thorax covered with robust, outstanding setae. Legs extremely long and thin. Prothoracic leg much longer and slender than meso- and metathoracic legs. Femora differing in pattern: prothoracic femur with small dark dots, mesothoracic femur with two parallel dark stripes, metathoracic femur with an apical dark marking. Tibial spurs absent (*G. variegata*, *G. editaerevayae*) or present (*G. mirabilis*). Tarsomeres 1–4 of prothoracic leg differentiated in size, with the first (basal) tarsomere at least as long as one and a half times the second tarsomere. Tarsal claws opposable, closing against a brush of thickened setae on the fifth tarsomere. Male (based on *G. variegata* and *G. editaerevayae*): ectoproct rounded, gonocoxites 11 arch-like, gonocoxites 9 partly encircling gonocoxites, 11 plate-like in shape. Female: gonocoxite 7 tooth-like, gonocoxites 8 digitiform, gonocoxites 9 covered with digging setae, ectoproct provided with digging setae.

Larval morphology (based on *G. variegata*). Mandible long and slender, provided with 3 teeth of which the apical and median are subequal in size. Ocular tubercle prominent. Mesothoracic spiracle raised on tubercle. Meso- and metathoracic setiferous processes scolus-like. Odontoid processes atrophied. Rastra with the internal pair of digging setae smaller than the others (Cesaroni et al. 2010, Badano and Pantaleoni 2014).

Gymnocnemia variegata (Schneider, 1845)

Figs 1B, 2A–C, 3A, 4B, 8A–B, 9A–B

Diagnosis. Medium-sized antlion with a variegated habitus, with an alternating ochre and dark brown pattern. Forewing Rs at half the wing length with at least 8 crossveins. Thorax covered with outstanding black and white setae. Tibia without spurs. Tarsus shorter than tibia.

Variability. (Based on examination of 7 males and 8 females, see Suppl. material 1)

G. variegata is a widely distributed but exceedingly localized species ranging from the Mediterranean to Central Asia (H. Aspöck and Hölzel 1996, H. Aspöck et al. 2001, Stange, 2004, Krivokhatsky 2011, Michel, 2013, Monserrat and Acevedo, 2013, Badano and Pantaleoni 2014, U. Aspöck et al. 2015, Kral and Devetak 2016). Despite a recent and exhaustive re-description (Michel 2013), the variability of this myrmeleontid remains unstudied, potentially confusing its identification. Indeed, *G. variegata* is a highly variable species with distinct pale and dark morphs, differing in the dimension and

shape of body markings. The pale morph is characterized by a sand-like body colour with relatively small brown markings. In this form, the vertex has small paired dots, while the pronotum is characterized by two pale spots per side and brown lateral margin (Fig. 2A). On the contrary, the dark morph has a darker tinge and the markings are much more contrasted and developed, resulting in an overall dark habitus. In particular, the pronotal markings blend with each other forming one dark brown stripe per side, while the brown marking on the lateral margin is larger and more evident (Fig. 2B). In exceptionally dark specimens, the dark markings on the vertex are fused in a transversal band, while the pronotum appears mostly dark with a very large stripe per side (Fig. 2C). The body pattern of the closely related *G. editaerevayae* falls in the variability range of *G. variegata*, thus the two species are best set apart on wing and genital characters (Fig. 2D) (Michel 2013).

Gymnocnemia mirabilis (Hölzel, 1980) comb. n.

Figs 1C–D, 2E, 3B, 4A, 6A, 7C–D

Megistopus mirabilis Hölzel, 1980 (ODescr): H. Aspöck and Hölzel 1996 (List), H. Aspöck et al. 2001 (Cat), Stange 2004 (Cat).

Diagnosis. Small-sized antlion with a variegated habitus, with an alternating ochre and dark brown pattern. Wing venation sparse. Forewing Rs at half the wing length, with few crossveins. Thorax and prothoracic leg covered with prominent white setae. Tarsus exceptionally elongated, longer than tibia.

Examined specimens. Oman 18.VIII.1988 / Wadi Bani Kharus / Al Misra / M.J. Ebejer, 1 ♀ (NHMW). Oman: JABAL SHAMS / 23°14'N, 57°14'E 1900M / 3Jul95 BSKule, 4 ♀, 1 ex. (NHMW); OMAN: Jabal Shams / Wadi Dar Sawda, 1865 m / 23°14'N, 57°12'E, 20.X.95 / to light, MD Gallagher, 1 ♀ (NHMW).

Redescription. Colouration. Vertex ochre dorsally and darker anteriorly. Frons dark brown. Clypeus dark brown with the ventral margin ochre. Labrum brown. Genae light brown. Maxillary and labial palpi ochre (Fig. 3B). Antennae light brown with dark brown scape and pedicel, basal antennomeres darker. Pronotum ochre, dorsal side with two dark brown stripes connected with the dark lateral margins (Fig. 2E). Mesonotum ochre medially, dark brown laterally; mesoscutellum with paired dark markings. Metanotum dark brown with a median, light brown stripe (Fig. 6A). Prothoracic leg ochre, femur and tibia dotted, tarsus ochre (Fig. 1C). Mesothoracic leg ochre, femur with parallel dark stripes, tibia dotted with the internal side dark brown. Metathoracic leg ochre, femur with a distal dark marking, tibia dotted. Wings hyaline, venation brown with alternating pale dashes. Pterostigma whitish, proximally with a faint brown marking. Forewing gradates with a faint dark marking. Cubital mark very faint (Fig. 4A). Abdomen with a variegated dark brown and

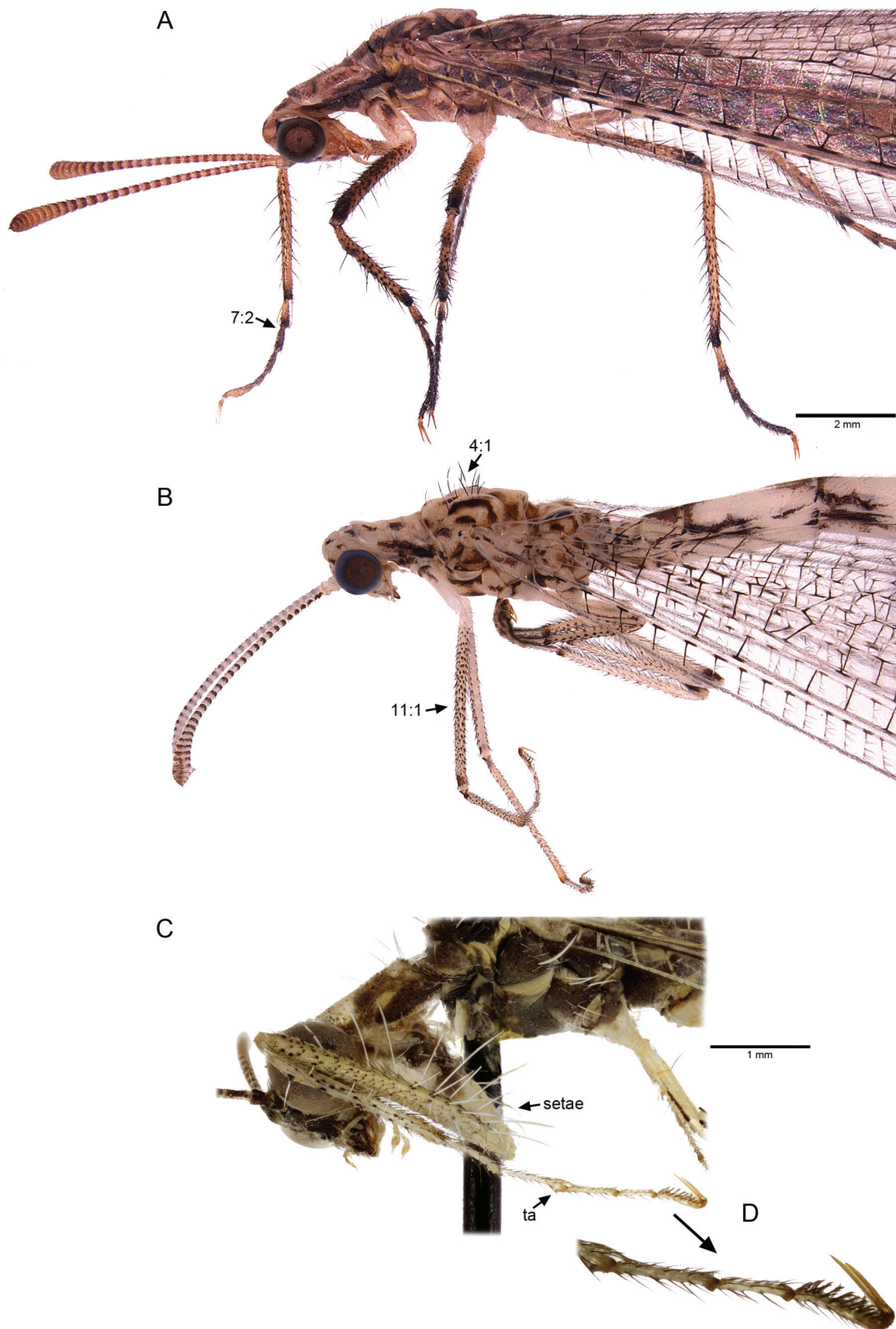


Figure 1. *Gymnocnemia* and *Megistopus*, habitus and details of thorax, lateral view. **A** *Megistopus lucasi* [Italy, Sardinia]; **B** *Gymnocnemia variegata* [Greece, Corfu]; **C–D** *Gymnocnemia mirabilis* [Oman, Jabal Shams], **C** thorax and prothoracic leg, **D** tarsus. Numbers indicate morphological characters of the data matrix and their state. Abbreviation: **ta** – tarsus.

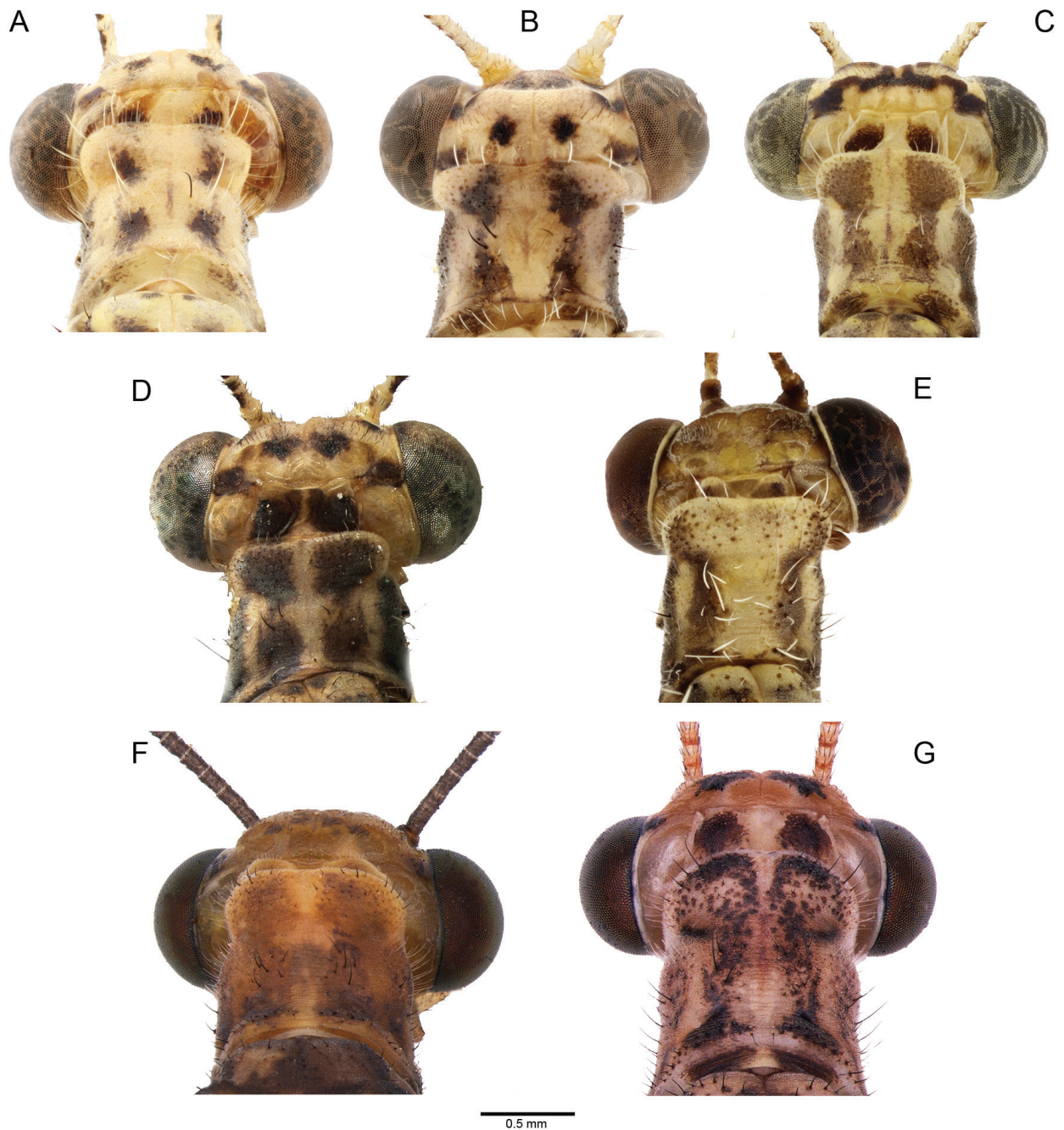


Figure 2. Head and pronotum of *Gymnocnemia* and *Megistopus*, dorsal view. **A–C** *Gymnocnemia variegata*, variability, **A** Italy, Lazio, Rome [type locality], **B** Slovenia, **C** Italy, Sardinia; **D** *Gymnocnemia editaerevayae*, holotype [Morocco, High Atlas] (Photo: B. Michel, CBGP); **E** *Gymnocnemia mirabilis* [Oman, Jabal Shams]; **F** *Megistopus flavicornis* [France, Gard]; **G** *Megistopus lucasi* [Italy, Sardinia].

ochre pattern, tergites dark brown with a dorsal ochre marking, sternites brown.

Dimensions (based on 5 specimens). Average body length 14.62 mm (min-max 14.02–15.23); forewing length 18.06 mm (16.66–18.25), ratio width/length 0.23; hind wing length 17.05 mm (15.39–19.04), ratio width/length 0.21.

Head. Vertex with a slightly raised transversal ridge (Fig. 2E). Labial palpi with distal palpomere fusiform,

palpimacula elliptical. Antenna clavate. Antennal chaetotaxy constituted by short black setae.

Thorax. Pronotum slightly longer than wide. Pronotum and mesonotum covered with white outstanding setae (Fig. 2E). Legs very long and slender. Tarsus of pro-, meso- and metathoracic legs much longer than tibia (Fig. 1C). Tibial spur present, minute, less than half the length of first tarsomere. Femur and tibia of prothoracic

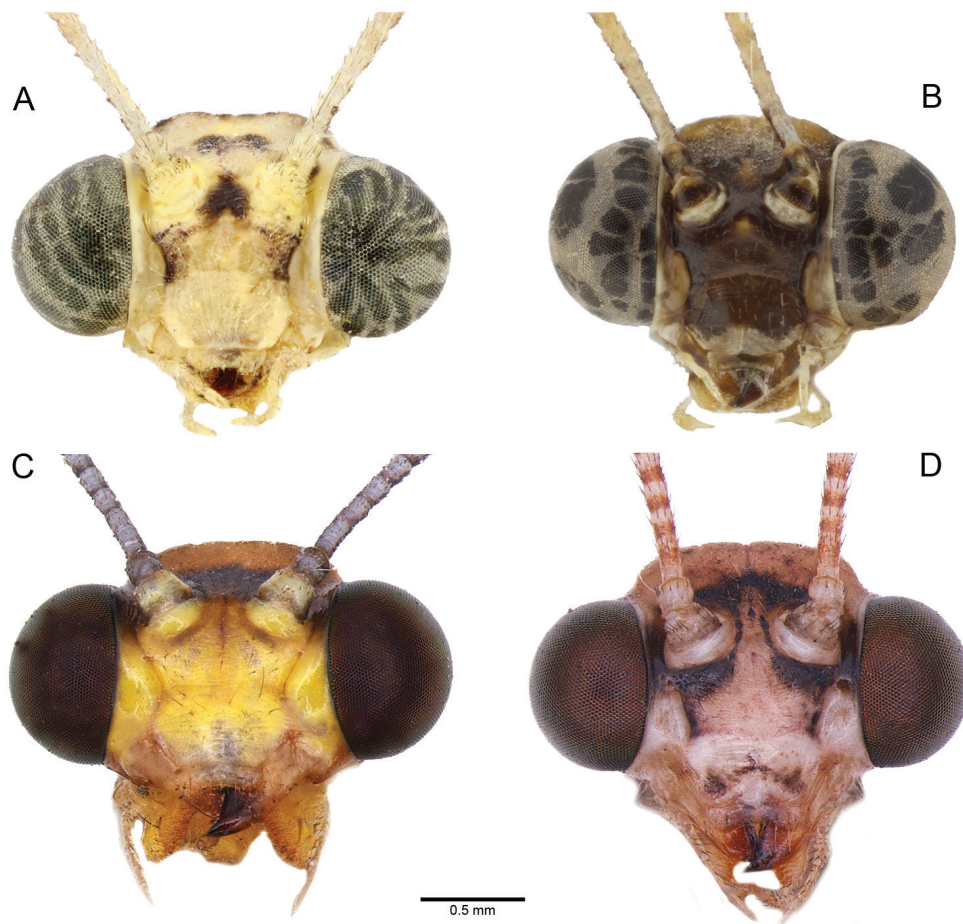


Figure 3. Head of *Gymnocnemia* and *Megistopus*, frontal view. **A** *Gymnocnemia variegata* [Italy, Sardinia]; **B** *Gymnocnemia mirabilis* [Oman, Jabal Shams]; **C** *Megistopus flavicornis* [France, Gard]; **D** *Megistopus lucasi* [Italy, Sardinia].

leg covered with white outstanding setae, similar to those on thorax, arranged in a comb-like row (Fig. 1C). Tarsus of prothoracic leg, one and a half time as long as tibia.

Wings. Relatively narrow with an acute apex (Figs 4A, 6A). Venation relatively sparse. Forewing with 7–8 presectoral crossveins. Radius sector arising at half of forewing length, distinctly distal to Cubital fork. Rs with few, well-spaced crossveins (4–6). Branches of the Cubital fork divergent. CuP + 1A gently converging with wing margin but not abruptly. Hind wing with 1 presectoral crossvein (Figs 4A, 6A).

Female genitalia. As for genus. Gonocoxite 7 relatively large and sclerotized, tooth-like in shape. Gonocoxites 8 covered with thin black setae. Gonapophyses 8 narrow, ribbon-like. Ectoproct with a short ventrocaudal projection, ventral side covered with stout setae.

Male. Unknown.

Distribution. The species was originally described from a single specimen found in the Sinai Peninsula (Egypt). The examined specimens are the first records of this species from Oman and the Arabian Peninsula, which significantly expands the known area of distribution (Fig. 12).

Megistopus Rambur, 1842

Megistopus Rambur, 1842: 343. Type species *Megistopus bisignatus* Rambur, 1842, by monotypy.

Recognition. Legs long and slender, not abruptly differentiated in size. Tibial spurs as long as the first tarsomere. Tarsomeres 1–3 of prothoracic leg of similar size, tarsomere 4 shorter than the others. Tarsal claws opposable. Male: ectoproct rounded, gonocoxites 11 arch-like, gonocoxites 9 plate-like, converging apically. Female: gonocoxite 7 tooth-like, gonocoxites 8 digitiform, gonocoxites 9 provided with digging setae, ectoproct equipped with digging setae.

Larval diagnosis. Mandible relatively long, armed with 3 teeth. Ocular tubercle prominent. Mesothoracic spiracle raised on tubercle. Mesothoracic setiferous processes scoli-like, metathoracic processes tubercle-like. Odontoid processes atrophied or absent. Rastra with the internal pair of digging setae less than 1/4 the length of the others (Steffan 1965, Cesaroni et al. 2010, Badano and Pantaleoni 2014). The larva of *M. flavicornis* is characterized by prominent abdominal spiracles, while *M. lucasi* has sessile spiracles (Badano and Pantaleoni 2014).

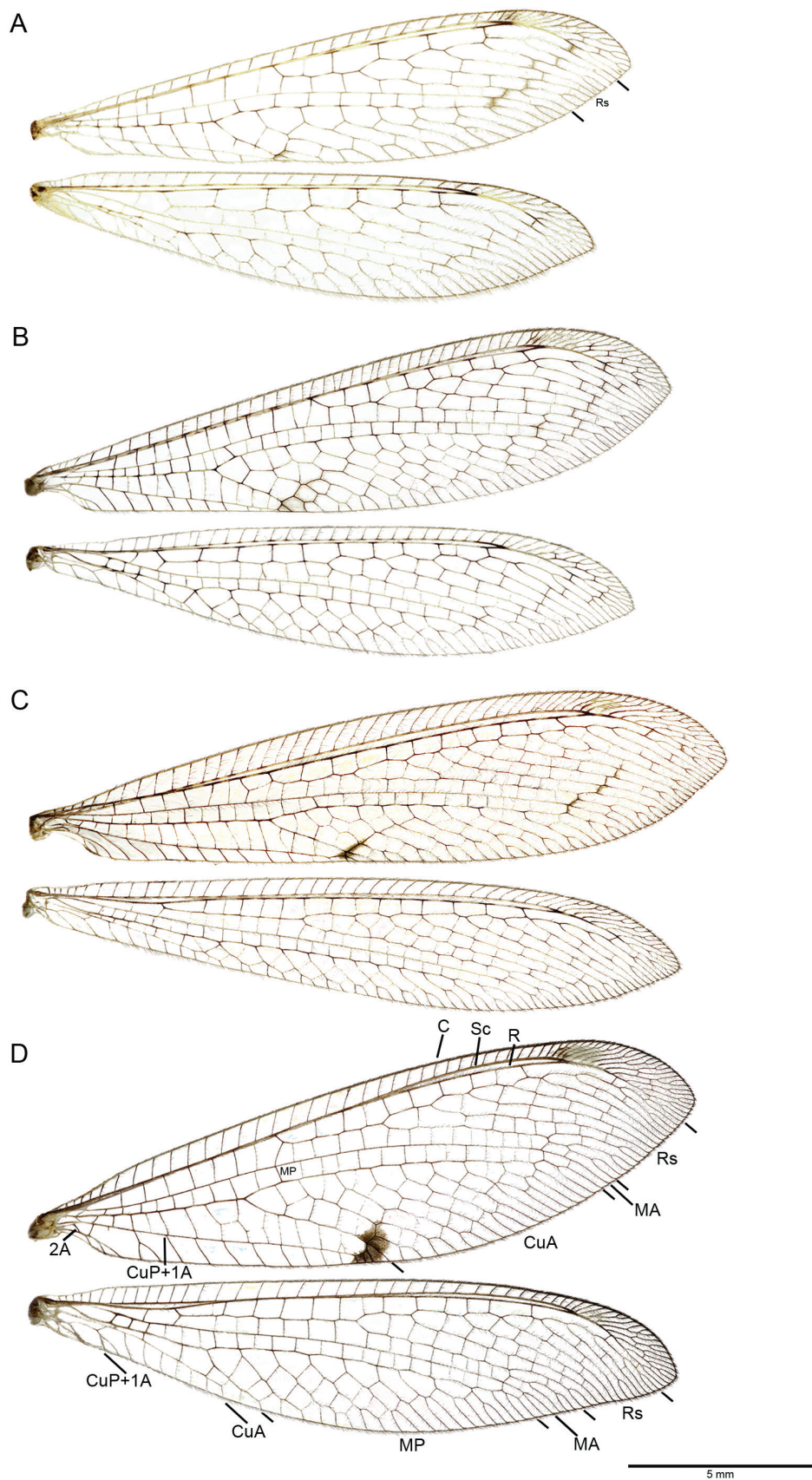


Figure 4. Wings of *Gymnocnemia* and *Megistopus*. **A** *Gymnocnemia mirabilis* [Oman, Jabal Shams]; **B** *Gymnocnemia variegata* [Italy, Lazio, Rome, type locality]; **C** *Megistopus lucasi* [Italy, Sardinia]; **D** *Megistopus flavicornis* [France, Gard]. Abbreviations: C – Costa, Sc – Subcosta, R – Radius, Rs – Radius sector, MA – Media anterior, MP – Media posterior, CuA – Cubitus anterior, CuP – Cubitus posterior, A – Anal vein.

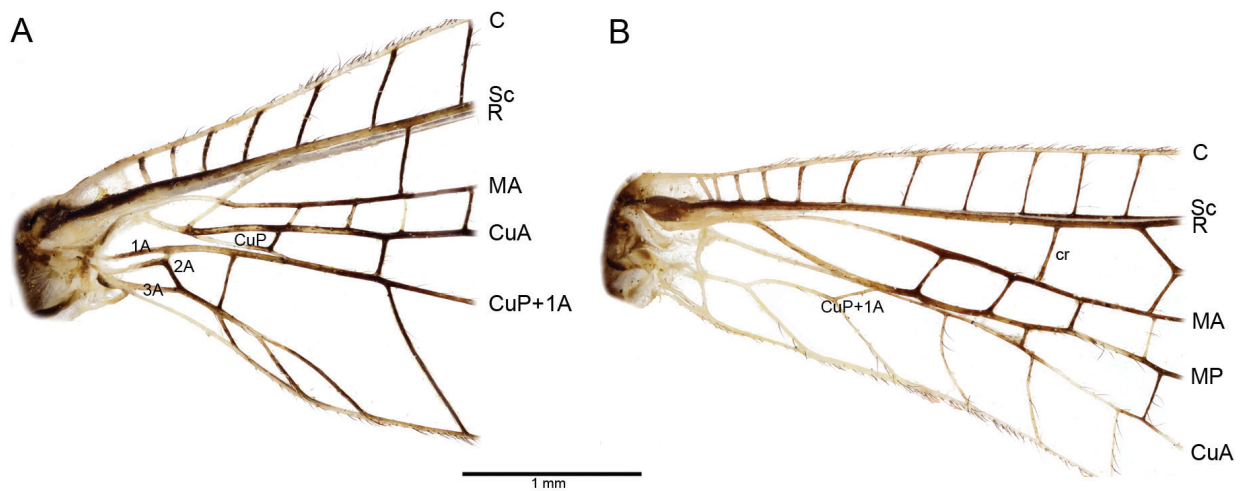


Figure 5. Base of fore- and hindwing of *Megistopus*, showing diagnostic wing characters of Nemoleontini. **A** forewing of *Megistopus flavicornis* [Italy, Liguria]; **B** hindwing of same specimen. Abbreviations: **C** – Costa, **Sc** – Subcosta, **R** – Radius, **Rs** – Radius sector, **MA** – Media anterior, **MP** – Media posterior, **CuA** – Cubitus anterior, **CuP** – Cubitus posterior, **A** – Anal vein, **cr** – presectoral crossvein.



Figure 6. *Gymnocnemia* spp., holotypes, dorsal view. **A** *Gymnocnemia mirabilis* [Sinai, Shreg]; **B** *Gymnocnemia editaerevayae* [Morocco, High Atlas, Oukaimeden] (Photo: B. Michel, CBGP).

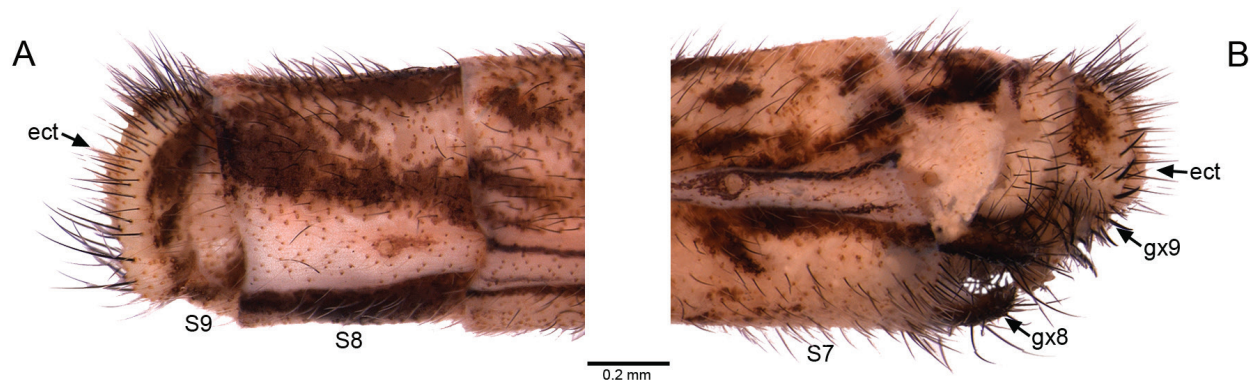


Figure 7. *Megistopus lucasi*: male and female terminalia, lateral view. **A** male [Italy, Sardinia]; **B** female [Italy, Sardinia]. Abbreviations: **ect** – ectoproct, **S9** – sternite 9, **gx9** – gonocoxite 9, **S8** – sternite 8, **gx8** – gonocoxite 8, **S7** – sternite 7.

Megistopus lucasi (Navás, 1912)

Figs 1A, 2G, 3D, 4C, 7, 8C–D

Nelees lucasi Navás, 1912 (ODescr): Banks 1913 (Com).

Neuroleon lucasi (Navás, 1912): H. Aspöck and Hölzel 1996 (Distr), H. Aspöck et al. 2001 (Cat), Stange 2004 (Cat).

Megistopus mirabilis Hölzel, 1980 (misidentification): [Bernardi] Iori et al. 1995 (List), Letardi and Pantaleoni 1996 (Distr), Letardi 1998 (Distr), Letardi 2006 (Distr), Popov and Letardi 2010 (Biogeogr), U. Aspöck et al. 2015 (List).

Megistopus lucasi (Navás, 1912): Güsten 2003 (Distr, Com), Badano and Pantaleoni 2014 (Biol), Letardi 2016 (Key), Badano et al. 2017 (photo).

Diagnosis. Medium-sized antlion with a mottled light and dark brown body pattern. Wings relatively narrow. Forewing Rs arising at the height of Cubital fork. Forewing gradates shaded with brown, cubital mark brown.

Examined specimens. Italy: Sardinia, Torre dei Corsari, 39°41'017"N 8°27'044"E, 28.V.2003, 50 m, H. and U. Aspöck and R.A. Pantaleoni leg, 3 ♀ (HUAC); Italy: Sardinia, Arbus (Oristano) / Torre dei Corsari, 39°41'23.09"N 8°27'14.50"E, coastal sand dunes /V.2010 D. Badano leg, 1 ♀ ex larva (DB); Italy: Sardinia, Arbus (Oristano)/ Torre dei Corsari, 39°41'23.09"N 8°27'14.50"E, coastal sand dunes /V.2011 D. Badano leg, 1 ♂ ex larva; Italy: Sardinia/ Chia (Cagliari), beach, XI.2011 (D. Badano), 1 ♂ ex larva (DB).

Redescription. Colouration. Vertex ochre with paired dark markings. Paired blackish markings extend from the anterior margin of the vertex to the lateral margins of the frons, surrounding the base of the antenna. Frons light brown, except the lateral margins. Clypeus light brown with suffused dark markings. Labrum brown. Genae, maxillary and labial palpi testaceous. Antennae light brown, scape with dark brown suffusions, antennomeres darker basally (Fig. 3D). Pronotum ochre, dorsal side with paired dark brown, variegated stripes connecting the dark brown anterior and posterior margins; lateral margins mottled (Fig. 2G). Mesothoracic proscutum light brown anteriorly, pos-

terior margins dark brown. Mesoscutum and mesoscutellum light brown with dark brown margins. Metathoracic proscutum brown with lighter margins. Metascutum and metascutellum with dark brown margins. Leg ochre, femur and tibia dotted (more thickly on the dorsal side) and with a dark marking near the articulation, tarsus ochre, darker near the articulation (Fig. 1A). Wings hyaline, venation brown with alternating pale dashes. Pterostigma whitish, with a faint brown proximal marking. Forewing gradates with a dark shade. Cubital mark elongated and clearly distinct (Fig. 4C). Abdomen mainly ochre, tergites with a darker median stripe on the anterior half and small darker spots on the margins. Abdomen covered with white and dark setae.

Dimensions (based on 2 specimens). Body length 20.31, 26.66 mm; forewing length 21.43, 26.61 mm, ratio width/length 0.24; hind wing length 20.8, 25.87 mm, ratio width/length 0.20.

Head. Vertex slightly inflated. Distal palpomere of labial palpi fusiform, relatively thin, palpmacula elliptical. Antennae clavate.

Thorax. Pronotum longer than wide (Fig. 2G). Thorax covered with short black setae. Legs extremely long and slender. Tibial spurs as long as the first tarsomere. Wings: relatively narrow with a rounded apex. Forewing costal area slightly wider at middle length. Forewing with ca. 6 presectoral crossveins. Origin of Radius sector at the same height of Cubital fork. Rs with more than ten crossveins. Branches of the Cubital fork divergent. CuP + 1A gently running toward the posterior wing margin but not abruptly. 2A gently curved before merging with 3A. Hind wing with 1 presectoral crossvein (Fig. 4C).

Male genitalia. As for genus. Gonocoxites 9 plate-like, converging apically (Fig. 8C). Ectoproct shell-like, ochre with a dark marking, covered with thin black setae (Fig. 7A).

Female genitalia. As for genus. Gonocoxites 8 dark brown, covered with thin black setae. Gonocoxites 9 and ectoproct covered with sparse stout setae (Fig. 7B).

Distribution. The species is only known from few coastal localities of Algeria, Tunisia and Italy (Lazio and Sardinia) (Letardi and Pantaleoni 1996 [*sub M. mirabilis*], Güsten 2003, Badano and Pantaleoni 2014) (Fig. 12).

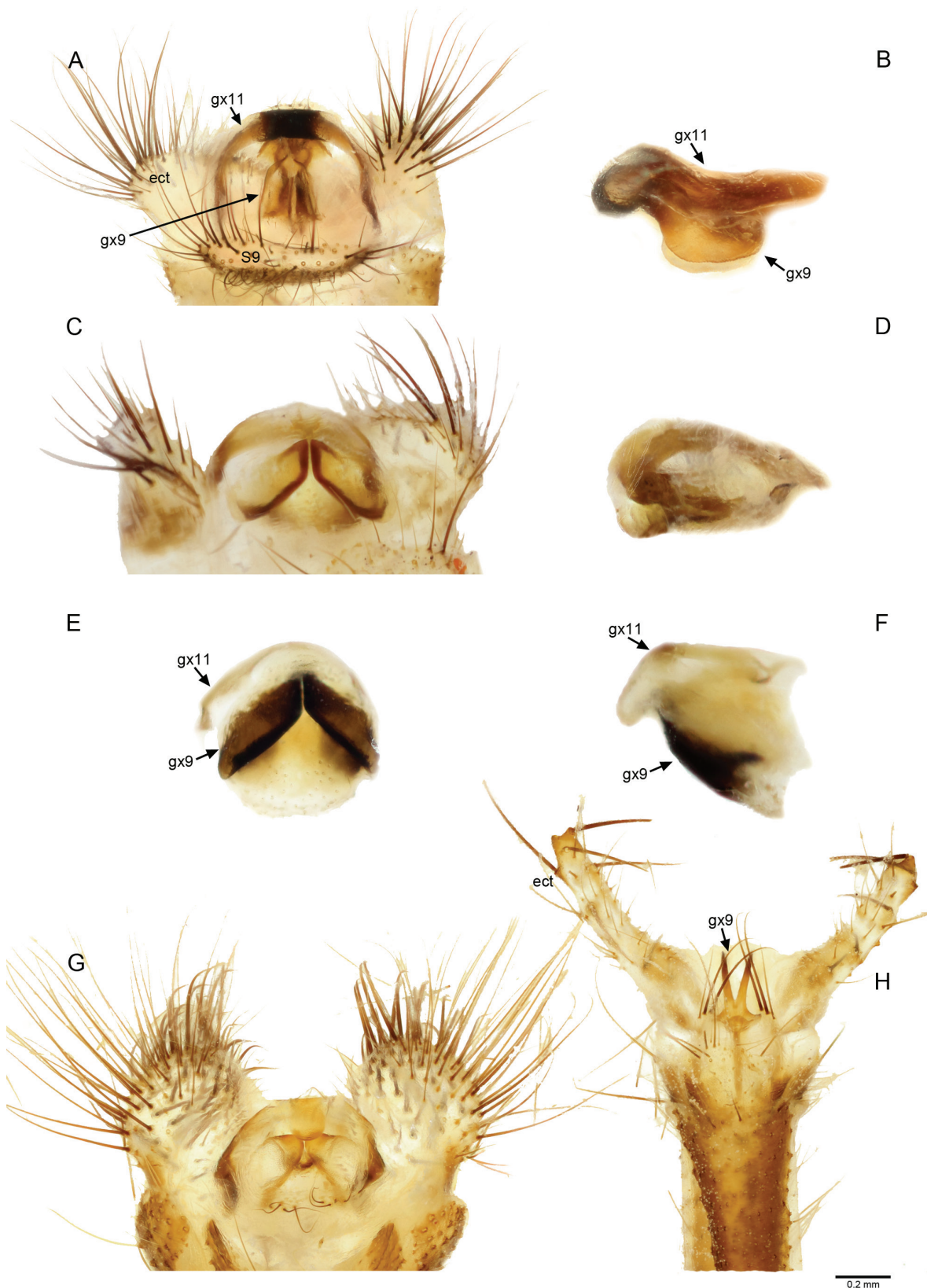


Figure 8. Male genitalia of Nemoleontini, complex of gonocoxites 9 + gonocoxites 11 *sensu* U. Aspöck and H. Aspöck (2008) (=gonarcus-parameres complex *sensu* H. Aspöck et al. 1980). **A–B** *Gymnocnemia variegata* [Greece, Corfu], **A** apex of abdomen, ventral view, **B** gx 9 + gx 11, lateral view; **C–D** *Megistopus lucasi* [Italy, Sardinia], **C** apex of abdomen, ventral view, **D** gx 9 + gx 11, lateral view; **E–F** *Megistopus flavicornis* [France, Gard], gx 9 + gx 11, **E** ventral view, **F** lateral view; **G** *Nedroledon iranensis* (Hölzel, 1972) [Iran], apex of abdomen, ventral view; **H** *Nemoleon notatus* [Italy, Sardinia], apex of abdomen, ventral view. Abbreviations: **ect** – ectoproct, **gx9** – gonocoxite 9, **gx11** – gonocoxite 11, **S9** – sternite 9.

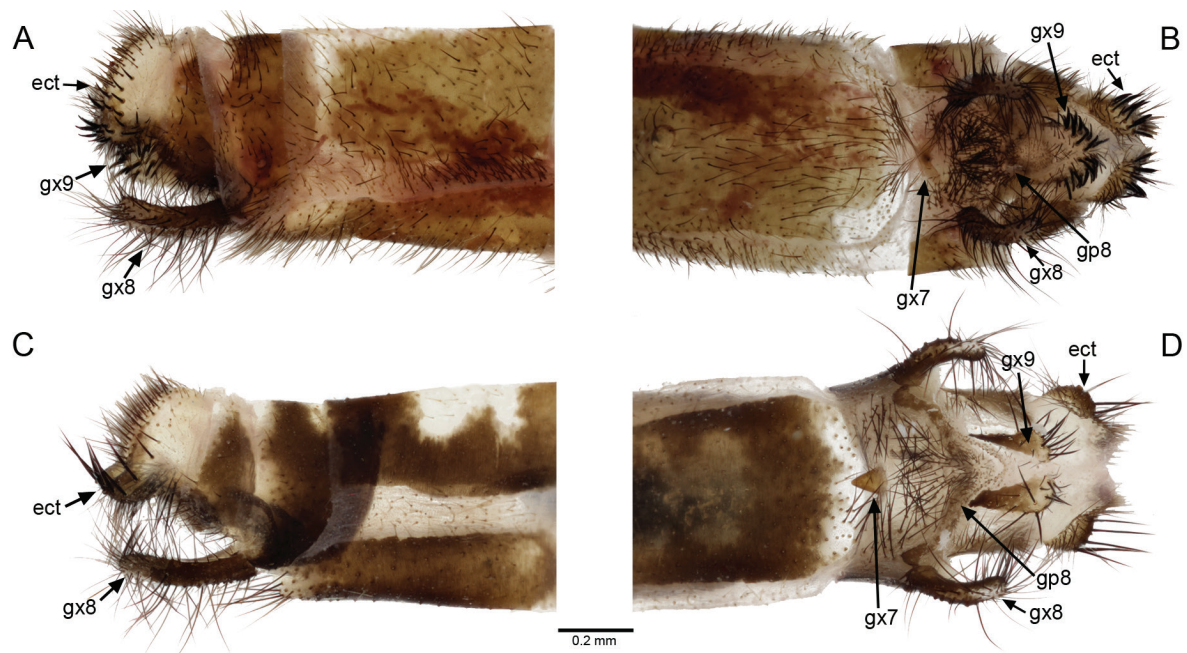


Figure 9. Female genitalia of *Gymnocnemia*. A–B *Gymnocnemia variegata* [Greece, Corfu], A lateral view, B ventral view; C–D *Gymnocnemia mirabilis* [Oman, Jabal Shams], C lateral view, D ventral view. Abbreviations: **ect** – ectoproct, **gp8** – gonapophysis 8, **gx7** – gonocoxites 7, **gx8** – gonocoxite 8, **gx9** – gonocoxite 9.

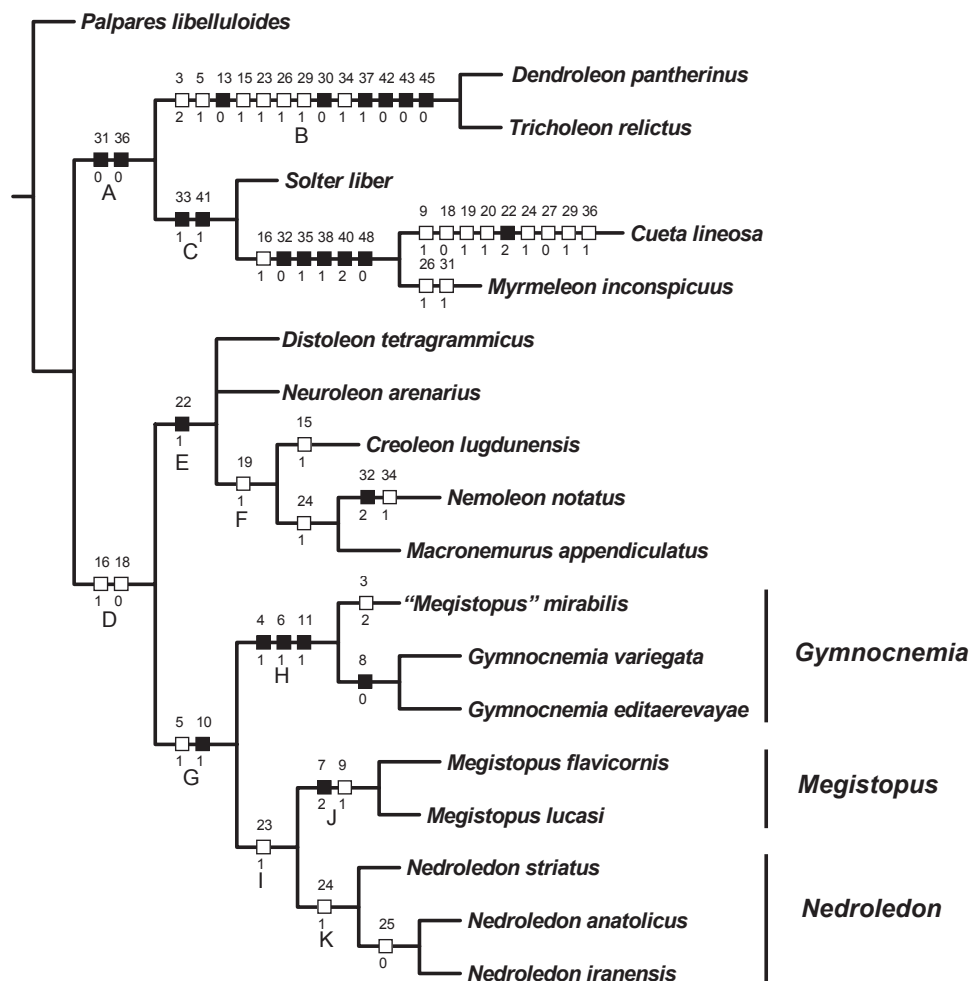


Figure 10. Preferred tree of the two most parsimonious trees (83 steps, C.I. 0.687) obtained in the analysis. Black squares indicate nonhomoplasious apomorphies, white squares homoplasious ones. Letters indicate clades discussed in the text.

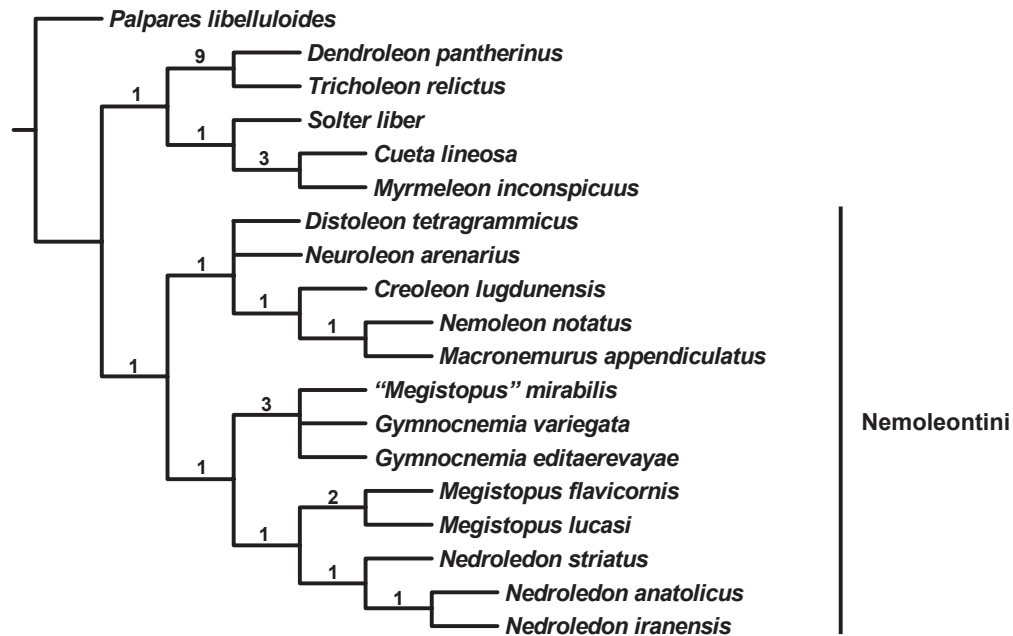


Figure 11. Strict consensus tree obtained from the two most-parsimonious trees with Bremer support values indicated above branches.



Figure 12. Distribution of *Gymnocnemia mirabilis* and *Megistopus lucasi*. Blue dots = *Gymnocnemia mirabilis*, red dots = *Megistopus lucasi*.

Ecology. *M. lucasi* is an extremely rare species and is exclusively known from well preserved coastal sand dunes and beaches with junipers. The unmistakable larva of this species (see Badano and Pantaleoni 2014) is an ambush hunter, dwelling at the base of junipers and amidst their

roots. The larva is parasitized by the generalist antlion parasitoid *Micomitra stupida* (Rossi) (Diptera, Bombyliidae) (Badano pers. obs.). This species of antlion is potentially endangered by human activities and exploitation of coastal sandy environments.

Identification key to the species of *Gymnocnemia* and *Megistopus* and the genus *Nedroledon*

- 1 Forewing vein Rs originating at or distal to cubital fork; forewing vein 2A strongly bent before merging with 3A (Fig. 5A); legs long and slender; tarsal claws folding against a brush of robust setae on fifth tarsomere (Fig. 1D) (Western Palaearctic)..... 2
- Other combination of characters other Myrmeleontidae

- 2 Thorax covered with outstanding, robust setae (Fig. 1B, 4:1); prothoracic leg much longer than the other legs (Fig. 1B, 11:1) 3...*Gymnocnemia*
- Thorax without outstanding setae; prothoracic leg as long as the other legs 5
- 3 Frons dark brown (Fig. 3B); wing venation sparse, forewing Rs with less than 8 crossveins (Fig. 4A); prothoracic femur with a fringe of long white setae (Fig. 1C); tibial spurs present, minute; tarsus much longer than tibia in all legs (Fig. 1C); pronotum Fig. 2E *G. mirabilis*
- Frons light brown (Fig. 3A); wing venation dense; forewing Rs with 10 or more crossveins (Fig. 4B); prothoracic femur without a fringe of long white setae; tibial spurs absent; tarsus shorter than tibia 4
- 4 Wings relatively broad; forewing with cubital and gradate markings faint (Fig. 4B); pronotum Fig. 2A, B, C, head Fig. 3A *G. variegata*
- Wings relatively narrow; forewing with cubital and gradate markings dark, well evident (Fig. 6B); pronotum Fig. 2D
..... *G. editaerevayae*
- 5 Tarsomere 1 as long as T2 or slightly shorter (Fig. 1A); male: abdomen shorter than wings, ectoproct without ventrocaudal projections (Fig. 8C) 6...*Megistopus*
- Tarsomere 1 as long as T2+T3; male: abdomen longer than wings, ectoproct with ventrocaudal projections (Fig. 8G) ...
..... *Nedroledon*
- 6 Body pattern: blackish with pale areas in the abdomen; frons yellow (Fig. 3C); pronotum reddish with a pale median stripe (Fig. 2F); forewing with only a black cubital marking, forewing vein Rs originating distal to cubital fork (Fig. 4D); male genitalia (Fig. 8E, F) *M. flavicornis*
- Body pattern: ochre with dark brown markings; frons ochre with brown markings below the base of the antennae (Fig. 3D); pronotum ochre with paired darker stripes (Fig. 2G); forewing with faint cubital and gradate markings, forewing vein Rs originating at the same height or slightly proximally of cubital fork (Fig. 4C); male genitalia (Fig. 8C, D) *M. lucasi*

Discussion

The phylogenetic analysis was conducted mainly to investigate the relationships among the species included in the genera *Gymnocnemia* and *Megistopus* and to test their respective monophyly. In addition, it is possible to draw some interesting, even if preliminary, observations on affinities at the tribal level. In agreement with Stange (1994, 2004), Nemoleontini was reconstructed as monophyletic, although it was only based on homoplasious apomorphies, thus obtaining only weak support. Michel et al. (2017) also retrieved this tribe as monophyletic in a phylogenetic analysis of the family based on molecular data. However, Badano et al. (2017), investigating the phylogeny of Myrmeleontiformia based on larval morphological characters, reconstructed Nemoleontini as paraphyletic with respect to Dendroleontini. Indeed, the members of these two tribes are characterised by strikingly similar larval morphology suggesting that further studies are necessary to clarify tribal level relationships. Stange (2004) noted that Nemoleontini is best delimited by a set of adult characters, such as the fusion of forewing veins 2A and 3A (16:1) and the absence of *pilula axillaris* in male forewing (18:0). The fusion of forewing anal veins also occurs in Nesoleontini and Myrmeleontini, while the *pilula axillaris* is probably an autapomorphy of Myrmeleontidae, which however, has been repeatedly and independently lost in several lineages at the tribal level (Acanthaclisini, Myrmecaelurini, Nesoleontini, Nemoleontini), generic level (e.g. *Dimares* Hagen, *Scotoleon* Banks) and species level (e.g. some *Brachynemurus* Hagen and *Myrmeleon* species) (Stange 1970a, 1994, 2004, Pantaleoni and Badano 2012). The retrieved subclades of Nemoleontini did not support the

subtribal level division into Nemoleontina and Neuroleontina as proposed by Stange (2004). In fact, *Nemoleon*, the only included member of Nemoleontina, was deeply nested within Neuroleontina. The presence of gonocoxites 9 fused in a Y-shaped structure (22:1) supported the monophyly of a clade (clade E) including *Distoleon*, *Neuroleon*, *Creoleon*, *Nemoleon* and *Macronemurus*. Further, subclade G was retrieved as monophyletic based on the presence of elongated legs (5:1) and opposable tarsal claws (10:1). The genera comprised in the latter group (i.e. *Gymnocnemia*, *Megistopus* and *Nedroledon*) were traditionally included in Glenurini (Markl 1954, Hölzel 1972, H. Aspöck et al. 2001). Markl (1954) distinguished Glenurini from Nemoleontini (which he divided into several tribes) based on the forked forewing vein 2A and simple 3A in the former tribe (vice versa in Nemoleontini). However, Stange (1970b) questioned the value of these characters, and Hölzel (1972) dismissed the importance of anal wing shape and bifurcations due to variability both among and within these tribes. Lastly, Stange and Miller (1990) synonymised Glenurini with Neuroleontina based on larval characters, thus including them within Nemoleontini. Krivokhatsky (2011) retained these groups as separate subfamilies, Nemoleontinae and Glenurinae, chiefly based on genital morphology. Our clade E corresponds to his characterisation of Nemoleontinae; however, we interpret the plate-like shape of the gonocoxites 9 (22:0) of the members of clade G as the plesiomorphic condition for Myrmeleontinae. This character is thus not warranted to delimit antlion taxa. A more extensive taxon sampling is necessary to test the relationships of “glenu-rines” with the other Nemoleontini.

Our analysis consistently recovered *Gymnocnemia mirabilis*, originally described as a member of *Megisto-*

pus, within the genus *Gymnocnemia*. The monophyly of this genus was well supported by elongated prothoracic legs, strikingly different pattern of leg pairs and the presence of robust, prominent thoracic setae. The characteristic shape of male gonocoxites 9, partly encircling gonocoxites 11, characterizes both *G. variegata* and *G. editaerevayae* (see also Michel 2013). Therefore, the discovery of the male of *G. mirabilis* is necessary to verify the value of this character to delimit the genus. The absence of tibial spurs, often used by antlion taxonomists to differentiate genera, is here re-interpreted as a weak homoplasious apomorphy that is not useful for systematic purposes questioning the importance of the character for generic delimitation. Furthermore, *Megistopus*, which now comprises only *M. flavicornis* and *M. lucasi*, is best distinguished by tarsomeres 1–4 being equally elongated and of similar size, while in other genera of Nemoleontini the first tarsomere is noticeably longer than the following articles (usually twice the length of the others).

The present analysis confirms the importance of a phylogenetic approach (i) to circumscribe genera as monophyletic groups in a family characterized by an overall homogeneous morphology, such as Myrmeleontidae, and (ii) to test the actual systematic value of commonly used diagnostic characters. A more inclusive taxon sampling and the integration of molecular data is advisable to delimit suprageneric taxa and to reconstruct the relationships within the family.

Acknowledgements

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Supplementary material 1 List of examined specimens

Authors: Davide Badano, Horst Aspöck, Ulrike Aspöck
Data type: RTF file

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Supplementary material 2 Data matrix for the phylogenetic analysis

Authors: Davide Badano, Horst Aspöck, Ulrike Aspöck
Data type: NEXUS file

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