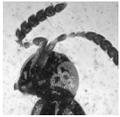


# Diverse scelionid wasps from Early Cretaceous Álava amber, Spain (Hymenoptera: Platygastroidea)

JAIME ORTEGA-BLANCO, RYAN C. MCKELLAR & MICHAEL S. ENGEL



Platygastroid wasp diversity in Álava amber is reviewed. Platygastroids are the most numerous group of Hymenoptera in Spanish amber, a pattern typical for many Cretaceous amber deposits, with species of the superfamily sometimes more abundant than all other arthropod lineages. Herein we report on 87 specimens, 62 of them sufficiently preserved to permit specific identification, and all dating from the Lower Cretaceous (middle Albian). Eight new genera and nine new species are described and figured as *Proterosceliopsis* gen. nov., *Proterosceliopsis masneri* sp. nov., *Bruescelio* gen. nov., *Bruescelio platycephalus* sp. nov., *Tithonoscelio* gen. nov., *Tithonoscelio resinalis* sp. nov., *Amissascelio* gen. nov., *Amissascelio temporarius* sp. nov., *Juxtascelio* gen. nov., *Juxtascelio interitus* sp. nov., *Alavascelio* gen. nov., *Alavascelio delvallei* sp. nov., *Electroteleioptis* gen. nov., *Electroteleioptis hebdomas* sp. nov., *Perimoscelio* gen. nov., *Perimoscelio tyrbastes* sp. nov., and *P. confector* sp. nov. Morphological interspecific variability is low, hindering identification, and as such, taxa are principally diagnosed on structure of the female antenna, tibial spur formula, mesoscutal form, and head and metasomal anatomy. The taxa are discussed in relation to other fossil lineages of platygastroids as well as modern counterparts. All species belong to the “Scelionidae”, a paraphyletic group relative to Platygastriidae as currently circumscribed (including Platygastriinae, Scelioninae, Teleasinae, Telenominae). Platygastroid diversity will certainly rise in Spanish amber as abundant new material becomes available from the El Soplao and San Just outcrops. The name *Jordanoscelio* nom. nov. is proposed to replace the homonymous *Microptera* Kaddumi for a Jordanian amber (Early Cretaceous) genus of Scelionidae, resulting in *Jordanoscelio attiki* (Kaddumi) comb. nov. • Key words: Insecta, Hymenoptera, Apocrita, Proctotrupomorpha, Platygastroidea, Scelionidae, Mesozoic, Spain, amber, taxonomy.

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The parasitoid Hymenoptera are diverse and well represented in Cretaceous amber outcrops throughout the world (e.g., Nel & Azar 2005, Grimaldi & Engel 2005, Masner *et al.* 2007, Johnson *et al.* 2008b; McKellar & Engel 2012). Nonetheless, the vast majority of these fossils belong to a single family. The sheer abundance of Scelionidae in Cretaceous ambers dwarfs the number of individuals typically recovered for nearly all other families (e.g., Grimaldi *et al.* 2002, McKellar & Engel 2012, Penney 2010, herein). It was apparently during the Cretaceous, particularly the

Early Cretaceous, that platygastroid wasps experienced their heyday relative to other hymenopteran groups, reflective of a remarkable diversification that was either taking place or had been ongoing since the latest part of the Jurassic. Many of these taxa intermingle features of the basal tribes and subfamilies of Platygastroidea (i.e., intermixing features of Nixonini, Sparasionini, and Scelioninae), and therefore may ultimately prove critical to resolving higher relationships within the clade. Before such a work, however, the incredible diversity of these wasps must be

surveyed and their characters elucidated for future phylogenetic studies.

Not surprisingly the monophyly of the Scelionidae has been seriously questioned, although the few studies addressing the issue have arrived at different placements for the offending tribes and genera (Austin & Field 1997, Murphy *et al.* 2007). Sharkey (2007) advocated the synonymy of Scelionidae within Platygastriidae, and this position has some merit and has been adopted by some (*e.g.*, Valerio *et al.* 2009). However, excluding a few genera, most Scelionidae have been recovered as monophyletic and this group represents a distinctively different morphology and biology from that seen in the Platygastriidae *s. str.* Accordingly, it seems perhaps more useful to retain Scelionidae in some restricted sense, excluding the tribes Sparasionini and Nixonini until such time as their relationships are more fully resolved (as was done by Engel & Krombein 2012). Herein we have retained the name Scelionidae but exclude the aforementioned tribes temporarily as Platygastroidea *incertae sedis*, pending final resolution of their placement at which time they, or subsets of their included genera, may require incorporation into newly defined Platygastriidae and Scelionidae, or elevation to family rank alongside these groups (*e.g.*, Engel & Krombein 2012). Such a system permits a more enriched classification, which more effectively communicates the diversity of lineages in the superfamily; reflects the fact that, while much remains to be clarified, some information on the hierarchy within the clade is available; avoids the difficulty that the superfamilial and familial names for the group become equivalent and serve no utility; and permits some historical continuance in the application of names through the literature.

Herein, we provide a taxonomic overview of the diversity of scelionid wasps found in Early Cretaceous Álava amber, from Spain. This work is intended to bring this diversity to the attention of hymenopterists and put on record the morphological character combinations embodied by these Lilliputian fossils. A key to the diversity of Scelionidae in Spanish amber is provided.

## Material and methods

This work is based on an extensive sample of 87 platygastroid wasps entombed in Early Cretaceous (Albian) amber from Álava, Spain. Specimens were prepared for optimal microscopic study following the procedure outlined by Corral *et al.* (1999). Measurements were made using Leica IM 1000 software. Photomicrographs were executed using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, then arranged and sharpened with CombineZ and edited with Photoshop CS3. Line drawings were prepared using a camera lucida attached to

an Olympus BX41 microscope. Material is deposited in the Museo de Ciencias Naturales de Álava (MCNA) and the Conjunto Paleontológico de Teruel (CPT). References to Peñacerrada I refer to the “Álava amber” deposit found in Burgos, to distinguish it from Peñacerrada II which is found in Basque Country (not cited in this article). The age, composition, and fauna of Spanish amber were briefly reviewed by Alonso *et al.* (2000), Delclòs *et al.* (2007), and Najarro *et al.* (2010).

Abbreviations and terms used in the text follow those generally employed elsewhere in the systematics of Platygastroidea (*e.g.*, Masner 1976, Masner *et al.* 2007b). Such abbreviations are as follows: A1, A2, ... A14: antennomeres 1, 2, ... 14; claval formula: distribution of the large, multiporous basiconic sensilla on the underside of apical antennomeres of the female, with the segment interval specified followed by the number of sensilla per segment, for example A10–A14, 1-2-2-2 (Bin 1981); antennal composition, number of clavomeres compared to number of flagellomeres; LOL: lateral ocellar line, being the shortest distance between inner margins of median and lateral ocelli; OOL: ocular ocellar line, being the shortest distance from inner orbit and outer margin of posterior ocellus; POL: posterior ocellar line, being the shortest distance between inner margins of posterior ocelli (Masner & Huggert 1989); epomial carina: the vertical portion of epomium on the pronotum; pronotal humeral carina: the horizontal portion of epomium on the pronotum; T1, T2, ... T7: metasomatic terga 1, 2, ... 7; S1, S2, ... S7: metasomatic sterna 1, 2, ... 7.

## Systematic palaeontology

### Scelionidae Haliday, 1839

#### *Proterosceliopsis* gen. nov.

*Etymology.* – The new genus-group name is a combination of the generic name *Proteroscelio* and the Greek suffix *-opsis*, meaning “looking like”. The name is feminine.

*Type species.* – *Proterosceliopsis masneri* sp. nov.

*Diagnosis.* – Antenna 14-merous; clava 7-merous; funicle 5-merous; lateral ocelli closer to compound eyes than to other ocelli; mesoscutal pits present; forewing not reaching metasomal apex; tibial spur combination 1-2-2; calcar with bifid apex; R with bulla before marginal vein; 2Rs not connecting with M; 3Rs about 3 times the length of r-rs; female with 6 terga visible, about as long as wide; tergum 1 longitudinally striate, slightly humped dorsally; ovipositor relatively short and wide. Among previously reported Cretaceous genera, new genus most similar to *Proteroscelio* Brues,

but differs by rounded head (strongly compressed and transverse in *Proteroscelio*), presence of occipital carina, presence of notauli, forewing not extending near to metasomal apex, and strongly transverse mesoscutellum bearing posterior mesoscutellar pits.

***Proterosceliopsis masneri* sp. nov.**

Figures 1, 6A, B

*Etymology.* – The specific epithet is a patronym for Dr. Lubomír Masner, world's authority on Proctotrupomorpha.

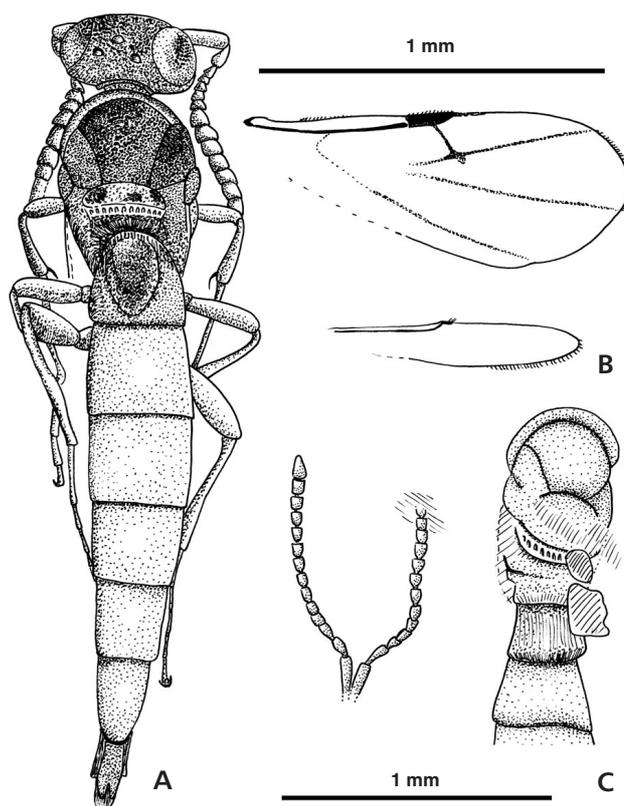
*Type material.* – Holotype MCNA 13631 (female); paratypes MCNA 12753 (female), MCNA 12579 (male), MCNA 12738 (female), MCNA 9837 (female).

*Type locality.* – Moraza – Peñacerrada I.

*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo-La Orden Member boundary, Escucha Formation.

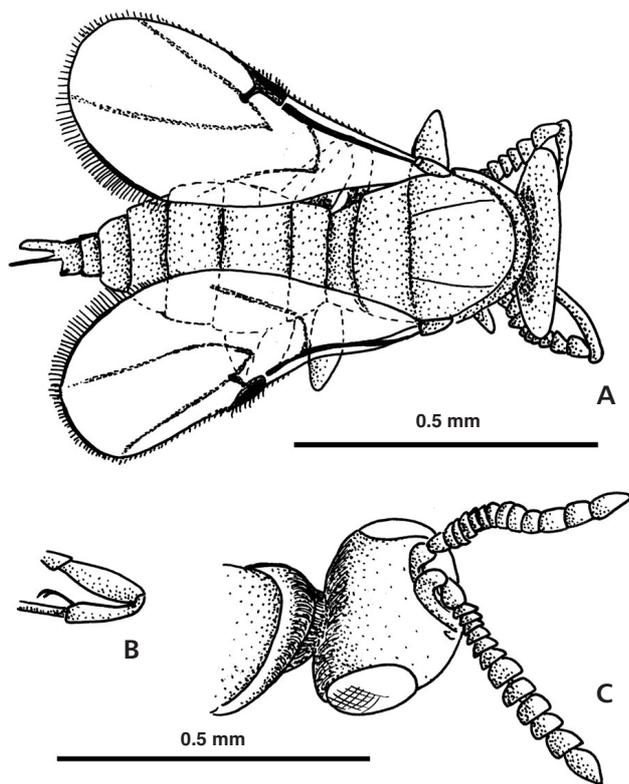
*Diagnosis.* – As for the genus (*vide supra*).

*Description.* – Total body length 2.14 mm (from holotype); forewing length 1.25 mm (from holotype). Head subglobose, not compressed or flattened, moderately transverse, 1.75 times wider than long, with punctured sculpture; vertex rounded; occipital carina present. Clypeus short, strongly transverse; malar sulcus apparently present (difficult to discern); mandibles tridentate (right slightly overlapping left, so not completely clear from holotype MCNA 13631 but apparently so from paratype MCNA 9837); maxillary palpus 5-segmented; labial palpus 3-segmented. Compound eye large, bare, occupying about 2/3 of head surface; orbital carina absent; inner orbits roughly parallel. Frons relatively flat, without frontal depression, median longitudinal carina absent, without raised interantennal process between toruli; toruli opening anteriorly. Male and female antenna 14-merous; radicle inserted apically into base of scape, parallel to longitudinal axis of A1; funicle 5-merous, slightly smaller than clava; first funicular segment slightly longer than wide, other 4 shaped as clavomeres (wider than long); clava 7-merous, with antennomeres wider than long; claval formula A8–A14, 2-2-2-2-2-2-1, with sensilla longitudinally arranged, sex segment not differentiated. Mesosoma not compressed, slightly longer than wide, semi-oval in dorsal view; pronotum with anterolateral corners rounded; transverse pronotal carina absent; epomial carina absent; pronotal humeral carina absent; lateral surface of pronotum convex, without scrobe; mesoscutum elongate, with punctured sculpture and notauli well impressed; parapsidal lines absent; transscutal articulation well developed, simple; mesoscutellum



**Figure 1.** A – dorsal view of *Proterosceliopsis masneri* gen. and sp. nov., holotype (MCNA 13631). • B – wings from paratype (MCNA 12753) at same scale as A. • C – details showing main differences with female of *P. masneri* found in male paratype (MCNA 12579), particularly the non-clavate antenna and first tergum without protuberance, and covered by full longitudinal striation in male.

strongly transverse, much wider than long, relatively flat, with transverse row of posterior mesoscutellar pits; mesoscutellum narrow, without processes (teeth, protuberances, spines...); propodeum unadorned, without tubercles, processes, keels, or teeth, or with only very weakly developed dorsolateral tubercles; metanotal depression present. Trochantellus present on all legs; femora weakly incrassate; tibiae without spines; tibial spur formula 1-2-2 (meso- and metatibial spurs fine, reduced, and difficult to discern); protibial calcar simple in both legs; tarsi pentamerous, tarsomeres cylindrical; probasitarsus with inner comb of setae, short but distinctly longer than the rest of tarsomeres; metabasitarsus shorter than combined lengths of remaining tarsomeres. Forewing not extending to metasomal apex; R faintly bent at position of basal vein; basal vein nebulous, very faint (nearly appearing absent) in most specimens; costal margin in costal cell basad of confluence of R with marginal vein slightly infumate; R with bulla immediately prior to marginal vein; thickened pigmented marginal vein, about three times longer than wide; r-rs (stigmatal vein) forming acute angle with costal margin, long, about as long as marginal vein; R1 distinct, well developed, continuing along



**Figure 2.** A – dorsal view of *Bruescelio platycephalus* gen. and sp. nov., paratype (MCNA 9536). • B – detail of bifid left calcar, holotype (MCNA 13284). • C – head in dorsal view, holotype (B and C at same scale).

costal margin to form postmarginal vein, nearly as long as marginal vein; 3Rs nebulous except for very short basal stub at apex of r-rs (even less pigmented), three times longer than r-rs; 2Rs (almost nonexistent, only the commented faint stub) nebulous, not connecting to M; M nebulous; Cu nebulous; M+Cu faintly nebulous. Hind wing with R tracheate throughout length, complete (bending apically to meet costal margin), with three hamuli on R at contact with costal margin; marginal fringe of setae short. Metasoma not compressed, cylindrical, about two times combined length of rest of body, somewhat lanceolate; terga sub-square, T1 apparently with dorsal hump (it could be an ovipositor holder); all segments except the apical subequal in length, slightly longer than wide; seven terga and sterna visible in male, six in female; laterotergites narrow; male T7 apically rounded, not reflexed; female T6 bluntly rounded at apex.

**Male:** Body length 2.34 mm. Antenna filiform, without clava; occipital carina present and more distinct, demarcated by small areolae; propodeum with weak dorsolateral tubercles; T1 with longitudinal striae along entire length; parameres with serrated tip.

**Comments.** – In several respects this genus is reminiscent of *Proteroscelio* Brues, known in Lebanese and Canadian

amber (Brues 1937, Johnson *et al.* 2008b), but it can be clearly differentiated on the basis of the characters included in the diagnosis (*vide supra*).

***Bruescelio* gen. nov.**

**Etymology.** – The new genus-group name is a combination of Brues, honoring the late Charles T. Brues who described the first Cretaceous platygastroids, and *Scelio*, type genus of the family Scelionidae. The name is masculine.

**Type species.** – *Bruescelio platycephalus* sp. nov.

**Diagnosis.** – Head and body highly flattened dorso-ventrally; occipital carina absent; antenna 14-merous; clava 6-merous; funicle 6-merous; ocelli apparently closer to each other than to compound eyes; mesoscutal pits absent; forewing overpassing metasomal apex; tibial spur combination 1-2-2; protibial spurs with bifid apex; R with bulla before marginal vein; 2Rs connecting with M; 3Rs about 6 times the length of r-rs; metasoma as long as the rest of the body; female with 6 terga visible, all wider than long; tergum 2 slightly longer than the rest; ovipositor relatively short. Among Cretaceous genera, *Bruescelio* superficially similar to *Cretoxenomerus* Nel & Azar, but new genus readily distinguished by distinctive head shape, well-developed antennal clava, and metasomal tergum 2 being longest (tergum 3 longest in *Cretoxenomerus*).

***Bruescelio platycephalus* sp. nov.**

Figures 2, 6C

**Etymology.** – The specific epithet is a combination of the Greek terms *platys* (meaning, “broad” or “flat”) and *kephale* (meaning, “head”).

**Type material.** – Holotype MCNA 9536 and paratypes MCNA13284, MCNA 9499 (all female).

**Type locality.** – Moraza – Peñacerrada I.

**Type horizon.** – Lower Cretaceous, upper Albian, Regachuelo – La Ordem Member boundary, Escucha Formation.

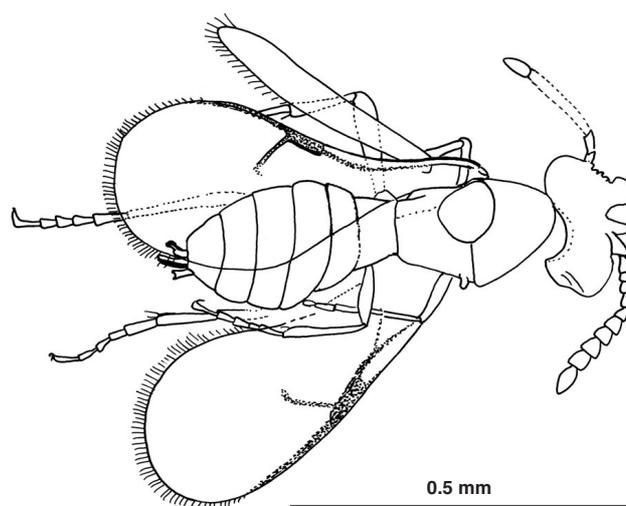
**Diagnosis.** – As for the genus (*vide supra*).

**Description.** – **Female:** Total body length 0.83–0.90 mm; forewing length 0.61 mm; integument black; apparently not setose. Head flattened in lateral view, wider than long; vertex rounded; occipital carina absent. Compound eye large, bare; orbital carina absent; inner orbits roughly parallel; ocelli not well visible but possibly closer to

each other than to compound eyes. Frons flat, without frontal depression, median longitudinal carina absent, without raised interantennal process between toruli; toruli opening anteriorly. Female antenna 14-merous; radicle inserted apically into base of scape, parallel to longitudinal axis of A1; scape robust, curved and elongate, representing more than 1/3 of antennal length, gradually widened to apex; pedicel around 2 times longer than apical width; funicle 6-merous; clava 6-merous; sex segment not differentiated; clava slightly wider than funicle; clavomeres about as wide as long. Mesosoma somewhat compressed dorso-ventrally, slightly longer than wide, as wide as head, semi-oval in dorsal view; pronotum with anterolateral corners rounded; transverse pronotal carina absent; epomial carina absent; pronotal humeral carina absent; lateral surface of pronotum convex, without scrobe; propleura elongate, making fore legs appear far from head; mesoscutum elongate; notauli present; parapsidal lines absent; transscutal articulation well developed, simple; mesoscutellum strongly transverse, much wider than long, relatively flat, without posterior pits; metascutellum narrow, without processes; propodeum unadorned, without tubercles, processes, keels, or teeth; metanotal depression present. Trochantellus present on all legs; femora weakly incrassate; tibiae without spines; tibial spur formula 1-2-2 (meso- and metatibial spurs fine, reduced, and difficult to discern); protibial calcar with bifurcate apex bifid (very clear on MCNA 13284); tarsi pentamerous, tarsomeres cylindrical; metabasitarsus shorter than combined lengths of remaining tarsomeres. Forewing extending just beyond metasomal apex; R faintly bent at position of basal vein; basal vein nebulous, very faint (nearly appearing absent); costal margin in costal cell basad of confluence of R with margin slightly infumate; R with bulla immediately prior to marginal vein; thickened weak pigmented marginal vein, about three times longer than wide; r-rs (stigmatal vein) forming acute angle with costal margin, short, distinctly shorter than marginal vein; R1 (postmarginal vein) absent; 3Rs nebulous except for very short basal stub at apex of r-rs, about six times longer than r-rs; 2Rs nebulous, connecting to M; M nebulous; Cu nebulous; M+Cu faintly nebulous. Hind wing with R tracheate throughout length, complete (bending apically to meet costal margin); marginal fringe of setae short. Metasoma apparently not setose, compressed dorso-ventrally, ovoid, about as long as head and mesosoma combined, with segments much wider than long; T2 largest tergum; six terga visible; laterotergites narrow; T6 bluntly rounded at apex; ovipositor and valves relatively short.

***Tithonoscelio* gen. nov.**

*Etymology.* – The new genus-group name is a combination of the Latin name *Tithonus*, a mythical consort of Aurora



**Figure 3.** Dorsal view of *Tithonoscelio resinalis* gen. nov. and. sp. holotype (MCNA 8633).

who symbolized decrepitude and old age, and *Scelio* (Latin, “rogue”), type genus of the family Scelionidae. The name is masculine.

*Type species.* – *Tithonoscelio resinalis* sp. nov.

*Diagnosis.* – Head flattened (transverse from dorsal view); ocelli not visible; antenna 12-merous; clava 5-merous; funicle 5-merous; notauli absent; mesoscutal pits absent; forewing overpassing metasomal apex; tibial spur combination 1-1-1; protibial spurs with simple apex; R without bulla before marginal vein; veins 3Rs, 2Rs, M, Cu and M+Cu absent; r-rs slightly shorter than marginal vein; metasoma as long as the rest of the body; female with 6 terga visible, all wider than long and of similar length; ovipositor short. New genus readily distinguished from previously described Cretaceous genera, due to 12-merous antenna (differences between new genera outlined in key herein, *vide infra*).

***Tithonoscelio resinalis* sp. nov.**

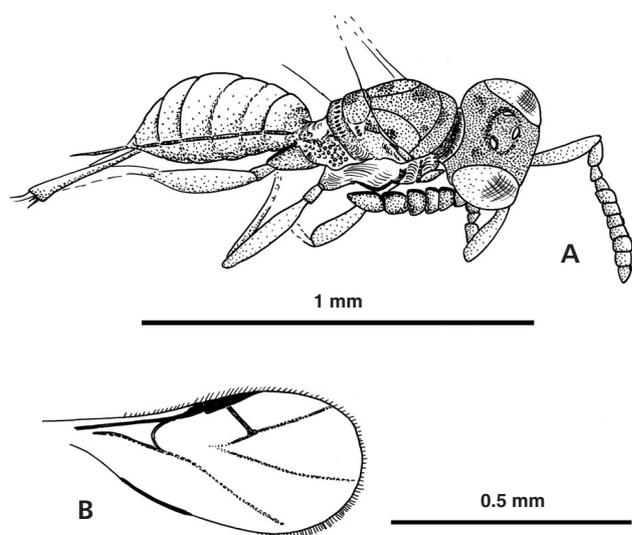
Figures 3, 6E, F

*Etymology.* – The specific epithet is the Latin term *resinalis*, meaning, “of resin”.

*Type material.* – Holotype MCNA 8633.3 (female). Syninclusions: 1 Psocoptera (?), 1 Acari, 9 Diptera, and numerous arthropod remains (at least a dipteran wing and long antenna)

*Type locality.* – Moraza – Peñacerrada I.

*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo – La Orden Member boundary, Escucha Formation.



**Figure 4.** A – dorso-lateral view of *Amissascelio temporarius* gen. and sp. nov., holotype (MCNA 13643). • B – forewing, paratype (MCNA 9978).

**Diagnosis.** – As for the genus (*vide supra*).

**Description.** – Female: Total body length 0.63 mm; forewing length 0.54 mm; integument black, not setose. Head flattened anteriorly, strongly wider than long in dorsal view. Antenna 12-merous; scape robust, curved and not very elongate; pedicel around 2 times longer than its apical width; funicle 5-merous, all slightly wider than long, all similar in size and shape; clava 5-merous, slightly wider than funicle, with clavomeres about as wide as long; sex segment not differentiated. Mesosoma not compressed, longer than wide, semi-oval in dorsal view, narrower than head; pronotum with anterolateral corners rounded; transverse pronotal carina absent; epomial carina absent; pronotal humeral carina absent; lateral surface of pronotum convex, without scrobe; mesoscutum elongate; notauli absent; parapsidal lines absent; transscutal articulation well developed, simple; mesoscutellum transverse, slightly wider than long, flat, without posterior pits; metascutellum without processes; propodeum unadorned, without tubercles, processes, keels, or teeth; metanotal depression present. Legs moderately setose; trochantellus present on all legs; femora weakly incrassate; tibiae without spines; tibial spur formula 1-2-2 (meso- and metatibial spurs fine, reduced, and difficult to discern); protibial calcar elongate and arched, with simple apex (seen in both legs); tarsi pentamerous, tarsomeres cylindrical; metabasitarsus much shorter than combined lengths of remaining tarsomeres. Forewing extending clearly beyond metasomal apex; R faintly bent at position of basal vein; basal vein nebulous; costal margin in costal cell basad of confluence of R with margin not infumate; R without bulla immediately prior to marginal vein; marginal vein extremely narrow, difficult to distinguish;

r-rs (stigmal vein) forming acute angle with costal margin, about as long as marginal vein, and arising from very apex of marginal vein; R1 (postmarginal vein) distinct and continuing along anterior margin even longer than r-rs; 3Rs, 2Rs, M, Cu and M+Cu absent. Hind wing without veins visible; marginal fringe of setae short. Metasoma apparently somewhat compressed dorso-ventrally and not setose, about as long as head and mesosoma combined; all terga of similar length, around 3–4 times wider than long; six terga and sterna visible; laterotergites narrow; T6 bluntly rounded at apex; ovipositor and valves relatively short, exerted.

***Amissascelio* gen. nov.**

**Etymology.** – The new genus-group name is a combination of the Latin term *amissus* (meaning, “lost”) and *Scelio*, type genus of the family Scelionidae. The name is masculine.

**Type species.** – *Amissascelio temporarius* sp. nov.

**Diagnosis.** – Head flattened dorso-ventrally; antenna 11-merous; clava 7-merous; funicle 2-merous; ocelli placed on low prominence; lateral ocelli within one ocellar diameter of compound eye, closer to compound eye than to the other lateral ocellus; occipital, epomial and pronotal humeral carinae present; mesoscutal pits present; forewing overpassing metasomal apex; tibial spur combination 1-2-2; protibial spurs with simple apex; R without bulla before marginal vein; 2Rs faintly connecting with M; 3Rs about 2–2.5 times the length of r-rs; r-rs slightly longer than marginal vein; metasoma as long as the rest of the body; female with 7 terga visible, all wider than long; ovipositor relatively short. Among previously described Cretaceous genera, new genus most similar to *Cenomanoscelio* Schlüter, but differs by increased number of claval articles and metasomal tergum being 2 slightly longer than others (5-merous clava, 4-merous funicle, and elongate tergum 3 present in *Cenomanoscelio*).

***Amissascelio temporarius* sp. nov.**

Figures 4, 6D

**Etymology.** – The specific epithet is the Latin term *temporarius*, meaning, “lasting only a time”.

**Type material.** – Holotype MCNA 13643 and paratypes MCNA 9584, MCNA 9978, MCNA 10015, MCNA 10744, MCNA 10776, MCNA 11389 and MCNA 12708 (all specimens female).

**Type locality.** – Moraza – Peñacerrada I.

*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo–La Orden Member boundary, Escucha Formation.

*Diagnosis.* – As for the genus (*vide supra*).

*Description.* – Female: Body length between 1.05 to 1.28 mm, hardly pigmented, with punctured sculpture among all visible sclerites. Head subglobose, somewhat flattened in lateral view, not strongly transverse, and 2 times wider than long; vertex rounded; occipital carina present. Mandibles tridentate (clear in MCNA 13643). Compound eye large, bare; orbital carina absent; inner orbits roughly parallel. Frons relatively flat, without frontal depression, with median longitudinal carina absent, without raised interantennal process between toruli; toruli opening anteriorly. Antenna 11-merous (currently unknown in males) densely setose; radicle inserted apically into base of scape, parallel to longitudinal axis of A1; scape around 5–6 times longer than wide; pedicel about 3 times longer than maximum width; flagellomeres around as long as wide; funicle dimerous; clava 7-merous; sex segment not differentiated. Mesosoma not compressed, slightly longer than wide, semi-oval in dorsal view; pronotum with anterolateral corners rounded, distinct dorsally; transverse pronotal carina absent; epomial carina present; pronotal humeral carina present; lateral surface of pronotum concave; mesoscutum short; notauli present faintly impressed; parapsidal lines absent; transscutal articulation well developed, crenulate; mesoscutellum transverse, slightly wider than long, relatively flat, with transverse row of posterior mesoscutellar pits; mesopleural depression broad, deep; metascutellum narrow, without processes; propodeum with dorsolateral tubercles; metanotal depression present. Legs densely covered by moderately long setae, slightly flattened laterally; trochantellus present on all legs; femora weakly incrassate; tibiae without spines; thin, slightly wide apically, with an inner row of stiff setae; tibial spur formula 1-2-2 (meso- and metatibial spurs fine, reduced, and difficult to discern); protibial calcar simple; tarsi pentamerous, tarsomeres cylindrical; probasitarsus with inner comb of setae; metabasitarsus slightly shorter than combined lengths of remaining tarsomeres. Forewing densely setose, extending just beyond metasomal apex; R faintly bent at position of basal vein; basal vein nebulous; costal margin in costal cell basad of confluence of R with margin not infumate; R without bulla immediately prior to marginal vein; thickened weakly pigmented marginal vein, about three times longer than wide; r-rs (stigmal vein) forming acute angle with costal margin, long, slightly longer than marginal vein; R1 distinct, well developed, continuing along costal margin to form postmarginal vein, slightly shorter than marginal vein; 3Rs faintly nebulous without tubular stub at apex of r-rs, and 2–2.5 times longer than r-rs; 2Rs nebulous, faintly

connecting to M; M nebulous; 1Rs extending less than one marginal vein length basally; Cu nebulous; M+Cu nebulous. Hind wing with R tracheate throughout length, complete (bending apically to meet costal margin), with three hamuli on R at contact with costal margin; marginal fringe of setae short. Metasoma somewhat compressed dorso-ventrally, ovoid, slightly shorter than head and mesosoma combined, with setose last terga; T2 slightly larger than remaining segments; six terga visible; laterotergites narrow; T6 bluntly rounded at apex; ovipositor relatively short, exerted, with short valves.

### ***Juxtascelio* gen. nov.**

*Etymology.* – The new genus-group name is a combination of the Latin term *juxta* (meaning, “near”) and *Scelio*, type genus of the family Scelionidae. The name is masculine.

*Type species.* – *Juxtascelio interitus* sp. nov.

*Diagnosis.* – Antenna 11-merous; clava 6-merous; funicle 3-merous; ocelli at equal distance between middle ocellus longitudinal axis and compound eyes, and surrounded by low ridge; mesoscutal pits present; forewing barely reaching metasomal apex; tibial spur combination 1-2-2; calcar with bifid apex; R without bulla before marginal vein; 2 Rs connecting with M; 3Rs about 3 times the length of r-rs; hind wing with Rs+M present; female with 7 terga visible, longer than wide; ovipositor long and thin. Among Cretaceous genera with 11-merous antennae, *Juxtascelio* most similar to *Amissascelio* (*vide supra*), but differs in antennal divisions (clava 7-merous, funicle 2-merous) and lack of crenulations in transscutal sulcus.

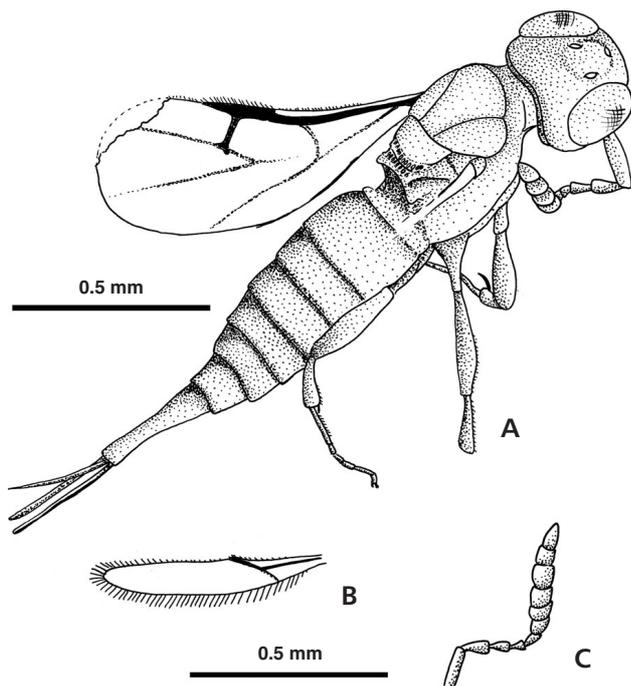
### ***Juxtascelio interitus* sp. nov.**

Figures 5, 6G

*Etymology.* – The specific epithet is the Latin term *interitus*, meaning, “perished”.

*Type material.* – Holotype MCNA 12600 and paratypes MCNA 8779, MCNA 8794, MCNA 9157, MCNA 9249, MCNA 9785, MCNA 9893, MCNA 11391 and MCNA 12557 (all specimens female).

*Additional material.* – MCNA 9412 agrees in most respects with the type series but is noticeably larger and with a somewhat more squared head, but the specimen is somewhat deformed. MCNA 9877 is noticeably smaller than most specimens in the type series but is otherwise in agreement with the diagnosis of the species.



**Figure 5.** A – dorso-lateral view of *Juxtascelio interitus* gen. and sp. nov., holotype (MCNA 12600). • B – detail of hind wing from paratype (MCNA 9785). • C – detail of antenna, paratype (MCNA 8779) (B and C at same scale).

*Type locality.* – Moraza – Peñacerrada I.

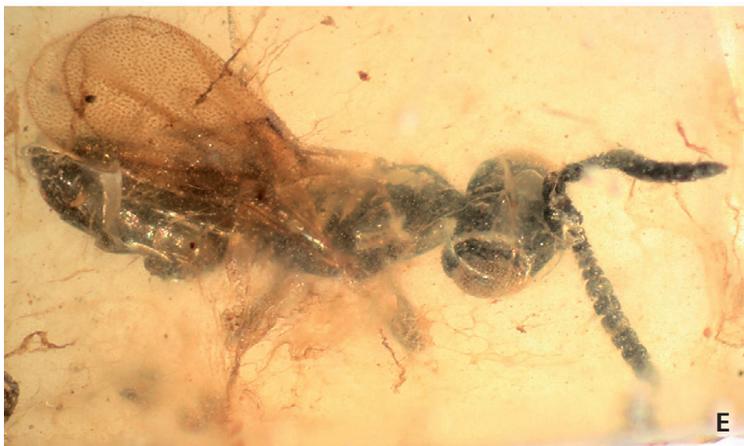
*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo – La Orden Member boundary, Escucha Formation.

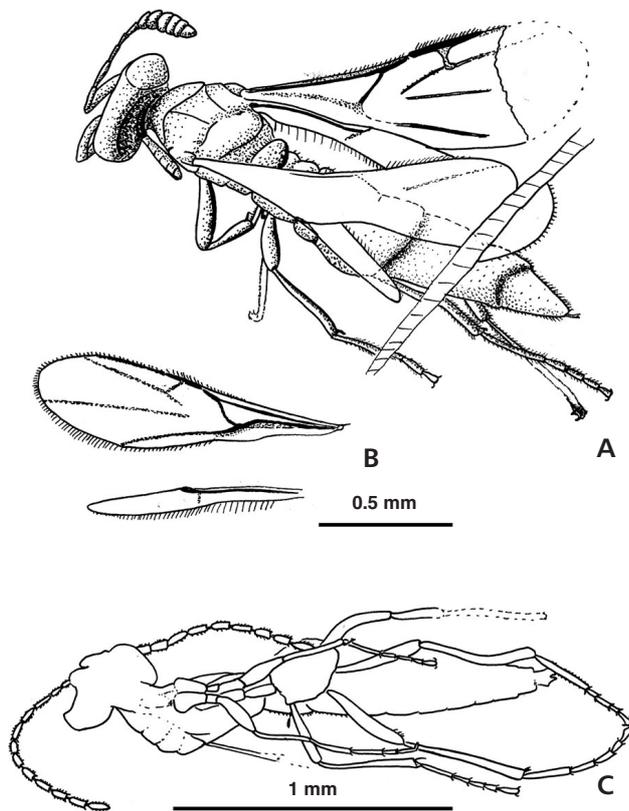
*Diagnosis.* – As for the genus (*vide supra*).

*Description.* – Female: Body size between 1.13 to 1.90 mm, heavily pigmented. Head subglobose, not compressed or flattened, not strongly transverse, slightly wider than long; vertex rounded; occipital carina present, laterally more distinct. Mandibles tridentate (clearly visible in MCNA 12600). Compound eye large, bare, postero-ventrally somewhat angular; orbital carina absent; inner orbits roughly parallel; ocelli at equal distance between mid ocellus longitudinal axis and compound eyes, and surrounded by low ridge. Frons with shallow frontal depression, median longitudinal carina present, without raised interantennal process between toruli; toruli opening anteriorly. Antenna 11-merous, covered in short setae; ra-

dicle inserted apically into base of scape, parallel to longitudinal axis of A1; scape 4 times longer than wide; pedicel 2.5–3 times longer than wide; funicle 3-merous; clava 6-merous, as long as wide clavomeres; sex segment not differentiated. Mesosoma not compressed, slightly longer than wide, semi-oval in dorsal view, as wide as head, with marked pointed sculpture; pronotum with anterolateral corners rounded; transverse pronotal carina absent; epomial carina absent; pronotal humeral carina absent; lateral surface of pronotum concave; mesoscutum short; notauli present; parapsidal lines absent; transscutal articulation well developed, simple; mesoscutellum transverse, slightly wider than long, relatively flat, with transverse row of posterior mesoscutellar pits; mesopleural depression broad, deep; metascutellum narrow, without processes; propodeum with elevated posterior margin and lateral sharp short processes; metanotal depression present. Legs densely setose with large tibiae; trochantellus present on all legs; femora weakly incrassate; tibiae without spines; tibial spur formula 1-2-2 (meso- and metatibial spurs fine, reduced, and difficult to discern); protibial calcar simple; tarsi pentamerous, tarsomeres cylindrical; metabasitarsus slightly shorter than combined lengths of remaining tarsomeres. Forewing extending to metasomal apex; R faintly bent at position of basal vein; basal vein nebulous; costal margin in costal cell basad of confluence of R with margin not infumate; R without bulla immediately prior to marginal vein; thickened weakly pigmented marginal vein, about 5–6 times longer than wide; r-rs (stigmal vein) forming acute angle with costal margin, long, slightly longer than marginal vein; R1 distinct, well developed, continuing along costal margin to form postmarginal vein, slightly shorter than marginal vein; 3Rs faintly nebulous without tubular stub at apex of r-rs, 2–2.5 times longer than r-rs; 2Rs nebulous, connecting to M; M nebulous; Cu nebulous; M+Cu nebulous. Hind wing with R tracheate throughout length, complete (bending apically to meet costal margin), with three hamuli on R at contact with costal margin; marginal fringe of setae short. Metasoma not compressed, cylindrical, slightly longer than head and mesosoma combined; metasomal segments 2–3 times wider than long, with first segment somewhat humped, and setose last terga; T2 slightly larger than remaining segments; seven terga visible (clear in holotype and other specimens); laterotergites narrow; T7 bluntly rounded at apex. Ovipositor and valves long and thin, in many cases extremely exerted and proximally covered by pigmented membrane.

**Figure 6.** General habitus. • A – *Proterosceliopsis masneri* gen. and sp. nov. female (MCNA 13631), B – *P. masneri* gen. and sp. nov. male (MCNA 12579). • C – *Tithonoscelio resinalis* gen. and sp. nov. female (MCNA 8633). • D – *Amisascelio temporarius* gen. and sp. nov. female (MCNA 13643). • E – *Bruescelio platycephalus* gen. and sp. nov. female (MCNA 13284) in dorsal view and F – in lateral view. • G – *Juxtascelio interitus* gen. and sp. nov. female (MCNA 12600).





**Figure 7.** A – dorsal view of female *Alavascelio delvallei* gen. and sp. nov., holotype (MCNA 9912.1). • B – detail of complete wings, paratype (MCNA 9892). C – ventral view of male (MCNA 9912.2) (A and C at same scale).

***Alavascelio* gen. nov.**

*Etymology.* – The new genus-group name is a combination of Álava and *Scelio*, type genus of the family Scelionidae. The name is masculine.

*Type species.* – *Alavascelio delvallei* sp. nov.

*Diagnosis.* – Head slightly anteriorly flattened; occipital carina weakly present; antenna 12-merous; clava 6-merous (with very wide clavomeres); funicle 4-merous; ocelli not visible; mesosoma short; mesoscutal pits absent; forewing not reaching metasomal apex; tibial spur combination 1-2-2; calcar with bifid apex; R with bulla before marginal vein; 1Rs long, about 3.5 times the length of r-rs; 2Rs not connecting with M; 3Rs about 5-6 times the length of r-rs; hind wing with Rs+M present; metasoma lanceolate, longer than the rest of the body; female with 6 terga visible (male 7), almost as long as wide; T1 somewhat humped dorsally in female; ovipositor very short and thin. In addition, new genus readily distinguished from previously described Cretaceous genera due to 12-merous antenna (differences between new genera outlined in key herein, *vide infra*).

***Alavascelio delvallei* sp. nov.**

Figures 7, 11A, B

*Etymology.* – The specific epithet honors Mr. Rafael López del Valle, geologist and gemologist from Álava who has prepared all the amber from Spain for its study.

*Type material.* – Holotype MCNA 9912.1 (female) and paratypes MCNA 9912.2 (male), MCNA 9782 (female), MCNA 12564 (6 males, 2 females), and 12726 (with a dip-teran and arthropod fragments).

*Additional material.* – MCNA 9892 and MCNA 12666 have the same characters as *Alavascelio delvallei* except for an apparent 4-merous clava (probably a visual effect) and hind wing crossvein angled toward base instead of toward wing apex.

*Type locality.* – Moraza – Peñacerrada I.

*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo-La Orden Member boundary, Escucha Formation.

*Description.* – Body heavily setose and elongated, around 1.94 mm. Head compressed in dorsal view, transverse, wider than long; vertex rounded; occipital carina present but weak. Mandible (right) apparently tridentate. Compound eye large, bare; orbital carina absent; inner orbits roughly parallel; ocelli not visible. Frons relatively flat, without frontal depression, median longitudinal carina absent, without raised interantennal process between toruli; toruli opening anteriorly. Male and female antenna 12-merous; scape, pedicel and funicle elongate; F1 as long as pedicel; funicle 4-merous, progressively shortening and widening, but clearly distinguished from clava; clava 6-merous, flattened, clavomeres 3 times wider than long; sex segment not differentiated. Mesosoma not compressed, slightly longer than wide, semi-oval in dorsal view, elongate, as wide as head; pronotum with anterolateral corners rounded; transverse pronotal carina absent; epomial carina absent; pronotal humeral carina absent; lateral surface of pronotum convex, without scrobe; mesoscutum short; notauli present; parapsidal lines absent; transscutal articulation well developed, simple; mesoscutellum transverse, much wider than long, without posterior pits; metascutellum narrow, without processes; propodeum unadorned, without tubercles, processes, keels, or teeth; metanotal depression present. Legs elongate and densely setose; trochantellus present on all legs; femora weakly incrassate; tibiae without spines; tibial spur formula 1-2-2 (seen in MCNA 12666); protibial calcars both bifid (well seen in MCNA 9912 ventral view); tarsi pentamerous, tarsomeres cylindrical; probasitarsus with well-developed inner comb of se-

tae; metafemur widened and flattened; metabasitarsus about as long as combined lengths of remaining tarsomeres, with inner comb of stiff setae. Forewing not extending to metasomal apex; R extending well beyond marginal vein but not contacting with 3Rs; faintly bent at position of basal vein; basal vein nebulous; costal margin in costal cell basad of confluence of R with margin slightly infumate; R with bulla immediately prior to marginal vein; thickened marginal vein present, about three (or more) times longer than wide and about as long as r-rs or longer; r-rs (stigmatal vein) convex with respect to apical margin, arising angled towards apical margin from marginal vein, long, and not expanded at apex; R1 distinct, elongate, continuing along costal margin to form postmarginal vein, about 3.5 times length of r-rs and nearly closing marginal cell; 3Rs nebulous, without basal stub at apex of r-rs, 5–6 times length of r-rs, reaching apical margin; 2Rs nebulous, not connecting to M; M nebulous; Cu nebulous; M+Cu nebulous, with a darkened area of membrane present around. Hind wing with R tracheate throughout length, complete (bending apically to meet costal margin), with three hamuli on R at contact with costal margin; Rs+M present, nebulous; marginal fringe of setae long. Metasoma not compressed, cylindrical, around 1.5 times as long as the rest of the body combined, around 5–6 times longer than wide; all segments except the apical subequal in length almost as long as wide, or slightly wider (except last, a little longer); seven terga and sterna visible in male, six in female; laterotergites narrow; male T7 apically rounded, not reflexed; female T6 narrowly rounded at apex with several longer setae on apical terga.

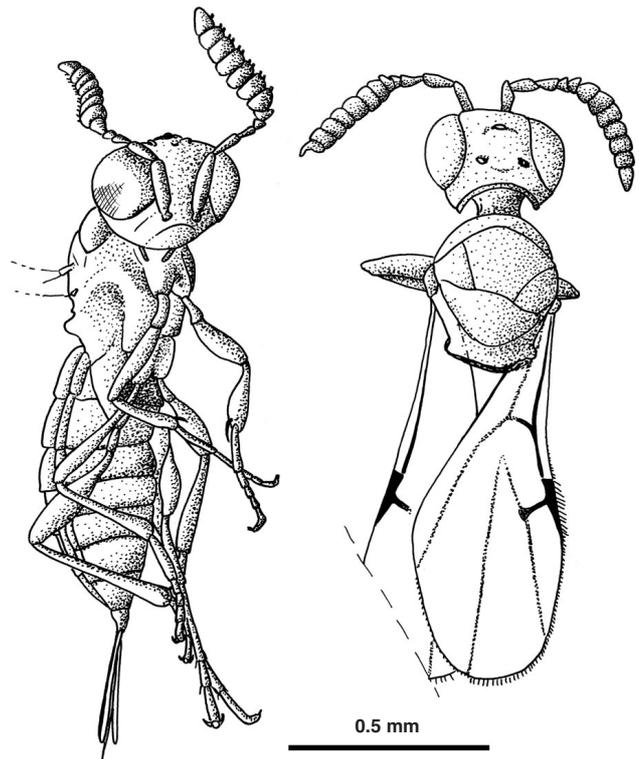
**Male:** As female except for: antenna densely setose, without clava, filiform with all flagellomeres elongated, around 3 times longer than wide; mesosoma and metasoma narrower than head, and the last apically rounded.

***Electroteleipsis* gen. nov.**

**Etymology.** – The new genus-group name is a combination of the generic name *Electroteleia* and the Greek suffix *-opsis*, meaning, “looking like”. The name is feminine.

**Type species.** – *Electroteleipsis hebdomas* sp. nov.

**Diagnosis.** – Head subglobose; ocelli placed in weak dorsal protuberance, separated for about an ocellar distance to compound eye, much more separated from the other lateral ocellus; antenna 12-merous; clava 7-merous; funicle 3-merous; mesosoma almost as wide as long; mesoscutal pits absent; forewings overpassing metasomal apex; tibial spur combination 1-2-2; calcar with bifid apex (at least right); R with bulla before marginal vein; 2Rs faintly connecting with M; 3Rs about 3.5 times the length of r-rs; me-



**Figure 8.** A – ventral view of *Electroteleipsis hebdomas* gen. and sp. nov., holotype (MCNA 8909.1). • B – dorsal view of paratype (MCNA 8793), both at same scale.

tasoma as long as the rest of the body; female with 7 terga visible, much wider than long; ovipositor and sheaths long and thin. In addition, new genus readily distinguished from previously described Cretaceous genera due to 12-merous antenna (differences between new genera outlined in key herein, *vide infra*).

**Comments.** – This genus is similar to *Electroteleia* Brues in middle Eocene Baltic amber, which is clearly a member of the Sparasionini. The new genus differs at least in the much smaller size (around 1.3 mm versus 3.5 mm), the funicular antennomeres much shorter than those of the clava (not so differentiated in size in *Electroteleia*), toruli opening anteriorly (laterally in *Electroteleia*, based on redescription of Johnson *et al.* 2008), transverse pronotal carina and vertical epomial carina absent (both present in *Electroteleia*), seven metasomal segments externally visible in female (vs. six), and wider laterotergites.

***Electroteleipsis hebdomas* sp. nov.**

Figures 8, 11C

**Etymology.** – The specific epithet is the Greek term *hebdomas*, meaning “seven”, typically in reference to the days of the week but here referring to the 7-merous clava.

*Type material.* – Holotype MCNA 8909.1 (with an indeterminate scelionid and a dipteran) and paratypes MCNA 8793 and MCNA 9878 (all specimens female).

*Additional material.* – MCNA 13834.1 (with several arthropod fragments) fits description except for its small size 0.98 mm and basitarsus apparently as long as  $t_2-t_4$ , not  $t_2-t_5$  combined.

*Type locality.* – Moraza – Peñacerrada I.

*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo – La Orden Member boundary, Escucha Formation.

*Description.* – Body size 1.23–1.38 mm, covered by fine setae. Head subglobose, not flattened, transverse, around two times wider than long; vertex rounded; occipital carina present, distinctly lateral. Clypeus short, strongly transverse; malar sulcus present. Compound eye large, bare, occupying large portion of head; orbital carina absent; inner orbits roughly parallel; ocelli placed in weak dorsal protuberance. Frons relatively flat, without frontal depression, median longitudinal carina absent, without raised interantennal process between toruli; toruli opening anteriorly. Female antenna 12-merous, flattened; scape elongate; pedicel 3 times longer than apical width, with basal constriction; funicle 3-merous, with F1 twice as long as wide and constrained basally; F3 wider than F1 and F2 but differentiated from clava; F4 somewhat reduced with respect to rest of apical claval segments; F5–F10 with short, wide sensilla.; clava 7-merous, claval formula A6–A12, 1-2-2-2-2-1, with pairs of sensilla longitudinally arranged; claval segments around 2.5 times wider than long; sex segment not differentiated. Mesosoma not compressed, slightly longer than wide, semi-oval in dorsal view, as wide as head; pronotum with anterolateral corners rounded; transverse pronotal carina absent; epomial carina absent; pronotal humeral carina absent; lateral surface of pronotum convex, without scrobe; mesoscutum elongate; notauli present; parapsidal lines absent; transscutal articulation well developed, foveolate; mesoscutellum transverse, slightly wider than long, relatively flat, apparently without posterior pits; metascutellum narrow, without processes; propodeum with dorsolateral tubercles; metanotal depression present. Legs moderately setose; trochantellus present on all legs; femora weakly incrassate; distal protibial comb of stiff setae; but without distinct spines; tibial spur formula 1-2-2 (meso- and metatibial spurs fine, reduced, and difficult to discern); left protibial calcar simple (MCNA 8909.1), right protibial calcar bifid (as a faint shadow in MCNA 8909.1, and clearly in MCNA 9878 in ventral view); tarsi pentamerous, tarsomeres cylindrical; metatibia around as long as metatarsus, 1/3 longer than metafemur, with posterior marginal row of setae; metabasitarsi as long

as  $t_2-t_5$ ; metabasitarsus slightly shorter than combined lengths of remaining tarsomeres. Forewing extending slightly beyond the metasomal apex; R present beyond marginal vein, and with very faint distal portion of Rs+M, faintly bent at position of basal vein; basal vein nebulous; costal margin in costal cell basad of confluence of R with margin not infumate; R with bulla immediately prior to marginal vein; thickened weakly pigmented marginal vein, about two times (or more) longer than wide; r-rs (stigmatal vein) forming nearly right angle with costal margin, long, about as long as marginal vein; R1 distinct, well developed, continuing along costal margin to form postmarginal vein nearly as long as marginal vein; 3Rs nebulous except for very short basal stub at apex of r-rs, 3.5 times longer than r-rs, slightly angled with respect to 2Rs; 2Rs nebulous, connecting to M; M nebulous; Cu nebulous; M+Cu faintly nebulous; Rs, M and Cu reaching wing margin. Hind wing with R tracheate throughout length, complete (bending apically to meet costal margin), with three hamuli on R at contact with costal margin; marginal fringe of setae short. Metasoma not compressed, longer than head and mesosoma combined; all segments except the apical subequal in length, wider than long, with narrow laterotergites, T2 slightly longer than others; seven terga visible in female; laterotergites narrow; T7 bluntly rounded at apex with long apical setae on terga; ovipositor and valves exerted, very thin, as long as half of metasoma.

#### *Perimoscelio* gen. nov.

*Etymology.* – The new genus-group name is a combination of the Latin term *perimo* (meaning “abolish”) and *Scelio*, type genus of the family Scelionidae. The name is masculine.

*Type species.* – *Perimoscelio tyrbastes* sp. nov.

*Diagnosis.* – Head subglobose, not compressed or flattened, about as long as wide; vertex rounded; occipital carina present. Clypeus short, strongly transverse; malar sulcus present; right mandible quadridentate, left tridentate (see holotype). Compound eye large, bare; orbital carina absent; inner orbits roughly parallel. Frons relatively flat, without frontal depression, median longitudinal carina absent, without raised interantennal process between toruli; toruli opening anteriorly. Male and female antenna 11-merous; radicle inserted laterally into base of scape, angled relative to longitudinal axis of A1; funicle 3- or 4-merous; clava 6- or 5-merous; sex segment not differentiated. Mesosoma not compressed, longer than wide, semi-oval in dorsal view; pronotum with anterolateral corners rounded; transverse pronotal carina absent; epomial carina absent; pronotal humeral carina absent; lateral surface of pronotum convex, without scrobe; mesoscutum elongate; notauli

present; parapsidal lines absent; transscutal articulation well developed, simple; mesoscutellum transverse, wider than long, relatively flat, with transverse row of posterior mesoscutellar pits; mesopleural depression broad, shallow; metascutellum narrow, without processes; propodeum with dorsolateral tubercles; metanotal depression present. Trochantellus present on all legs; femora weakly incrassate; tibiae without spines; tibial spur formula 1-2-2 (see ventral view of MCNA 8987 *P. tyrbastes*, or right middle and left hind from *P. confector* MCNA 9438); protibial calcar on right bifid and on left simple (in *P. tyrbastes*, clear in MCNA 9900, in *P. confector* very clear in MCNA 9438); tarsi pentamerous, tarsomeres cylindrical; metabasitarsus shorter than combined lengths of remaining tarsomeres. Forewing not or barely extending to metasomal apex; R faintly bent at position of basal vein; basal vein nebulous; costal margin in costal cell basad of confluence of R not infumate; R with bulla immediately prior to marginal vein; thickened weakly pigmented marginal vein, about three times longer than wide; r-rs (stigmatal vein) forming acute or right angle with costal margin, long, about as long as marginal vein; R1 distinct, well developed, continuing along costal margin to form postmarginal vein, almost three-quarters length of marginal vein; 3Rs nebulous, without tubular stub at apex of r-rs, 3.5 times longer than r-rs; 2Rs nebulous, connecting to M; M nebulous; Cu nebulous; M+Cu nebulous. Hind wing with R tracheate throughout length, complete (bending apically to meet costal margin), with three hamuli on R at contact with costal margin; marginal fringe of setae short. Metasoma slightly compressed dorso-ventrally, about as long as head and mesosoma combined; all segments except the apical subequal in length, T2 slightly longer than others; seven terga and sterna visible in male and female; laterotergites narrow; male T7 apically rounded, not reflexed; female T7 bluntly rounded at apex. New genus similar to previously described Cretaceous genus *Cenomanoscelio* in terms of antennal structure, but differs by lack of elongate tergum 3.

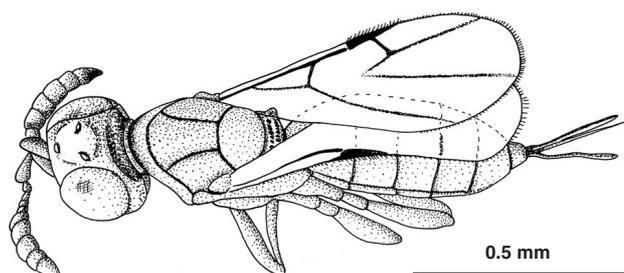
***Perimoscelio tyrbastes* sp. nov.**

Figures 9, 11E

*Etymology.* – The specific epithet is the Greek term *tyrbastes*, meaning, “agitator” or “disturber”.

*Type material.* – Holotype MCNA 9844 and paratypes MCNA 8987, MCNA 9900 and MCNA 10002 (all specimens female).

*Additional material.* – MCNA 9921 seems to have a slightly different body structure (smaller and wider) but it could be due to deformation and its position as preserved. However, it appears as though both calcars are bifid.



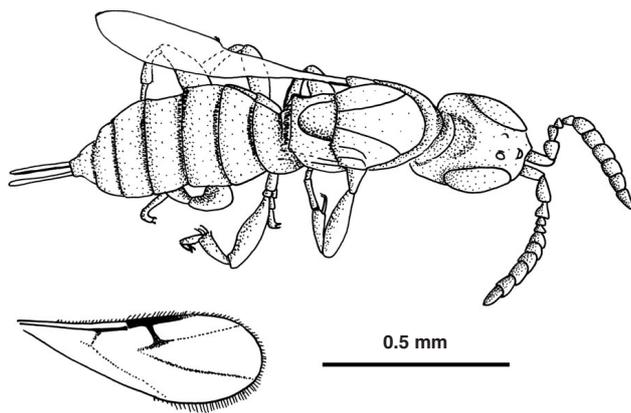
**Figure 9.** Dorsal view of *Perimoscelio tyrbastes* gen. and sp. nov., holotype (MCNA 9844)

*Type locality.* – Moraza – Peñacerrada I.

*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo – La Orden Member boundary, Escucha Formation.

*Diagnosis.* – Ocelli in low prominence surrounded by shallow pit; lateral ocelli closer to compound eyes (at about one ocellar diameter) than to mid ocellus longitudinal axis; mesoscutellum apically unadorned (or at least with less marked transverse row of pits); r-rs at slightly more acute angle relative to costal margin (more right in *P. confector*); antennal clava 5-merous, and funicle 4-merous.

*Description.* – Female: Body length between 0.80 to 1.15 mm, hardly pigmented, punctated sculpture. Head 1.25 times wider than long. Compound eyes circular, without flattened ventral margin, occupying large portion of head. Occipital carina laterally distinct, shortened dorsally. Scape 4–5 times longer than wide; pedicel 2 times longer than maximum width; clavomeres around as wide as long. F1 reduced but twice long as wide; F2 and F3 reduced and much wider than long; F4 wide, with shape similar to that of clavomeres but differentiated by smaller size. Pronotum dorsally distinct; propodeum somewhat elevated posteriorly. Metatibia and metabasitarsus with inner and distal marginal row of stiff setae. Calcar slightly sinuous; probasitarsal comb of setae present. Wings with membrane densely setose. Rs, M and Cu reaching apical margin; marginal vein and marginal sector between M and Cu with distinctly longer marginal setae than in the rest of anterior margin of wing (this is a character shared by all taxa described in this study); posterior margin of wing with darkened line, probably corresponding to A. 3Rs slightly angled with respect to 2Rs, which is slightly more posterior than 3Rs instead of aligned with it, and both are separated by small posterior expansion of r-rs. Hind wing with setae distinctly longer and more separated in the concave posterior sector (this is also shared by all taxa described here). Metasoma with setose last terga; ovipositor exerted with distinct long valves.



**Figure 10.** A – dorsal view of *Perimoscelio confector* gen. and sp. nov., holotype (MCNA 9438). • B – forewing, paratype (MCNA 8774), both at same scale.

***Perimoscelio confector* sp. nov.**

Figures 10, 11F

*Etymology.* – The specific epithet is the Latin term *confector*, meaning “destroyer”.

*Type material.* – Holotype MCNA 9806 and paratypes MCNA 8755.1 (together with a male with 14-antennomeres), MCNA 8774 (with two dipterans), MCNA 9227, MCNA 9438, MCNA 10737, MCNA 10754, MCNA 12584 and MCNA 12586 (type series all female specimens).

*Additional material.* – MCNA 9773 has unclear clava and severely damaged wings but the general aspect is of *P. confector*, while MCNA 9812 is very damaged but the right calcar is clearly bifurcate, and its size and body structure correspond with *P. confector*.

*Type locality.* – Moraza – Peñacerrada I.

*Type horizon.* – Lower Cretaceous, upper Albian, Regachuelo – La Orden Member boundary, Escucha Formation.

*Diagnosis.* – All ocelli equidistant to each other, in low prominence, removed by one ocellar diameter from compound eyes. Mesoscutellum apically with transverse row of pits (more marked than in *P. tyrbastes*); r-rs orthogonal with respect costal margin; antennal clava 6-merous, funicle 3-merous.

*Description.* – Female: Body length around 0.96 to 1.82 mm, well-pigmented. Head around as long as wide,

with very short occipital carina; compound eyes not perfectly ovate, slightly angular between posterior and ventral margins. Antenna slightly flattened, not very setose; scape around 4 times longer than wide; pedicel around twice long as apical width; claval segments around as long as wide; F1 proximally constricted, two times longer than wide; F2 and F3 half as long as F1. Mesosoma as wide as head; pronotum dorsally short; scutellum short, not elevated with respect to rest of mesosoma. Propodeal tubercles very small. Legs densely setose; calcar sinuous; metatibia with inner row of stiff short setae; metabasitarsus very short (1/3 of metatibial length at most), apparently with inner comb (see MCNA 9806). Forewing with postero-apical marginal setae distinctly longer; marginal vein elongate; Rs, M and Cu reach wing margin; 3Rs not angled with respect to 2Rs. Hind wing with only marginal vein; posterior marginal setae distinctly longer than anterior. Metasomal segments much wider than long, with distinct longer setae on apical terga. Ovipositor extremely thin, exerted as valves.

**Genus and species indet.**

The following specimens are insufficiently preserved (and often in darkly turbid amber), to permit placement within any of the above taxa or to diagnose as new species. We provide a list of the specimens, with very brief comments on what little information could be discerned.

MCNA 8764: antennal composition 6/3; with elongate body, resembling *Juxtascelio*.

MCNA 8876: wide profemur; body wide (of robust aspect) and shorter than wings; no antenna preserved; unknown sex.

MCNA 8956: very fragmented remains, barely assignable to Scelionidae.

MCNA 8997: very poorly preserved, assigned to Scelionidae based on structure of remains of mesosoma and remains of wing venation.

MCNA 9090: clearly scelionid forewings.

MCNA 9215: body structure similar to *Perimoscelio*, but antennal structure unclear (though looks like 7/5); left calcar simple.

MCNA 9379: very poorly preserved, only seen as 11-merous antenna (6/3 composition).

MCNA 9512: severely damaged; possibly 6/3 antennal composition.

MCNA 9589: two Scelionidae very obscured, one male and other probably female; found together with an indeterminate stigmaphronid.

**Figure 11.** General habitus. • A – *Alavascelio delvallei* gen. nov. and sp. male (MCNA 9912.2) and B – female (MCNA 9912.1). • C – *Electroteleopsis hebdomas* gen. and sp. nov. female (MCNA 8909.1). • D – *Perimoscelio confector* gen. and sp. nov. female (MCNA 9438). • E – *Perimoscelio tyrbastes* gen. and sp. nov. female (MCNA 9844).



MCNA 9606: very poor posterior remains, identified as scelionid by part of wing venation.

MCNA 9819: antenna 14-merous, 7/5 composition with loose clava; Rs around 3 times as long as r-rs; elongate body, but apparently not as much as in *Proterosceliopsis masneri* (metasoma less than half the total body length and terga look wider than long)

MCNA 9836: antennal composition 6/3; with body structure resembling *Perimoscelio confector*.

MCNA 10011: looks very much like a male *Perimoscelio*, with 11 antennomeres, but it is not possible to place it in one of the species confidently.

MCNA 10046: antennal composition 6/3; with body structure resembling *Perimoscelio confector*.

MCNA 10055: antennal composition 6/3; with body structure resembling *Perimoscelio confector*; found with 3 other undetermined arthropods.

MCNA 12527: antennal composition clearly 6/3, but body very damaged.

MCNA 12533: antennal composition 6/3; with body structure resembling *Perimoscelio confector*.

MCNA 12573: antennal composition 6/3; only one hind leg preserved with body structure resembling *Perimoscelio confector*.

MCNA 12612: two specimens with antennal composition 6/3; with body structure resembling *Perimoscelio confector*.

MCNA 12626: very damaged, but elongated and apparently with antennal composition 4/6; clava well defined (3 apical clavomeres fused or nearly so); antenna very setose; specimen slightly resembling *Alavascelio* in a few details but clearly different.

MCNA 12792.1: antennal composition unknown; severely damaged wings; long ovipositor; specimen close to an anterior half of a male of moderately large size.

MCNA 12792.2: probably male 11-merous, gradually increasing size (similar in aspect to MCNA 9773).

MCNA 12793: fragmented specimen with incomplete antenna; body shape as in *Perimoscelio confector*; with tibial spur combination 1-2-2, apparently with right calcar bifid and with left simple.

MCNA 13276: small total body size; antenna apparently of 6/4 composition, with very compressed funicle; very short r-rs.

MCNA 13288: apparently with 5/4 antennal composition, but distinctly smaller and with narrower body structure than *Perimoscelio tyrbastes*.

### Key to species of Scelionidae in Spanish amber

1. Antenna 14-merous; tibial spur formula 1-2-2; calcar bifid . . . . . 2

- Antenna 11- or 12-merous; tibial spur formula 1-2-2 or 1-1-1; calcar bifid, simple or mixed (with right calcar bifid, and left calcar simple) . . . . . 3
- 2. Clava/funicle 6/6; occipital carina absent; extremely flattened head; first metasomal segment without striation . . . . . *Bruescelio platycephalus* gen. et sp. nov.
- Clava/funicle 7/5; occipital carina present; globular head; first metasomal segment with longitudinal sculpture. . . . . *Proterosceliopsis masneri* gen et sp. nov.
- 3. Antenna 12-merous . . . . . 4
- Antenna 11-merous . . . . . 6
- 4. Very small size (around 0.63 mm); strongly flattened head; clava/funicle 5/5; notauli absent; tibial spur formula 1-1-1; Rs vein absent in forewing . . . . . *Tithonoselio resinalis* gen. et sp. nov.
- Size around 1.20 mm to 2 mm; head globular or not extremely flat; clava/funicle not 5/5; notauli present; tibial spur formula 1-2-2; forewing with Rs . . . . . 5
- 5. Clava/funicle 6/4; bifid calcar; forewing with Rs vein very elongate and very thin Rs cell; metasoma longer than the rest of the body. . . . . *Alavascelio delvallei* gen. et sp. nov.
- Clava/funicle 7/3; calcar mixed; forewing with typical scelionid length for Rs vein and cell; metasoma about as long as the rest of the body . . . . . *Electroteleopsis hebdomas* gen. et sp. nov.
- 6. Mixed calcar; right mandible with 4 teeth, left with 3 . . . . . 7
- Simple calcar; both mandibles tridentate . . . . . 8
- 7. Clava/funicle 5/4; mesonotum wider than long. . . . . *Perimoscelio tyrbastes* gen. et sp. nov.
- Clava/funicle 6/3; mesonotum slightly longer than wide . . . . . *Perimoscelio confector* gen. et sp. nov.
- 8. Clava/funicle 7/2; epomial carina present; pronotal humeral carina present; transscutal sulcus crenulate . . . . . *Amissascelio temporarius* gen. et sp. nov.
- Clava/funicle 6/3; epomial carina absent; pronotal humeral carina absent; transscutal sulcus simple . . . . . *Juxtascelio interitus* gen. et sp. nov.

### Discussion

The main challenges for any study of Cretaceous Scelionidae are the low number of specific characters observable, and their diminutive size, made all the more difficult by their presence in sometimes turbid amber. Diagnostic characters lay mainly on antennal composition and especially on funicle-clava composition. The result of this is that

females are most easily identified and we emphasized the females in our taxonomic treatment, except in a few cases where the morphology of males obviously matched and permitted easy correspondence with particular females or they were preserved in association.

We did not initially wish to establish several new genera, instead attempting to place the species into already defined Cretaceous genera. However, the character variation simply did not permit such a classification, as it would have required radically redefining several already well-circumscribed fossil genera, rendering them meaningless and hypervariable relative to modern counterparts. Some specimens are superficially similar to other fossil genera, but upon finer examination are clearly distinct in a number of minute details, many of which are likely of phylogenetic importance. For example, although *Electroteleiopsis* seems very similar to *Electroteleia* (discussed above) or *Proterosceliopsis*, and similar to other 14-merous taxa like *Proteroscelio*, *Archaeoscelio*, or *Nixonia*, numerous characters distinguish each from all other known genera. *Janzenella* (Masner & Johnson 2007) resembles greatly *Bruescelio* at first sight, but the antenna is 14-merous in *Bruescelio* and 11-merous in *Janzenella*, the tibial spur combination is 1-1-2 (1-2-2 in *Bruescelio*), and the wing venation is dramatically more reduced than in *Bruescelio*. A recent review of *Platyscelio* (Taekul et al. 2010) also shows strong similarity between general body habitus with *Bruescelio* but differences in many characters, such as the much larger size (3–5.6 mm of *Platyscelio* vs. 0.83–0.9 mm of *Bruescelio*), the apically expanded scape, the medial longitudinal line of the frons, and also the much reduced venation in *Platyscelio*.

The antennomere number is clearly a relatively conservative character among platygastroids, as is the tibial spur formula (Johnson & Masner 2006), and these characters proved quite useful in segregating the groups within the Spanish amber fauna, but necessitated the establishment of several presently monospecific genera so as to avoid creating genera with radically different antennomere counts and structures as well as varied tibial spur formulae. Uniting some of these into genera of disparate morphologies would certainly have created paraphyletic groups or even genera with species that are distantly related (polyphyletic).

Many sources indicate scelionids as egg parasitoids of various arthropod lineages and some of them show specific structures, which could be related to escape from eggs, like *Sparasion*, *Acanthoscelio*, or *Tyrannoscelio* (Johnson & Masner 2006, Johnson et al. 2008a, Masner et al. 2007a). Interestingly, none of these unique modifications are observable in the Spanish amber species. The elongate ovipositor in many of them suggest they oviposited into a thick body of some kind, needing to perforate plant or animal tissues, or perhaps deep into piles of eggs. It is worth considering that these early scelionids may not have been

specialized for parasitizing eggs and that such a shift took place later in their evolution. Certainly a great deal remains to be discovered about Mesozoic Scelionidae, but it is clear that a remarkable variety of species existed and that their morphologies suggest they may have had a different, likely plesiomorphic, mode of parasitism relative to several modern lineages in the superfamily. For the moment, much remains speculative but it is hoped that continued and on-going studies on other deposits (e.g., McKellar et al., in prep.) will continue to unravel the complexity of Cretaceous Platygastroidea and contribute significantly to resolving basal relationships within the superfamily.

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## Appendix

Nomenclatural correction for the Cretaceous amber scelionid genus *Microptera*

### ***Jordanoscelio* nom. nov.**

*Microptera* Kaddumi, 2005, *nomen praeoccupatum*, nec Fleming, 1822 (Pisces), Robineau-Desvoidy, 1830 (Diptera), Nuttall, 1834 (Aves). Type species: *Microptera attiki* Kaddumi, 2005, by original designation.

*Type species.* – *Microptera attiki* Kaddumi, 2005, autobasic.

*Etymology.* – The new genus-group name is a combination of Jordan and *Scelio*, type genus of the family.

*Included species.* – The genus presently includes only the type species, *Jordanoscelio attiki* (Kaddumi), comb. nov.

*Comments.* – This genus was placed originally in an unavailable, monogeneric, purportedly-new family group, the Platychalidae (*nomen invalidum*, ICZN 1999: Art. 11.7.1, name not formed from stem of available generic name). Regardless of the various nomenclatorial difficulties surrounding this taxon, the genus is definitively a scelionid, making Platychalidae an invalid synonym thereof. The number of metasomal segments appears to be seven in the available photographs, rather than six as originally described, but this requires confirmation. Unfortunately, the type resides in a private collection and is not available for study. For now the genus is simply retained as *incertae sedis* until such time as the holotype can be examined and the description corrected.