



Revalidation of the polymorphic genus *Acephalonomia* (Hymenoptera: Bethyliidae) and description of a new species from Micronesia

WESLEY D. COLOMBO and CELSO O. AZEVEDO

Universidade Federal do Espírito Santo, Ciências Biológicas, Av. Fernando Ferrari 514, Goiabeiras, Vitória 29075-910, Brazil; e-mails: wesleycolombo@gmail.com, bethyliidae@gmail.com

Key words. Hymenoptera, Bethyliidae, Scleroderminae, *Acephalonomia*, taxonomy, new species, Coleoptera, Ciidae, parasitoids, Micronesia

Abstract. The genus *Acephalonomia* Strejček, 1990 is revalidated and its single species, *Acephalonomia cisidophaga* Strejček, 1990, from Czech Republic and Slovakia is restituted in the original combination. The revalidation is based on distinct characters: antennae with eight flagellomeres and prestigmal abscissa of R1 vein dilated. The intraspecific polymorphism is also relevant for revalidation, although not exclusively so. We redescribe and illustrate the type species *Acephalonomia cisidophaga* and describe and illustrate a second new species with eight antennal flagellomeres from the Mariana Islands, *Acephalonomia micronesica* sp. n., and provide a key to this genus.

ZooBank Article Registration: <http://zoobank.org/urn:lsid:zoobank.org:pub:900C0CE0-650A-4321-B90C-02FDFB2EE9B0>

INTRODUCTION

The monotypic genus *Acephalonomia* was described by Strejček (1990) to accommodate a new species, *Acephalonomia cisidophaga* Strejček, 1990, having only 8 flagellomeres. So far only the type species has been known with such antennae. The author stated that *Acephalonomia* is similar to *Cephalonomia* Westwood, especially *C. formiciformis* Westwood, but he did not explain the nature of that similarity; at the same time he did affirm that the body plan of both genera is very different.

De Rond (2001) commented that the male genitalia, the wing pattern and the general body plan of *Acephalonomia* did not justify a genus separate from *Cephalonomia*. Thus, he proposed *Acephalonomia* as a junior synonym of *Cephalonomia*.

While examining the collection of the Bernice Pauahi Bishop Museum (Honolulu, U.S.A.) we discovered a species of bethylid that perfectly matched the concept of *Acephalonomia* proposed by Strejček (1990) with eight antennal flagellomeres, wing polymorphism and the same hosts, Ciidae beetles inhabiting polypore fungus.

Thus, the main goal of this contribution is to revalidate *Acephalonomia*, and the description of the second species of *Acephalonomia*. We also take the opportunity to summarize the available information on the biology and taxonomy of *Acephalonomia cisidophaga* and amend the generic diagnosis by including additional characters.

MATERIAL AND METHODS

The type material of *Acephalonomia cisidophaga* is deposited in the Entomology Department of the National Museum, Praha, Czech Republic (NMPC, curator: Jan Macek) and was examined for the redescription and new images were prepared by J. Hájek and M. Tkoč.

The specimens of *Acephalonomia micronesica* sp. n., were collected on Mount Lasso on Tinian Island, one of the three principal islands of the Commonwealth of the Northern Mariana Islands. This material belongs to the Bernice P. Bishop Museum, Honolulu, Hawaii, USA (BPBM, curator: James Boone). The micropterous and macropterous specimens were obtained by breeding and emerged from the same host.

The nomenclature of the sculpturing on the integument follows Harris (1979) and the general morphological terms follow Kawada et al. (2015) and Azevedo et al. (2018). Measurements and indices used in this study are as follows: Body length measured from the apex of clypeus to the posterior margin of the last metasomal segment; length of forewing, the distance from the tegula to distal margin; LH – length of head, measured in frontal view, from crest of vertex to median apical margin of clypeus; WH – width of head, measured in frontal view, maximum width including eyes; WF – width of frons, measured in frontal view, minimum width, usually just below the eyes; HE – height of eye, measured in lateral view, its maximum height (length); OOL – ocellocular line, measured in laterodorsal view, the shortest distance from top of eye to posterior ocellus; WOT – width of ocellar triangle, measured in frontal view, maximum width, including ocelli; VOL – vertex-ocular line, measured in dorsal view, distance from top of eye to apex of vertex.

The images were taken under a Leica Z16 APO stereomicroscope coupled to a Leica DFC 2 video camera and using the Modular Dome Illumination System of Kawada & Buffington (2016). Helicon Focus was used to combine the images.

The data in the section on the specimens examined is literally transcribed from the labels, additional data are in square brackets.

RESULTS

Genus *Acephalonomia* Strejček, 1990 stat. rev.

Type species. *Acephalonomia cisidophaga* Strejček, 1990: 47 (by original designation).

Redescription

Female. Body with scattered short setae. Head elliptical in lateral view. Malar space conspicuous. Mandible with dorsal margin not denticulate. Clypeus short, subvertical, median carina present. Antenna with eight flagellomeres. Eye scarcely setose. Gena hidden by eye in dorsal view. Dorsal pronotal area ecarinate, not depressed forward, cervical pronotal area short and subvertical. Notaulus absent. First abdominal spiracle located on lateral surface of metapectal-propodeal complex. Propleuron with anterior corners not prominent in dorsal view. Prosternum small, much smaller than ventral surface of procoxa. Metasoma robust, cross-section subcylindrical, very poorly setose; without tubercles; apical segments orientated downward.

Micropterous form. Mandible wide proximally and progressively narrowing distally. Parapsidal signum absent. Mesoscutum-mesoscutellar sulcus absent. Micropterous, cells and veins indistinguishable. **Macropterous form.** Mandible narrow. Ocelli present. Parapsidal signum present. Mesoscutum-mesoscutellar sulcus complete. Macropterous. Forewing with anterior margin incurved, without closed cells; only Subcostal+Radial (Sc+R) and prestigmal abscissa of R1 veins present, latter very dilated; pterostigma semicircular; line of flexion not bifurcated. Hind wing with three distal hamuli.

Male. Head elliptical in lateral view. Mandible with dorsal margin not denticulate. Antenna with eight flagellomeres. Eye scarcely setose. Gena hidden by eye in dorsal view. Metasoma robust, cross-section subcylindrical, very poorly setose; without tubercles; apical segments orientated downward. **Macropterous form.** Ocelli present. Notaulus present. Parapsidal signum present. Mesoscutum-mesoscutellar sulcus complete. Macropterous. Forewing with anterior margin incurved, without closed cells; only Subcostal+Radial (Sc+R) and prestigmal abscissa of R1 veins present, latter very dilated; pterostigma semicircular. **Micropterous form.** Parapsidal signum absent. Mesoscutum-mesoscutellar sulcus absent. Micropterous, cells and veins indistinguishable.

Included species. *Acephalonomia cisidophaga* Strejček, 1990; *Acephalonomia micronesica* sp. n.

Hosts. Coleoptera: Ciidae (Strejček, 1990, and present paper).

Distribution. Western Palaearctic Region (known from Czech Republic and Slovakia) and Oceanian Region (Northern Mariana Islands).

Key to species of *Acephalonomia*

- 1 Macropterous form 2
- Micropterous form 3
- 2 Flagellomere I shorter than flagellomere II; metapectal-propodeal disc polished with lateral carina complete *A. micronesica* sp. n.
- Flagellomere I as long as flagellomere II; metapectal-propodeal disc punctate with lateral carina incomplete *A. cisidophaga*
- 3 Ocelli present *A. cisidophaga*
- Ocelli absent *A. micronesica* sp. n.

Acephalonomia cisidophaga Strejček, 1990 comb. rest.

Figs 1–4

Strejček, 1990: 47.

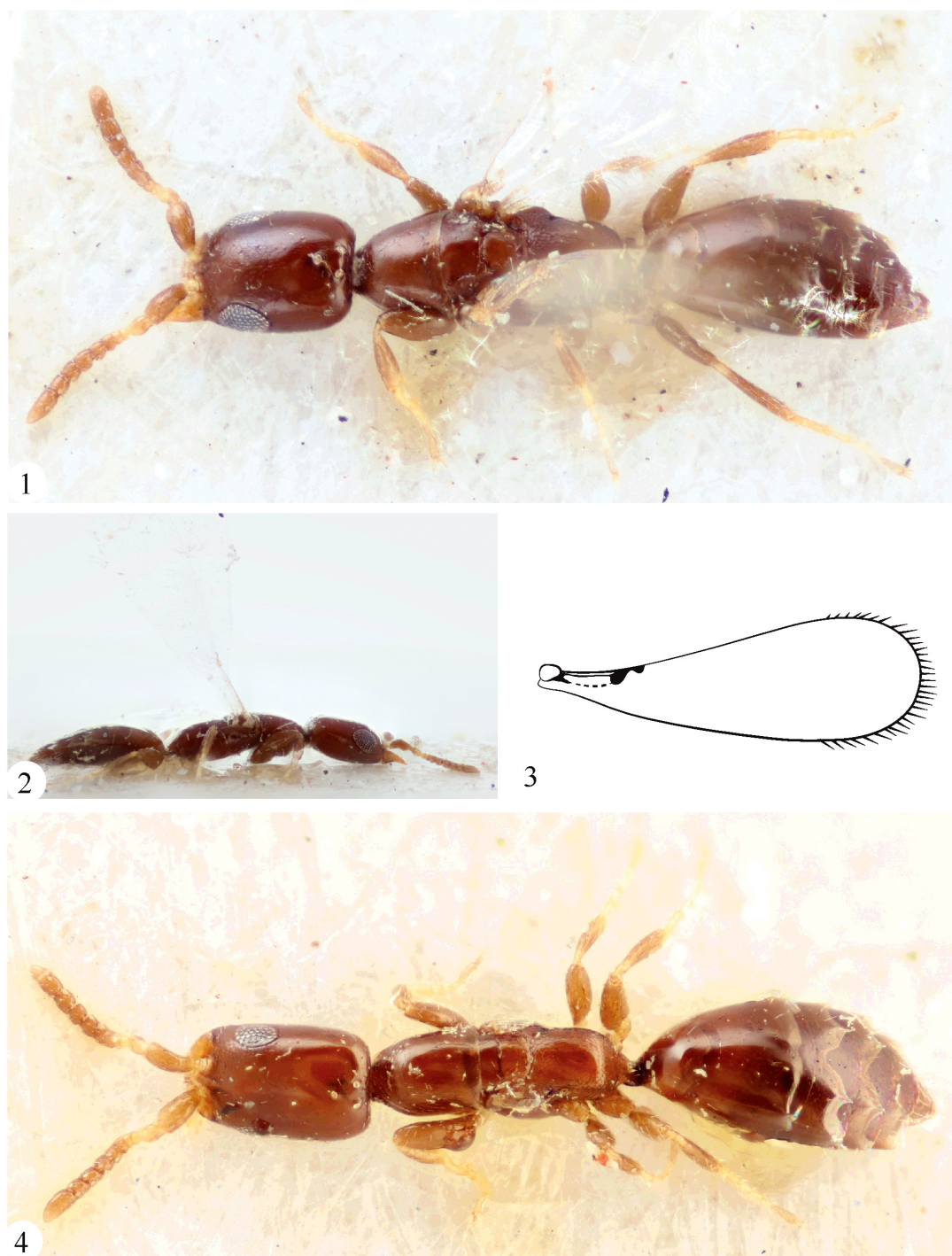
Cephalonomia cisidophaga: De Rond, 2001.

Redescription

Macropterous female (Figs 1–3). Body 1.3 mm long. Colour. Body castaneous, except mandibles, tibiae yellowish, tarsi and setae dark brown, wings hyaline, veins castaneous. Head subrectangular in dorsal profile, weakly coriaceous. Mandible apparently with three large distal teeth, lowermost largest. Antennal scape distinctly elongated, as long as flagellomere VIII; flagellomeres I–II distinctly shorter than others. Ocelli present. Dorsal pronotal area bell-shaped, progressively widening posteriorly. Mesoscutum transverse, $2 \times$ as long as wide and as long as mesoscutellum; notaulus absent; parapsidal signum subparallel. Mesoscutellum progressively narrowing posteriorly, anterior margin straight and posterior margin outcurved. Mesoscutum-mesoscutellar suture sulcate, foveae distinct. Metapectal-propodeal disc longer than dorsal pronotal area, transverse anterior, transverse posterior, metapostnotal median carinae absent, lateral carina incomplete. Mesotibia not spinose. Metasoma elongated, slightly flattened, polished; petiole very short; metasomal tergum II longer than others, posterior margin with short setae.

Micropterous female (Fig. 4). Body 1.2 mm long. Head rectangular, weakly coriaceous. Mandibles apparently with two large distal teeth, lowermost largest. Antennal scape distinctly elongated, as long as flagellomere VIII; flagellomeres I–II distinctly shorter than others. Ocelli present. Dorsal pronotal area rectangular, evenly wide along its length. Mesoscutum transverse, $2 \times$ as long as wide, about $0.5 \times$ as long as mesoscutellum; notaulus and parapsidal signum absent. Mesoscutellum wider medially and progressively narrowing both anteriorly and posteriorly. Mesoscutum-mesoscutellar suture absent. Metapectal-propodeal disc as long as dorsal pronotal area, rounded corners, transverse anterior, transverse posterior, lateral, metapostnotal median carinae absent, not punctate. Mesotibia not spinose.

Macropterous male. Body 1.2 mm long. Head as long as wide, subpentagonal in dorsal profile, with side outcurved, weakly coriaceous. Mandible apparently with three large distal teeth, lowermost largest. Antennal scape distinctly elongated, longer than flagellomere VIII; flagellomeres I–II shorter than the others. Dorsal pronotal area

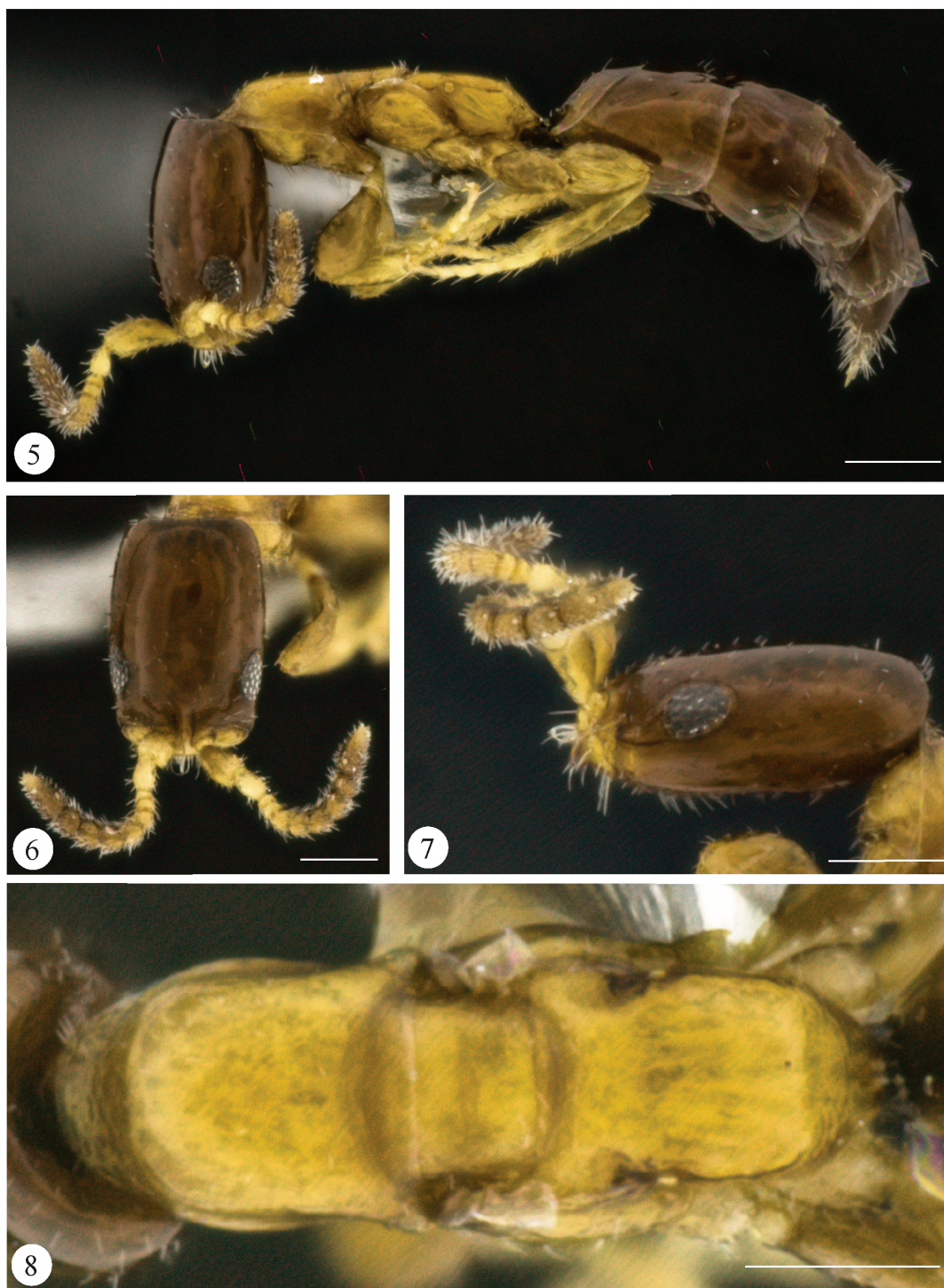


Figs 1–4. *Acephalonomia cisidophaga* Strejček. 1 – holotype macropterous female, habitus dorsal view; 2 – holotype macropterous female, habitus lateral view; 3 – holotype macropterous female, forewing dorsal view; 4 – paratype micropterous female, habitus dorsal view.

bell-shaped, progressively widening posteriorly. Mesoscutum transverse, $2 \times$ as long as wide; notaulus absent; parapsidal signum almost parallel. Mesoscutellum progressively narrowing posteriorly, anterior margin straight and posterior margin out curved. Metapectal-propodeal disc as long as dorsal pronotal area, rounded corners, transverse anterior, transverse posterior, lateral, metapostnotal median carinae absent, with very few minute punctures. Mesotibia not spinose.

Micropterous male. Body 1.0 mm long. Head subrectangular in dorsal profile, rounded corners, weakly coria-

ceous. Mandible apparently with two large distal teeth, lowermost largest. Antennal scape distinctly elongated, as long as flagellomere VIII; flagellomeres I–II shorter than the others. Dorsal pronotal area rectangular, similar width along its length. Mesoscutum transverse, $2 \times$ as long as wide; notaulus and parapsidal signum absent. Mesoscutellum wider medially and progressively narrowing both anteriorly and posteriorly. Metapectal-propodeal disc as long as dorsal pronotal area, transverse anterior, transverse posterior, lateral, metapostnotal median carinae absent, not punctate. Mesotibia not spinose.



Figs 5–8. *Acephalonomia micronesica* sp. n., holotype micropterous female. 5 – habitus, lateral view; 6 – head, dorsal view; 7 – head, lateral view; 8 – mesosoma, dorsal view. Scale: 100 μ m.

Remarks. The description of this species was based on a large series of micropterous and macropterous specimens of both males and females from polypore fungi collected in the Czech Republic and Slovakia. The holotype was collected from burrows of a ciid beetle, *Rhopalodontus* Mellié, in *Trametes* sp. on *Fagus sylvatica* (Strejček 1990). The sexual dimorphism of micropterous specimens is minimal. In the macropterous forms the only prominent difference between the sexes is the shape of head in dorsal profile:

subpentagonal in males and subrectangular in females. Interestingly, macropterous females are more similar to micropterous males and females than to macropterous males.

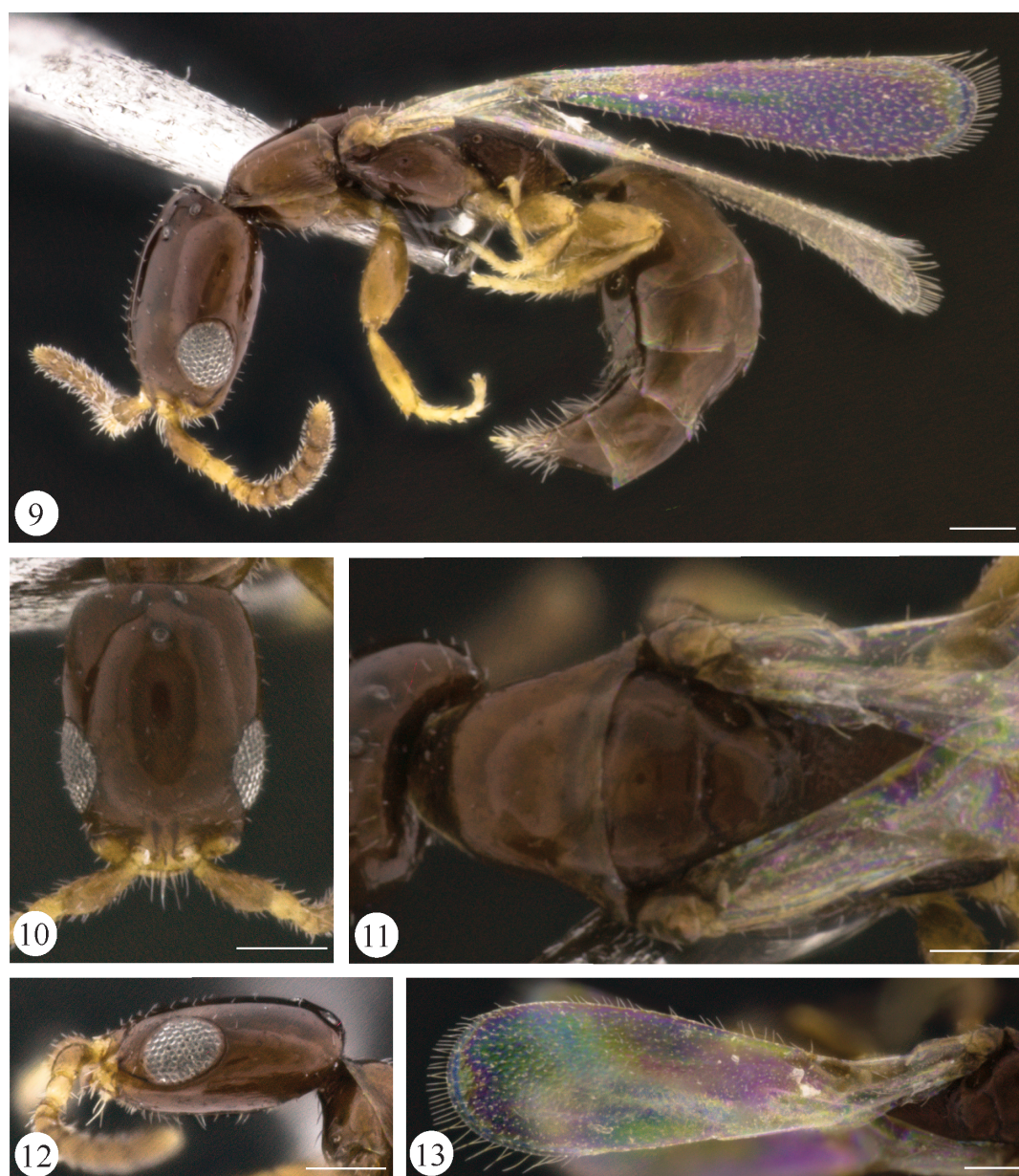
Distribution. Czech Republic and Slovakia.

***Acephalonomia micronesica* sp. n.**

Figs 5–13

ZooBank taxon LSID:

08A193D2-BEB1-4200-94FC-501CBC6A3BC9



Figs 9–13. *Acephalonomia micronesica* sp. n., macropterous female. 9 – habitus, lateral view; 10 – head, dorsal view; 11 – mesosoma, dorsal view; 12 – head, lateral view; 13 – forewing, dorsal view. Scale: 100 µm.

Description

Micropterous female (Figs 5–8). Body 1.22 mm long. Forewing 0.06 mm long. LH 0.29 mm. WH 0.19 mm. WF 0.13 mm. HE 0.07 mm. Colour. Head and metasoma, dark castaneous; mesosoma, clypeus, mandible, antenna, palpi and legs light castaneous. Head. Mandible apparently with two large distal teeth, lower tooth largest. Median clypeal lobe trapezoidal. Inter-torular space slightly less than torular diameter. Ratio of first four antennomeres about 7:2:1:1, pubescence on flagellomeres suberect. Ocelli absent. Frons polished, with very few minute punctures. WH $0.66 \times$ LH. WF $0.7 \times$ WH. WF $2.07 \times$ HE. VOL much longer than HE. Mesosoma. Mesoscutum and mesoscutellum transverse, almost equally long. Metapectal-propodeal disc slightly longer than wide, surface of anterior corners

deflected, transverse anterior, transverse posterior, meta-postnotal median carinae absent, lateral carina incomplete posteriorly; first abdominal spiracle subcircular. Propodeal declivity without median carina. Mesotibia not spinose. Mesopleural pit minute.

Macropterous female (Figs 9–13). Body 1.23 mm long. Forewing 0.85 mm long. LH 0.31 mm. WH 0.22 mm. WF 0.14 mm. HE 0.12 mm. WOT 0.07 mm. OOL 0.12 mm. Colour. Body, clypeus, mandible, antenna and proleg dark castaneous, meso- and metalegs and palpi castaneous; wings hyaline, veins light castaneous. Head. Mandible apparently with two large distal teeth, lower tooth largest. Median clypeal lobe trapezoidal. Inter-torular space slightly less than torular diameter. Ratio of first four antennomeres about 6:2.5:1:1, pubescence on flagello-

meres suberect. Ocelli present. Frons polished, with very few minute punctures. WH $0.7 \times$ LH. WF $0.64 \times$ WH. WF $1.13 \times$ HE. OOL $1.9 \times$ WOT. Frontal angle of ocellar triangle acute. VOL slightly longer than HE. Anterior ocellus well posterior of supra-ocellar line. Mesosoma. Parapsidal signum incomplete anteriorly, inconspicuous, straight, slightly converging posteriorly. Mesoscutum-mesoscutellar suture evenly narrow, slightly arched laterally. Metapectal-propodeal disc slightly longer than wide, surface of anterior corners deflected, transverse anterior, transverse posterior, metapostnotal median carinae absent, lateral carina complete; first abdominal spiracle subcircular. Propodeal declivity without median carina. Mesotibia not spinose. Mesopleural pit small.

Male. Unknown.

Type material. Holotype ♀, [Northern Mariana Islands], Tinian I., Mt. Lasso, NE slope, 18.III.45, Col. & pres. by Henri S. Dybas, Lot 987, bred from polypore fungus, 4 Hymenopt. (#987) assoc. with Cisiidae in polypore fungus (BPBM). Paratypes: 3 ♀, same data as holotype (BPBM); 12 ♀, Tinian I., Mt. Lasso, NE slope, 14.IV.45, Col. & pres. by Henri S. Dybas, Lot 962, bred from polypore fungus, 12 Hymenopt. (#962) assoc. with Cisiidae in polypore fungus (BPBM); 12 ♀, Tinian I., Mt. Lasso, NE slope, 14.IV.45, Col. & pres. by Henri S. Dybas, Lot 988, in polypore fungus (BPBM).

Type locality. Northern Mariana Islands, Tinian Island, Mount Lasso.

Etymology. The specific epithet *micronesica* denotes the origin from Micronesia.

Distribution. Known only from the type locality.

Remarks. The specimens of this species emerged from beetles of the family Ciidae living in polypore fungus. A total of 27 micropterous and one macropterous female were reared. Although this is a case of evident polymorphism, the difference between them is minimal, restricted to expected characters such as absence of ocelli and reduction of mesoscutum and mesoscutellum. There are only minute difference in measurements of the micropterous specimens.

A. cisidophaga and *A. micronesica* have some morphological similarities, such as antennae with eight flagellomeres; polymorphism with macropterous and micropterous forms; notaulus absent; parapsidal signum present only in macropterous form; forewing of macropterous form with Radial (R) cell closed, C and 2r-rs&Rs veins absent, Rs&M vein and prestigmal abscissa of R1 vein dilated and pterostigma wide and semicircular; metapectal-propodeal disc without anterior, posterior and median carinae.

However, the micropterous form of *A. cisidophaga* has ocelli, wings that surpass the posterior margin of mesoscutellum; and flagellomere I of the macropterous form is as long as flagellomere II, metapectal-propodeal complex punctate and lateral carina incomplete; whereas the micropterous form of *A. micronesica* does not have ocelli and the wings surpass posterior margin of mesoscutellum; and flagellomere I of the macropterous form is shorter than flagellomere II, metapectal-propodeal disc polished and lateral carina complete.

DISCUSSION

Flat wasps evolved to exploit small larvae occurring in cryptic situations like soil, stems, wood or seeds (Evans, 1964). The host preference of bethylids is exceptionally uniform. Bethylinae, and a few Epyrinae, attack larvae of Lepidoptera, while the other subfamilies attack larvae of Coleoptera. However, the host range of Bethylinidae is poorly known (Azevedo et al., 2018).

There are records of two other genera of bethylids (*Cephalonomia* and *Plastanoxus* excluding *Acephalonomia*) attacking ciid beetles feeding on fungus. *Cephalonomia hammi* Richards is associated with fungus infested with Ciidae (Richards, 1939); *Cephalonomia formiciformis* is recorded in polyporus fungus infested with *Cis bidentatus* Olivier on a birch stump and *Cis bilamellatus* Wood, *Cis boleti* (Scopoli), *Cis fagi* Waltl (as *Cis fuscatus* Mellié), *Cis laminatus* Mellié, *Cis micans* (Fabricius) (as *Cis hispidus* Paykull), *Cis pygmaeus* (Marsham) and *Cis villosulus* (Marsham) (as *Cis setigera* Mellié); and, *Cephalonomia perpusilla* Evans are recorded as reared from shelf fungus infested with Ciidae in western North America (Evans, 1963, 1964, 1978). *Plastanoxus chittendenii* Ashmead is reported being reared from *Cis* sp. (Ashmead, 1893), parasitizing *Cis fuscipes* Mellié (Kieffer, 1914) and *Cis festivus* (Panzer) (Perkins, 1976) and *Plastanoxus amamiensis* Terayama & Tachikawa reared from *Octotemnus laminifrons* Motschulsky (Tachikawa & Oda, 1977; Terayama & Tachikawa, 1987). Finally, *Acephalonomia cisidophaga* and *Acephalonomia micronesica* are recorded in burrows of *Rhopalodontus* sp. (Strejček, 1990; De Rond, 2001).

Among the flat wasps, sclerodermine wasps have very variable wings, with apterous forms (e.g. *Sclerodermus* Latreille), micropterous forms (e.g. *Platepyris* Lanes & Azevedo), brachypterous forms (e.g. *Bethylopsis* Fouts) and macropterous forms (e.g. *Nothepyris* Evans). Their number of antennomeres is also very variable and widely used throughout the group's taxonomic history. Evans (1964) for instance, divided them into two tribes, Sclerodermini and Cephalonomiini based on the number of flagellomeres (for more details, see Lanes & Azevedo, 2008; Alencar & Azevedo, 2013).

Wing polymorphism is recorded for several Scleroderminae. *Cephalonomia perpusilla* Evans has an unusually complex polymorphism (Evans, 1963). Yang et al. (2012) suggest that a long photoperiod and strong light promotes the development of winged females in *Sclerodermus pupariae* Yang & Yao. *Acephalonomia* may also be influenced by photoperiod as it is morphologically similar to the genus *Sclerodermus*. The cosmopolitan genus *Sclerodermus* is interspecifically variable with macropterous, micropterous and apterous forms, as well as intraspecifically variable (e.g. *S. pupariae*). However, there are only two species of *Acephalonomia*, both with micropterous and macropterous individuals, so polymorphism is probably a generic feature.

The forewing venation of *Acephalonomia* is also very characteristic in lacking a closed cell, C and 2r-rs&Rs

veins, and with Rs&M vein and prestigmal abscissa of vein R dilated. In this respect this genus is similar to *Megaprosternum*. Nevertheless, in *Megaprosternum* the pterostigma is small and linear, whereas in *Acephalonomia* it is large and subcircular (Azevedo, 2006; Gupta et al., 2017).

Polymorphism and simple morphology are more evident in Scleroderminae than in other bethylids.

Cephalonomia and *Acephalonomia* have some morphological similarities, such as a tiny body; forewing without C, 2r-rs&Rs and A veins. However, *Cephalonomia* has antennae with 10 flagellomeres; mesonotum with scutum and scutellum fused in micropterous and apterous forms; metapectal-propodeal complex margined on sides by carinae, occasionally with median carina; and apterous forms; whereas, *Acephalonomia* has antenna with eight flagellomeres; mesonotum with scutum and scutellum not fused in micropterous form; metapectal-propodeal complex occasionally margined on sides by carinae; and lacks an apterous form. These characters led us to revalidate the genus.

This genus can be keyed by modifying the key of Azevedo et al. (2019) by simply adding one couplet to couplet 3 for micropterous forms and 23 for macropterous form, as follows:

- 3 Antenna with 10 flagellomeres, or less.....3a
- Antenna with 11 flagellomeres 4
- 3a Antenna with 10 flagellomeres *Cephalonomia*
- Antenna with 8 flagellomeres *Acephalonomia*
- 23 Forewing with R cell closed *Israelius*
- Forewing with R cell open.....23a
- 23a Antenna with 10 flagellomeres *Cephalonomia*
- Antenna with 8 flagellomeres *Acephalonomia*

The genus has an accentuated disjunct distribution with *Acephalonomia cisidophaga* in Europe (Czech Republic and Slovakia) and *A. micronesica* sp. n. on Tinian Island (Mariana Islands). This widely broadens the known distribution of the genus, and the geographical gap indicates that this genus may be more widely distributed. One particular reason for this gap could be few collectors. The specimens of *Acephalonomia* are tiny and are parasitoids of a tiny ciid beetle, which occur in polypore fungus, so they are collected using only by a very specific field protocol. Future studies that focus on them will undoubtedly increase the number of species in this genus and possibly partially fill the geographical gap.

ACKNOWLEDGEMENTS. We thank the anonymous reviewers for their useful suggestions. We also thank the curators cited in the text for loaning us the specimens used in this study, and to J. Hájek and M. Tkoč (Dept. of Entomology, National Museum, Prague) for locating and photographing the types of *A. cisidophaga*. We also thanks CNPq/CAPES/FAPs call #16/2014 for providing a bursary to F.B. Fraga under the project INCT-Hymenoptera Parasitoides #8887.136354/2017-00 coordinated by A.M. Penteado-Dias, who took the pictures of *A. micronesica*. This paper was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), grant # 465562/2014-0. WDC has a doctoral bursary of Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). COA has a bursary funded by CNPq grant # 303748/2018-4.

REFERENCES

- ALENCAR I.D.C.C. & AZEVEDO C.O. 2013: Reclassification of Epyrini (Hymenoptera: Bethyidae): a tribal approach with commentary on their genera. — *Syst. Entomol.* **38**: 45–80.
- ASHMEAD W.H. 1893: A monograph of the North American Proctotrypidae. — *Bull. U. S. Natn. Mus.* **45**: 1–472.
- AZEVEDO C.O. 2006: Two new genera of Sclerodermini (Hymenoptera, Bethyidae, Epyrinae) with large scolebythid-like prosternums. — *Zootaxa* **1191**: 35–47.
- AZEVEDO C.O., ALENCAR I.D.C.C., RAMOS M.S., BARBOSA D.N., COLOMBO W.D., VARGAS J.M.R. & LIM J. 2018: Global guide of the flat wasps (Hymenoptera, Bethyidae). — *Zootaxa* **4489**: 1–294.
- AZEVEDO C.O., ALENCAR I.D.C.C., RAMOS M.S., BARBOSA D.N., COLOMBO W.D., VARGAS J.M.R. & LIM J. 2019: Erratum, Global guide of the flat wasps (Hymenoptera, Bethyidae) (vol. 4489, 1–294, 2018). — *Zootaxa* **4571**: 597–600.
- DE ROND J. 2001: Bethyidae. In Dathe H.H., Taeger A. & Blank S.M. (eds): Verzeichnis der Hautflügler Deutschlands. — *Entomol. Nachr. Ber. (Beiheft 7)*: 117–119.
- EVANS H.E. 1963: A new species of *Cephalonomia* exhibiting an unusually complex polymorphism (Hymenoptera, Bethyidae). — *Psyche* **70**: 151–163.
- EVANS H.E. 1964: A synopsis of the American Bethyidae (Hymenoptera, Aculeata). — *Bull. Mus. Compar. Zool.* **132**: 1–122.
- EVANS H.E. 1973: Further studies on South American Bethyidae (Hymenoptera). — *Proc. Entomol. Soc. Wash.* **75**: 194–204.
- EVANS H.E. 1978: The Bethyidae of America North of Mexico. — *Mem. Am. Entomol. Inst.* **27**: 1–332.
- FOUTS R.M. 1935: New serphoid, bethylid, and anteonid wasps from the Marquesas and Society Islands. — *Pac. Entomol. Surv. Publ.* **8**: 151–157.
- GUPTA A., RAJESHWARI S.K. & AZEVEDO C.O. 2017: Biology and description of *Megaprosternum cleonarovororum* sp. nov. (Hymenoptera: Bethyidae) a gregarious larval ectoparasitoid of *Cleonaria bicolor* Thomson (Coleoptera: Cerambycidae) from India. — *Zootaxa* **4237**: 78–90.
- HARRIS R.A. 1979: A glossary of surface sculpturing. — *Occas. Pap. Entomol.* **28**: 1–31.
- KAWADA R. & BUFFINGTON M.L. 2016: A scalable and modular dome illumination system for scientific microphotography on a budget. — *PLoS ONE* **11**(5): e0153426, 20 pp.
- KAWADA R., LANES G.O. & AZEVEDO C.O. 2015: Evolution of metapostnotum in flat wasps (Hymenoptera, Bethyidae): implications for homology assessments in Chrysidoidea. — *PLoS ONE* **10**(10): e0140051, 17 pp.
- KIEFFER J.J. 1914: Bethyidae. In Schulze F.E. (ed.): *Das Tierreich* **41**. Friedländer und Sohn, Berlin, xxvi+595 pp.
- LANES G.O. & AZEVEDO C.O. 2008: Phylogeny and taxonomy of Sclerodermini (Hymenoptera, Bethyidae, Epyrinae). — *Insect Syst. Evol.* **39**: 55–86.
- LATREILLE P.A. 1809: *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias desposita, iconibus exemplisque plurimis explicata. Tomus quartus et ultimus*. Amand Koenig, Paris, 399 pp.
- PERKINS J.F. 1976: *Handbooks for the Identification of British Insects. Vol. 6. Hymenoptera Bethyloidea (Excluding Chrysidoidea)*. Royal Entomological Society, London, 38 pp.
- RICHARDS O.W. 1939: The British Bethyidae (s.l.) (Hymenoptera). — *Trans. R. Entomol. Soc. Lond.* **89**: 185–344.
- STREJČEK J. 1990: Beschreibung einer neuen Gattung und Art der Familie Bethyidae aus der Tschechoslowakei: *Acephalonomia cisidophaga* gen. et. sp. n. (Insecta, Hymenoptera, Bethyloidea). — *Reichenbachia* **28**: 47–50.

- TACHIKAWA T. & ODA A. 1977: A bethylid parasite (Hymenoptera) of *Octotemnus laminifrons* (Coleoptera: Ciidae). — *Trans. Shikoku Entomol. Soc.* **13**: 129.
- TERAYAMA M. & TACHIKAWA T. 1987: A new species of the genus *Plastanoxus* (Hymenoptera: Bethylidae) from Japan. — *Trans. Shikoku Entomol. Soc.* **18**: 311–314.
- YANG Z.Q., WANG X.Y., YAO Y.X., GOULD J.R. & CAO L.M. 2012: A new species of *Sclerodermus* (Hymenoptera: Bethylidae) parasitizing *Agrilus planipennis* (Coleoptera: Buprestidae) from China, with a key to Chinese species in the genus. — *Ann. Entomol. Soc. Am.* **105**: 619–627.

Received December 20, 2019; revised and accepted March 25, 2020
Published online May 5, 2020