

Cretaceous Digger Wasps of the New Genus *Bestiola* Pulawski and Rasnitsyn (Hymenoptera: Sphecidae: Angarosphecinae)

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Abstract.—The new genus *Bestiola* Pulawski and Rasnitsyn, characterized by a unique wing venation, is described for the following four new species from the Lower Cretaceous: *hispanica* Martínez Delclòs and Rasnitsyn (type species) from northeastern Spain, *communis* Pulawski and Rasnitsyn from central Mongolia, *subpetiolata* Pulawski and Rasnitsyn from central Mongolia, and *tenuipes* Pulawski and Rasnitsyn from Eastern Siberia. The genus is assigned to Angarosphecinae Rasnitsyn, 1975, new status by Rasnitsyn, which is treated as a paraphyletic Lower Cretaceous subfamily of Sphecidae. The family name Baissodidae Rasnitsyn, 1975, is synonymized with Angarosphecidae Rasnitsyn, 1975, by Rasnitsyn.

Sphecid wasps of the archaic subfamily Angarosphecinae (= Baissodinae) are the most abundant taxa among the Early Cretaceous Hymenoptera, particularly in the middle interval of that epoch, probably after Berriasian and before Albian, 140–113 myr before present (Rasnitsyn et al. 1998). Only a fraction of the material accumulated in the collections has been described (Evans 1969; Rasnitsyn 1975, 1986, 1990; Hong 1984; Zhang 1985, 1992; Darling and Sharkey 1990; Jarzembowski 1991; Ansorge 1993; Ren et al. 1995; Rasnitsyn et al. 1998). The Early Cretaceous fossils described here originate from three distant areas of Eurasia (central Mongolia, Eastern Siberia, and Spain), but have a unique wing venation and are all approximately the same age.

Most of the specimens examined were collected in Bon Tsagan, Central Mongolia, a rich fossil site 5–8 km north of Bon Tsagan Nuur (= Bon Tsagan Lake), in Bayanhongor Aymag (= Region). Specimens were impressed in marl of the Khurilt rock unit, Bon Tsagan Series (Sinitza

1993), possibly of Aptian age (Ponomarenko 1990). This hymenopteran assemblage is related to the Wealden Supergroup of the Southern England (Valanginian to Barremian: Rasnitsyn et al. 1998).

Siberian material was collected in two localities east of Lake Baikal. One is Baisa, a riverside outcrop on the left bank of the Vitim River, 3 km downstream of the former lodge Baisa and 45 air km upstream of the Romanovka Village, Buryat Republic. The fossils, impressed in marl of the Zaza Formation, are related to the Purbeck of South England (Berriasian), based on their hymenopteran assemblages (Rasnitsyn et al. 1998). The other Siberian locality, Semyon, is at Semyon Creek, 3.5 km SW of Elizavetino Village, west of Chita, Chita Oblast'. The age of insectiferous mudstones, disputable within the Early Cretaceous, is correlated either with Baisa (Zherikhin 1978) or with Bon-Tsagan (Dmitriev and Zherikhin 1988).

The Spanish specimen originates from the Montsec Range, central Lerida Province, and comes from lithographic lime-

stones named La Pedrera de Meià, located 5 km W of Santa Maria de Meià in La Noguera comarca, possibly of Berriassian-Vallanginian age (Martínez-Delclòs 1995).

The following morphological structures, variously termed in the literature, are here defined or redefined as follows for clarity and convenience sake:

- mesosoma: thorax and propodeum combined;
- metasoma: abdomen excluding the propodeum (= gaster of Bohart and Menke 1976);
- metapostnotum: propodeal enclosure of Bohart and Menke 1976;
- spiracular lobe (as in Rasnitsyn 1988): pronotal lobe of Bohart and Menke 1976;
- adlateral lines: parapsidal line of Bohart and Menke (1976); we prefer this term to avoid confusion, as parapsidal lines of other entomologists correspond to notauli of most hymenopterists;
- cell 1+2r: submarginal cell I of Bohart and Menke (1976);
- 3r: marginal cell of Bohart and Menke (1976);
- 2rm and 3rm: submarginal cells II and III of Bohart and Menke (1976);
- 1mcu and 2 mcu: discoidal cells I and II of Bohart and Menke (1976);
- crossveins 2r-m and 3r-m: distal margins of 2rm and 3rm, respectively (as in Richards, 1956, and Gauld and Bolton, 1988), and corresponding to 1r-m and 2r-m of Bohart and Menke, 1976); unlike the latter two authors, we call 1r-m the vein that extends from cell 1+2r to cell 1mcu (i.e., the vein that separates the basal cell from cell 2rm) in the xyelid genus *Pleroneura*;
- vein 1RS: a veinlet between basal cell (= medial cell of Bohart and Menke, 1976) and cell 1+2r;
- vein 2RS: a veinlet between cells 1+2r and 2rm;
- vein 2r-rs: a veinlet between cells 1+2r and 3r, called 2r by Bohart and Menke, 1976.

The abbreviation PIN stands for the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

TAXONOMY

Family Sphecidae Latreille

Subfamily Angarosphecinae Rasnitsyn, **new status**

Angarosphecidae Rasnitsyn 1975:109. Type genus: *Angarosphe* Rasnitsyn 1975:110.

Baissodidae Rasnitsyn:1975:122. Type genus: *Baissodes* Rasnitsyn 1975:123. **New synonym** by Rasnitsyn.

Angarosphecinae are archaic Mesozoic wasps that lack the synapomorphies of any extant sphecids subfamily. They may be paraphyletic with respect to other Apoidea because they are not defined by any synapomorphy. They are treated here as a subfamily of Sphecidae because there is evidence in some specimens of two unique synapomorphies of Apoidea (they also lack any synapomorphy that would ally them with any other Aculeata). In particular, *Pompilopterus corpus* Rasnitsyn and Jarzembowski has an elongate spiracular lobe, pronotum thickened preapically, and an enlarged metapostnotum (Rasnitsyn, Jarzembowski, Ross 1998, Fig. 36), and *Angarosphe myrmicopterus* Rasnitsyn has an enlarged metapostnotum (Rasnitsyn 1980, Fig. 172). A large metapostnotum is also found in *Bestiola tenuipes* (Fig. 7). None of the Angarosphecinae has plumose setae or enlarged hindbasitarsi typical of bees. The form of the adlateral line of *Bestiola* and other Angarosphecidae differs from that of all extant Apoidea in that it extends to the posterior margin of the mesoscutum, as pointed out to us by M. A. Prentice (oral communication). This indicates that Angarosphecinae very probably represent the most basal lineage of known Apoidea.

Rasnitsyn (1975) recognized Baissodidae based on the presence of a unique median scutal sulcus believed to be lacking in all other non-bethylid Aculeata (in-

cluding Angarosphecidae). Subsequently, he (Rasnitsyn 1980) included *Angarosphex* in the Sphecidae and hypothesized that the Baissodidae were sphecid ancestors. However, ?*Angarosphex pallidus* Rasnitsyn, 1986, from the lowermost Lower Cretaceous of Mongolia, combines the wing venation of *Angarosphex* with the presence of a median scutal sulcus, although the latter is only slightly indicated. Because of this combination, Baissodidae are here synonymized with Angarosphecidae.

***Bestiola* Pulawski et Rasnitsyn, new genus**

Name derivation.—*Bestiola*, Latin for small beast. Gender feminine.

Type species.—*Bestiola hispanica* Martínez Delclòs et Rasnitsyn, new species, Lower Cretaceous of Spain.

Recognition.—*Bestiola* is easily recognized by its unique wing venation (Figs 1–8). It has three radiomedian (= submarginal) cells, and cell 2rm receives veins 1m-cu and 2m-cu (= both recurrent veins). The combination of three unusual features differentiates it from all other sphecid genera with these characteristics, both extinct and extant: 1. cell 3rm broader on the costal side than on the anal side (as in the North American genus *Xenosphex* and some *Palarus*); 2. crossvein 3r-m joining RS near the distal end of the latter (as in the North American genus *Eucerceris* and some *Palarus*); and 3. crossvein 2r-m equidistant from 2m-cu and 3r-m or closer to the latter (as in the Old World *Tachysphex brevipennis* Mercet, and several other Larrini and some *Diploplectron* approach this condition).

Description.—Size medium to large, length of forewing 5–15 mm. Antenna with no conspicuous modifications, at least basal flagellomeres longer than wide (all flagellomeres in most species). Occipital carina almost circular, reaching hypostomal carina. Ocelli not modified, distant from eye. Pronotum short, wide, thickened preapically, separated from mesonotum by a groove (Fig. 8). Mesoscutum

without median scutal sulcus, with long notauli and adlateral lines; mesopleuron with episternal and scrobal sulci, hypersternaulus, and possibly omaulus. Metanotum short, metapostnotum long, truncated, with median line. Propodeal spiracle elongate, slit-like. Forewing: pterostigma well defined; basal vein distant from pterostigma, evenly arched; cell 3r acuminate at wing foremargin; crossvein 2r-rs longer than width of pterostigma; 2r-m sinuate or arching outwardly, closer to 2r-rs than to 3r-m on RS, equidistant from 2m-cu and 3r-m on M or closer to the latter; 3r-m straight or arching outwardly; 1m-cu received near base of cell 2rm; M sharply angled at 2m-cu; cu-a interstitial with M or narrowly postfurcal. Hindwing venation complete, cu-a meeting Cu well beyond M+Cu fork. Fore and midfemora with well-defined, narrow trochantellus (hindleg condition unknown), but no obvious specializations. Metasoma rounded basally (neither petiolate nor pedunculate).

Composition.—Four species from the Lower Cretaceous of Spain, Eastern Siberia, and Mongolia, as described hereafter.

Taxonomic position.—*Bestiola* is a member of Aculeata s. s. (= Vespoidea + Apoidea) as evidenced by its sexually dimorphic antennal flagellum of 10 (female) and 11 articles (male). Unlike all Chrysidoidea, it possesses a complete set of forewing and hindwing cells. It belongs to Apoidea because it shares two unique synapomorphies of the superfamily: an elongate metapostnotum and a pronotum thickened preapically. The genus belongs to Sphecidae because it lacks the enlarged hindbasitarsus and plumose body setae of Apidae s. l. The genus shares with most other Angarosphecinae the position of 1m-cu which inserts near the RS+M fork. This feature occurs elsewhere only in some other Apoidea. The genus also lacks any synapomorphy that would place it in any extant sphecid subfamily and so we attribute it to Angarosphecinae.

KEY TO SPECIES OF *BESTIOLA*

1. Forewing cell 2rm conspicuously narrowing anterad, its costal margin markedly shorter than crossvein 2r-rs; the latter emerging shortly after pterostigma's midlength (Fig. 8) *Bestiola subpetiolata* Pulawski and Rasnitsyn, new species
- Forewing cell 2rm moderately narrowing anterad, its costal margin about as long as crossvein 2r-rs; the latter emerging markedly beyond pterostigma's midlength 2
2. Forewing length 5 mm; crossvein 2r-rs markedly shorter than 2RS (Fig. 1); hindfemur and gastral terga with pale spots (Fig. 1); metasoma conspicuously setose (Fig. 1) *Bestiola hispanica* Martínez Delclòs and Rasnitsyn, new species
- Forewing length 11.0–14.5 mm; crossvein 2r-rs longer to minimally shorter than 2RS (Figs. 2–7); hindfemur and gastral terga without pale spots (Figs. 2–7); metasoma not setose or less conspicuously setose (Fig. 5) 3
3. Head, wing veins, and legs except coxae light; forefemur slightly more elongate (Fig. 7) *Bestiola tenuipes* Pulawski and Rasnitsyn, new species
- Head, wing veins, and legs dark; forefemur slightly stouter (Figs. 2, 3) *Bestiola communis* Pulawski and Rasnitsyn, new species

***Bestiola hispanica* Martínez Delclòs and
Rasnitsyn, sp. n.**
(Fig. 1)

Name derivation.—Hispanica, Latin for Spanish.

Recognition.—*Bestiola hispanica* differs from its congeners by its small size (forewing length 5 mm rather than 11.0–14.5 mm), crossvein 2r-rs markedly shorter than 2RS (longer to minimally shorter in the other species), the presence of pale spots on the hindfemur and gastral terga, and a conspicuously setose metasoma.

Description.—Female unknown, male: Fig. 1. Body dark (including wing veins), but hindfemur with pale spot posteroapically and terga I–IV each with a pair of preapical spots. Head and metasoma conspicuously setose. Flagellomeres nearly equal in width, longer than wide, becoming shorter toward apex. Head relatively small, narrowing toward mouthparts; gena somewhat inflated; malar space half length of eye; clypeal free margin projecting mesally; hindocellus separated from eye by about its own diameter. Forewing: posterior pterostigmal margin straight; 2r-rs joining pterostigma near the latter's apex, about as long as costal margin of cell 2rm and half as long as 2RS; 3r-m straight;

costal margin of cell 2rm about twice as long as anal margin; cu-a almost interstitial with M+Cu fork. Hindwing with long row of hamuli (10 preserved) and cu-a angling at Cu. Legs not elongate; hindfemur as long as head width, moderately thick subbasally, not attenuated apically, its dorsal margin convex except subapically, ventral margin almost straight (ventral margin slightly convex on right femur, probably due to fossil compression). Hindtibia 1.25 times as long as femur, with no spines but with one spur. Hindtarsus slightly longer than tibia, basitarsus longer than tarsomeres II–IV combined. Apical gastral segments and genitalia not preserved. Body length ca 9 mm, distance from forewing base to apex of cell 3rm 5.1 mm.

Material examined.—Holotype (LP92/SC/3662): male, Spain: Lerida Province: La Pedrera de Meià 5 km W Santa Maria de Meià (Institut d'Estudis Ilerdencs, Lerida, Spain).

***Bestiola communis* Pulawski et
Rasnitsyn, new species**
(Figs. 2–6)

Name derivation.—Communis, Latin for common.

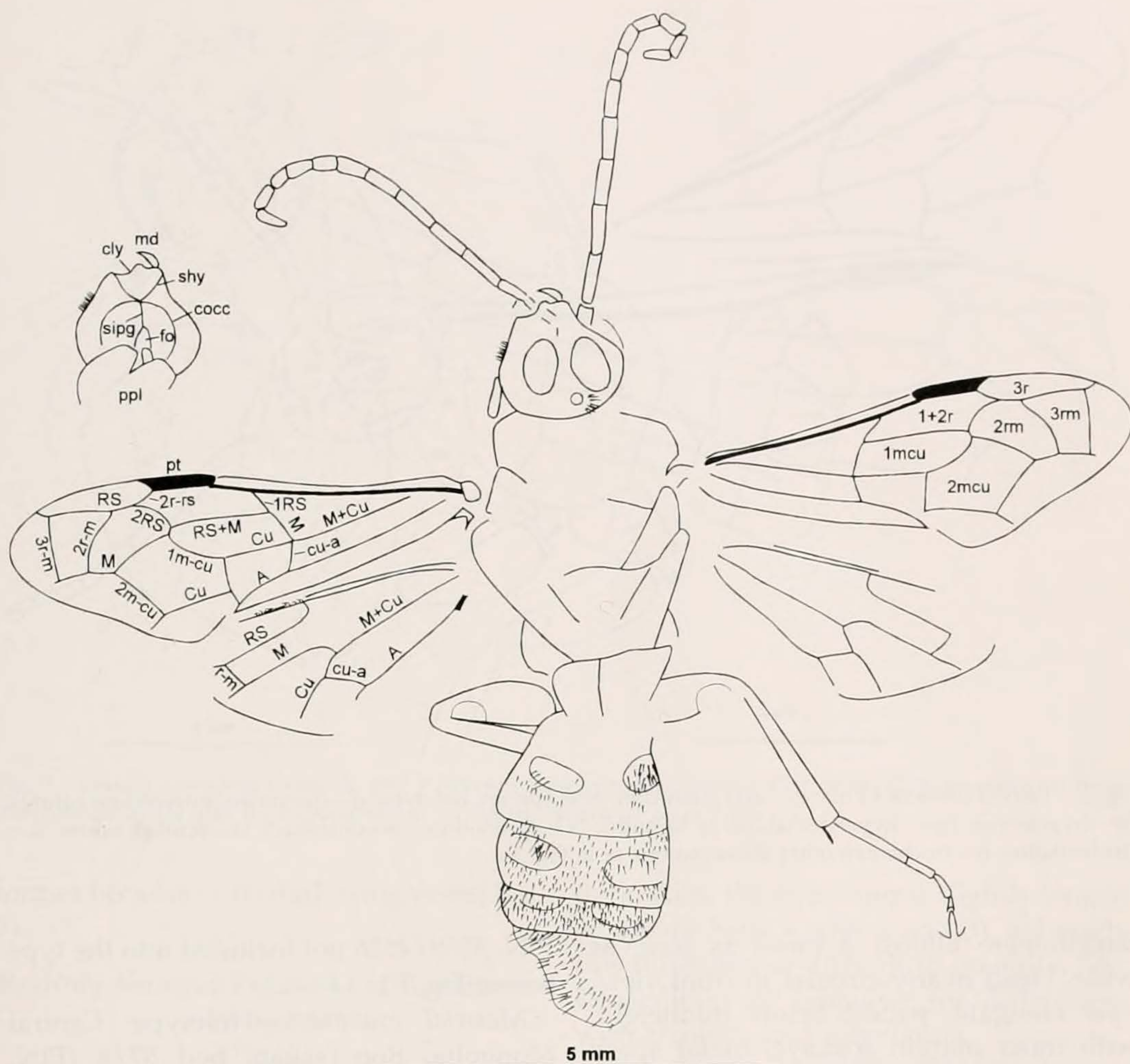


Fig. 1. *Bestiola hispanica* Martinez-Delclòs and Rasnitsyn, new species, holotype: cly—clypeus; cocc—occipital carina; f—femur; fo—occipital foramen; md—mandible; ppl—propleuron; shy—hypostomal suture; sipg—interpostgenal suture.

Recognition.—The following combination of characters is unique to *Bestiola communis*: forewing length 11.0–14.5 mm (5 mm in *hispanica*); costal margin of cell 2rm about as long as crossvein 2r-rs (markedly shorter in *subpetiolata*); 2r-rs longer to minimally shorter than 2RS (markedly shorter in *hispanica*), emerging markedly beyond pterostigma's midlength (near pterostigma's midlength in *subpetiolata*); hindfemur and gastral terga without pale spots (with pale spots in *hispanica*); and forefemur not elongate (slightly elongate in *tenuipes*,

compare Figs. 2 and 3 and 7). Unlike *tenuipes*, the body of *communis* is all dark, including the wing veins.

Description.—Female (Fig. 2), sex unknown in remaining specimens (Figs. 3–6). Body and appendages uniformly dark, metasoma inconspicuously setose (Fig. 5). Scape about as long as midflagellar articles; pedicel transverse; flagellomeres more than twice as long as wide, flagellomere I almost as long as II and III combined, following ones gradually shorter and thinner toward antennal apex, apical

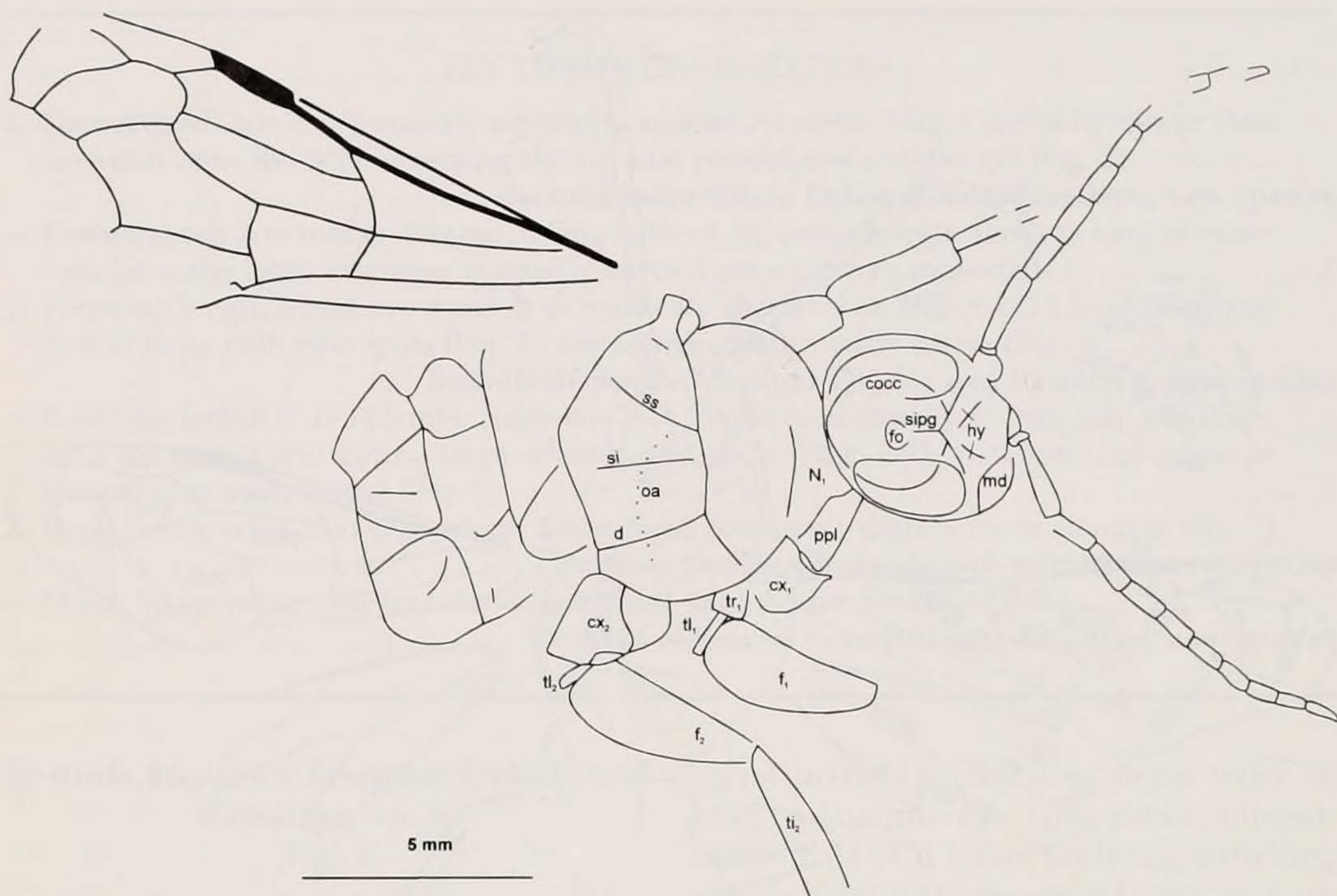


Fig. 2. *Bestiola communis* Pulawski and Rasnitsyn, new species, holotype: d—discrimen (interpleural suture); hy—hypostoma; hys—hypersternaulus or signum?; N₁—pronotum; oa—omaulus?; ss—scrobal suture; tl—trochantellus; tr—trochanter; other abbreviations as in Fig. 1.

flagellomere almost 3 times as long as wide. Head nearly circular in front view; eyes elongate, widest below midheight, with inner margin concave; malar space present; anterior clypeal margin protruding into wide medial lobe that is shallowly emarginate apically. Notauli and adlateral lines complete or nearly so. Mesopleuron with long, almost straight scrobal sulcus and hypersternaulus, possibly also with omaulus. Wing venation as in *hispanica* except 2r-rs subequal in length to 2RS and 3r-m arched. Fore- and midfemora thickest subbasally, narrow apically, with dorsal margin straight and ventral convex; forefemur as long as head width, midfemur slightly longer; fore- and possibly midtibiae shorter than respective femora. Metasoma missing in type series but present in specimen PIN 3559/4526 (that is excluded from type series). Forewing length 13.0–14.5 mm (11.0 mm in the specimen

PIN, 3559/4526 not included into the type series, Fig. 5).

Material examined.—Holotype: Central Mongolia, Bon-Tsagan, bed 87/8 (PIN. 3559/4525, incomplete female specimen with propodeum, hindlegs and metasoma missing).

Paratypes: same locality and bed (PIN, 3559/4528, incomplete specimen with most of antennae and legs, part of thorax and all metasoma missing; PIN, 3559/4530, two damaged wings mixed with other insect remains in vertebrate dropping).

Excluded from type series but possibly conspecific: same locality and bed (PIN, 3559/4526, a somewhat damaged specimen: Fig. 5); Eastern Siberia, Semyon (PIN, 2385/2392, an isolated wing with venation nearly identical to those of *communis* and *tenuipes*, and attributed to the

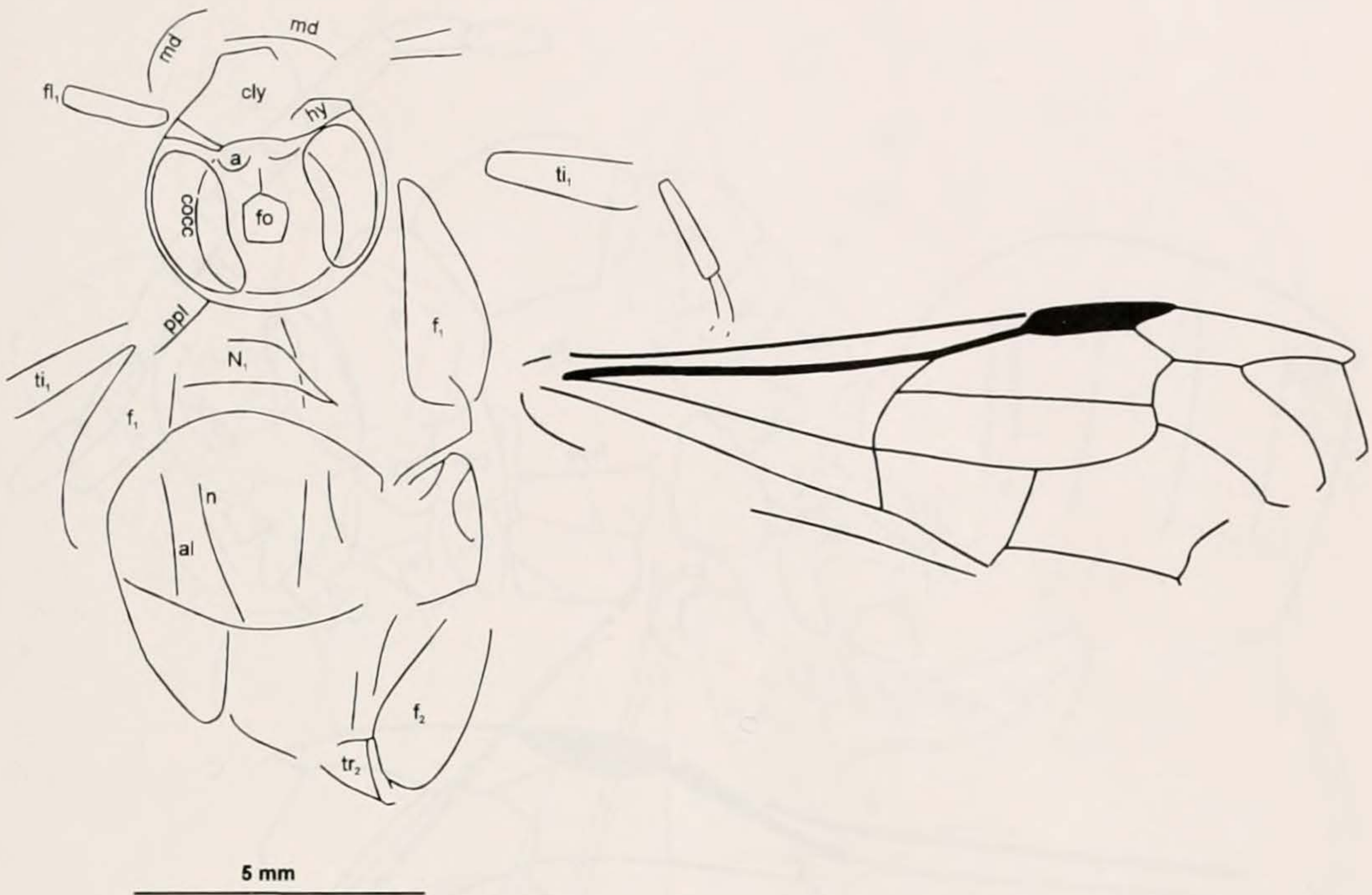


Fig. 3. *Bestiola communis* Pulawski and Rasnitsyn, new species, paratype PIN, 3559/4528: a—antennal foramen; al—adlateral line; h—hypostome; n—notaulus; otherwise as in Figs. 1, 2.

former because of its dark wing veins; Fig. 6).

***Bestiola tenuipes* Pulawski et Rasnitsyn,
new species**
(Fig. 7)

Name derivation.—*Tenuipes*, from the Latin words *tenuis*, thin, and *pes*, leg; with reference to the elongate forefemur.

Recognition.—The wing venation of *B. tenuipes* is as in *communis*, but the head, wing veins, and legs are light rather than

dark. Also, the forefemur is slightly longer (compare Figs. 7 with 2 and 3), although this difference is difficult to quantify. See Recognition of *communis* for differences with *hispanica* and *subpetiolata*.

Description.—Male (Fig. 7). Female unknown. Antenna and mesosoma (possibly in part) dark, metasoma infuscated toward apex, otherwise coloration light (including wing venation). Thorax with well-defined although shallow punctures that are about 1 diameter apart, and with moderately short and moderately dense setae. Basal flagellomeres unrecognizable, remaining flagellomeres 2.0–2.5 times as long as wide, gradually becoming shorter and thinner toward apex. Adlateral line of mesoscutum complete; scutellum wide, elongate; metascutellum contrastingly short; metapostnotum trapezoid, with basal impression, median longitudinal line, and rounded posterior angles. Propodeal spiracle elongate, narrow, slightly bent S-like. Wing venation

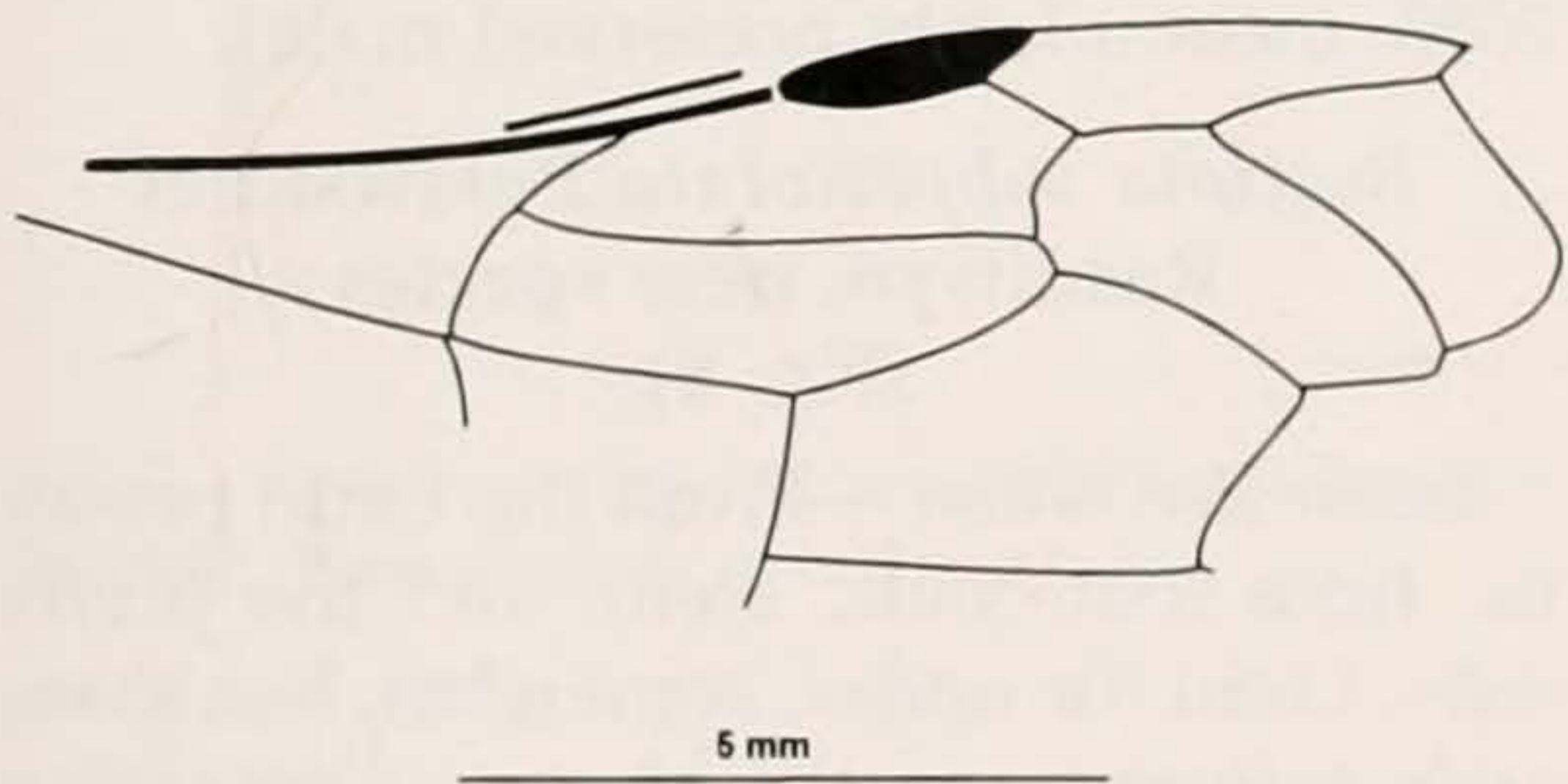


Fig. 4. *Bestiola communis* Pulawski and Rasnitsyn, new species, paratype, PIN, 3559/4530.

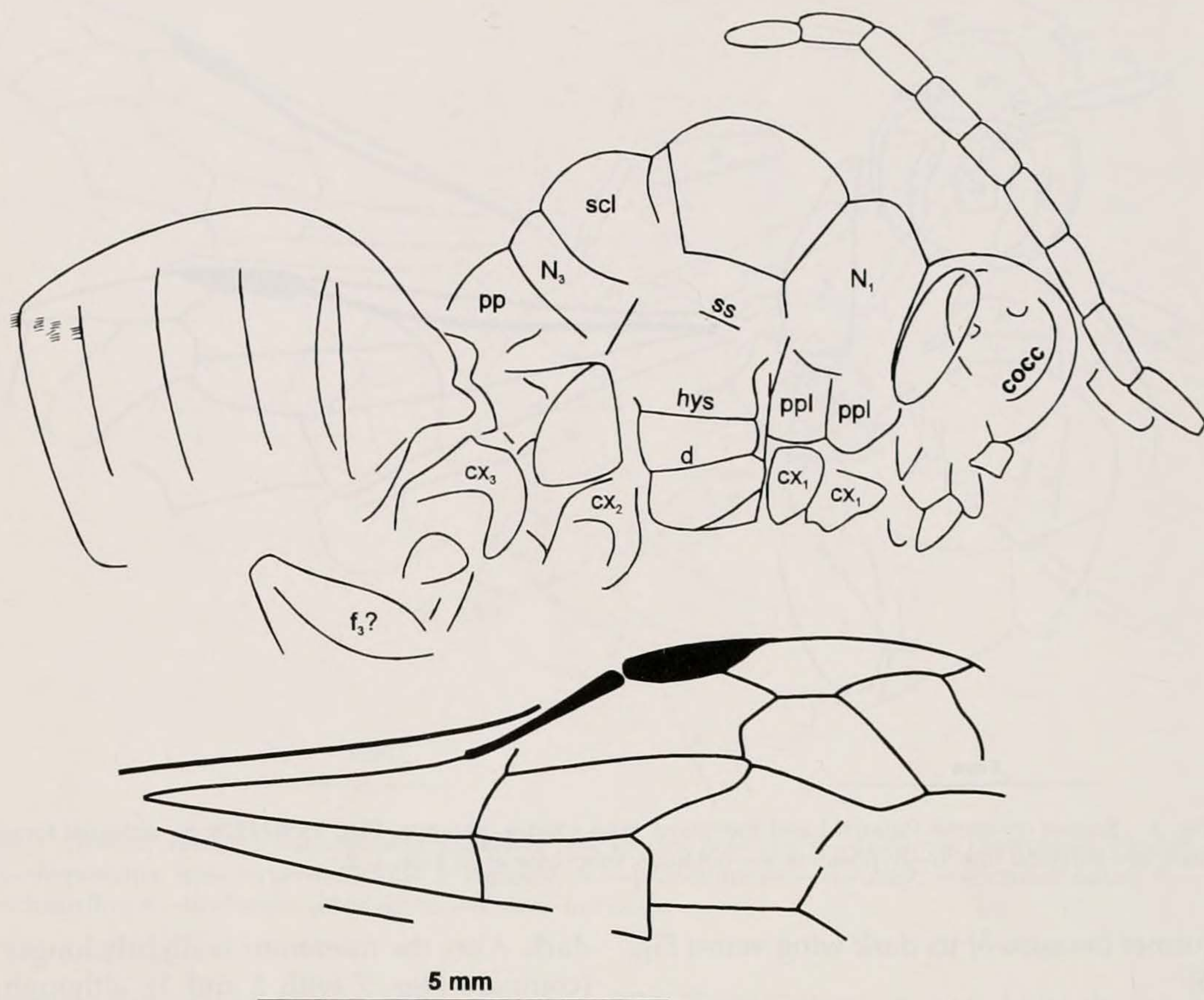


Fig. 5. *Bestiola ? communis* Pulawski and Rasnitsyn, new species, PIN, 3559/4526; N3—metanotum; pp—propodeum; scl—scutellum; other abbreviations as in Figs. 1–3.

as in *communis*. Legs relatively long, forefemur slightly longer than head width, with dorsal margin straight and ventral margin convex; hindfemur elongate, almost symmetrical, attenuated apically, both dorsal and ventral margins straight (except basally); midtarsus markedly longer than midfemur; midbasitarsus shorter

than three following tarsomeres combined. Genitalia elongate, ovoid, with smooth contour, with gonostyle apex narrow rounded. Body length 21 mm as preserved, forewing length 11.5 mm.

Material examined.—Holotype: Russia: Eastern Siberia: Baissa, bed 31 (PIN, 3064/2055, incompletely preserved male).

***Bestiola subpetiolata* Pulawski et
Rasnitsyn, new species**
(Fig. 8)

Name derivation.—From the Latin petiolus, little foot, stalk, stem; and the prefix sub-, Latin for under, somewhat, less than; with reference to the shape of forewing cell 2rm.

Recognition.—The following details of

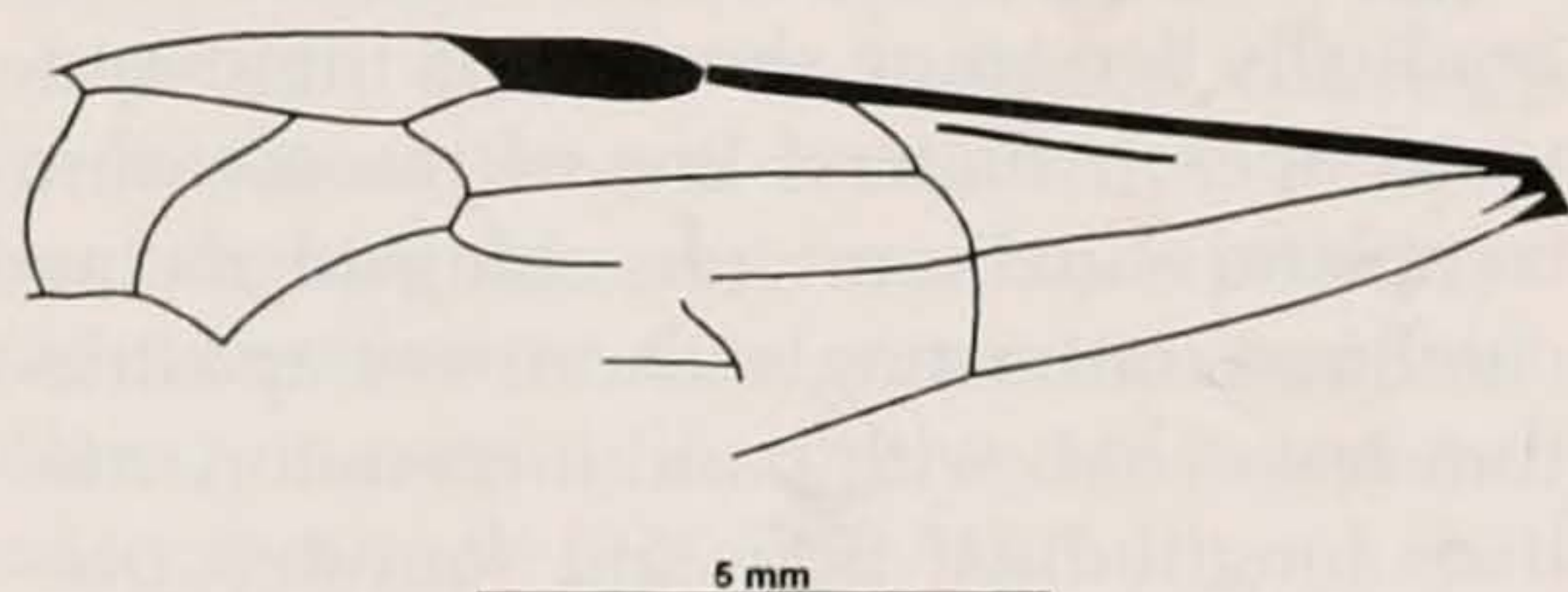


Fig. 6. *Bestiola ? communis* Pulawski and Rasnitsyn, new species, PIN, 2385/2392.

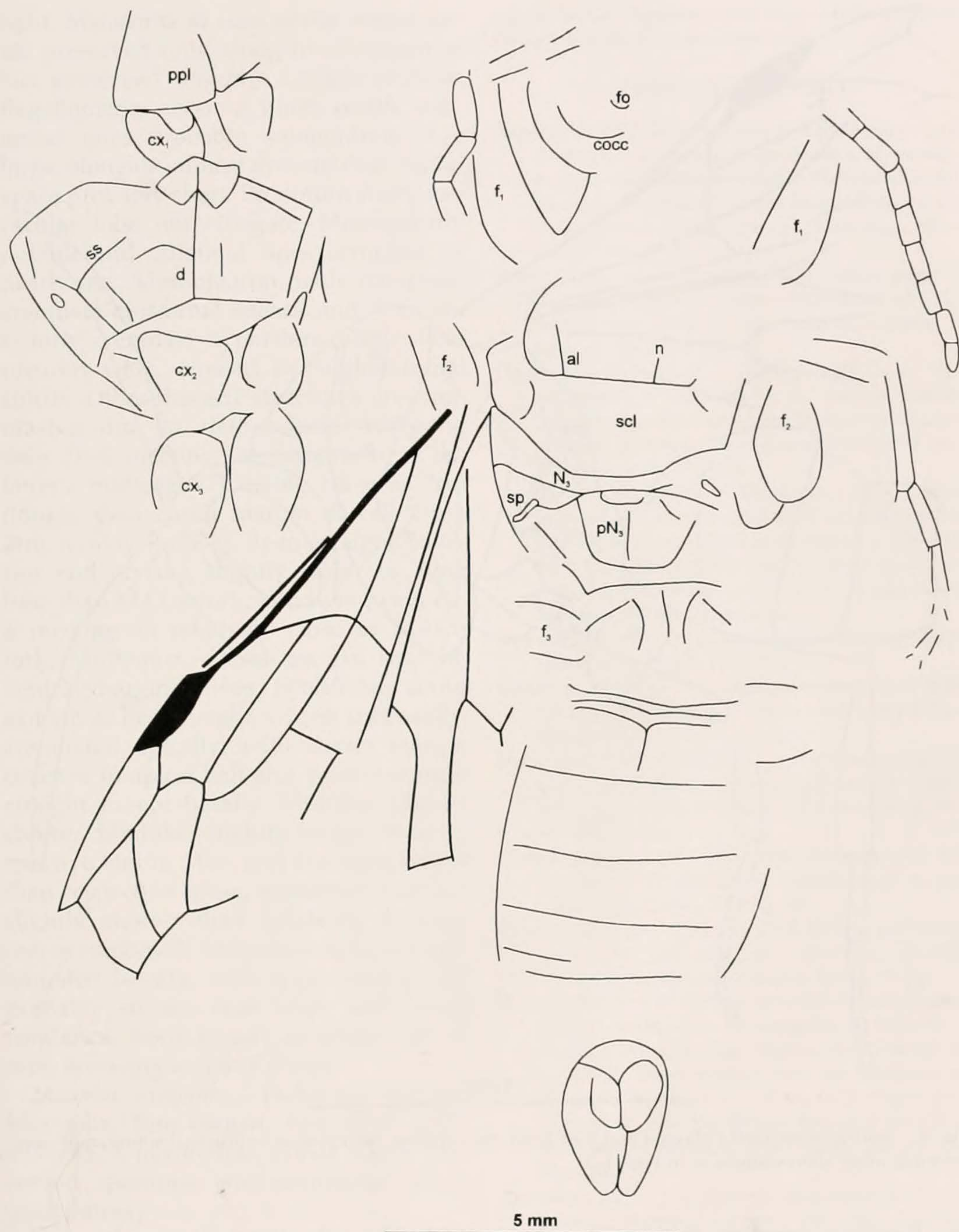


Fig. 7. *Bestiola tenuipes* Pulawski and Rasnitsyn, new species, holotype: pN3—metapostnotum; sp—propodeal spiracle; other symbols as in Figs. 1-5.

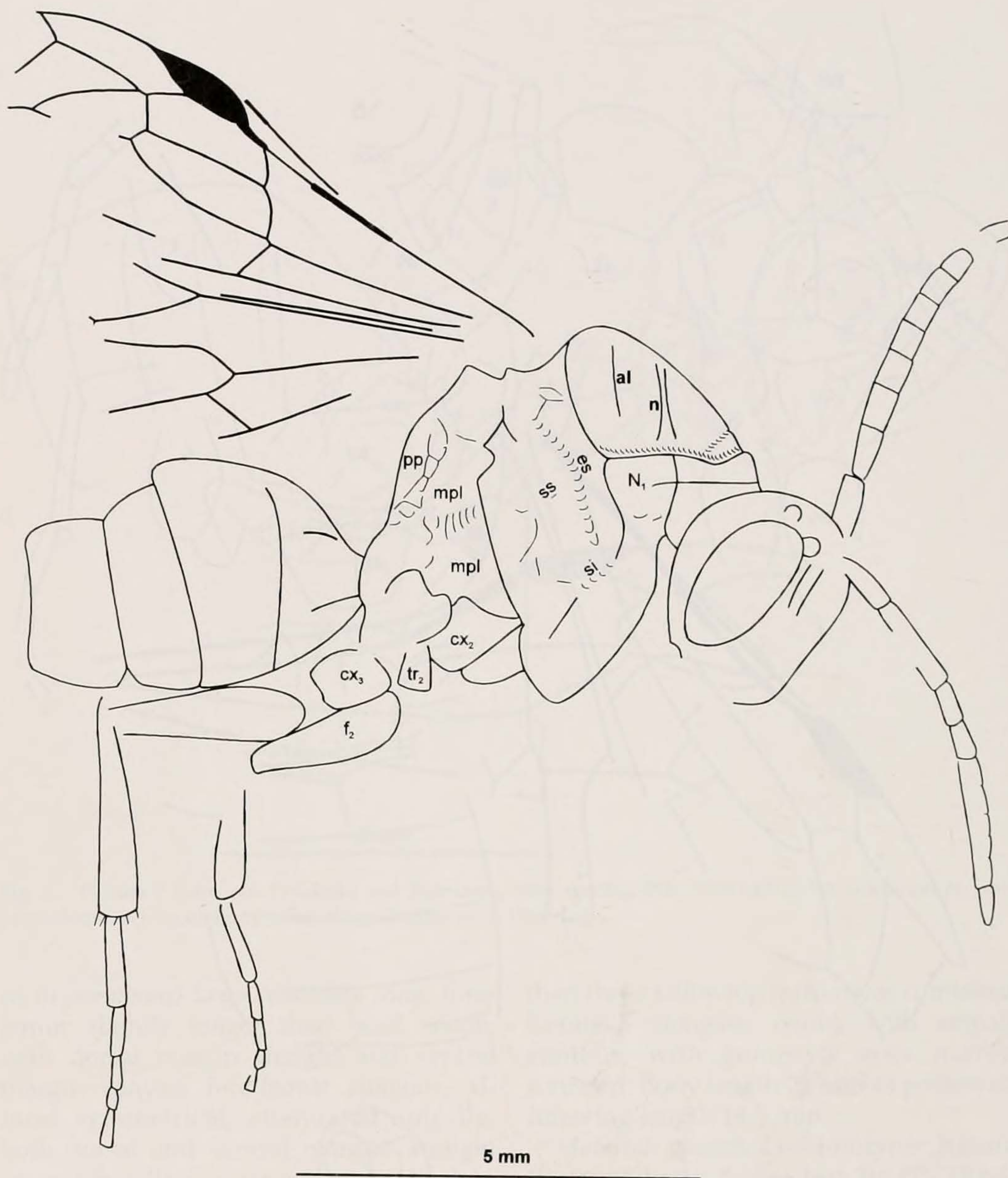


Fig. 8. *Bestiola subpetiolata* Pulawski and Rasnitsyn, new species, holotype: es—episternal suture; mpl—metapleura; other abbreviations as in Figs. 1–7.

the forewing venation distinguish *subpetiolata* from all of its congeners: vein 2r-rs meeting pterostigma near the latter's mid-length, costal margin of cell 2rm markedly shorter than 2r-rs, and anterior end of vein cu-a closer to wing base than M+Cu fork. In addition, subapical flagellomeres ap-

pear to be only slightly longer than wide, thus markedly shorter than in other *Bestiola*.

Description.—Sex unknown (Fig. 8). Body moderately dark (including wing veins) but antennal apex, tarsi (except hindbasitarsus basally), and metasoma

light. Metasoma at least partly setose (setae preserved only along hind margin of last preserved tergum). Length of basal flagellomeres about 3 times width, subapical ones probably subquadrate. Eye large, elongate, almost symmetrical. Malar space probably short. Pronotum short, spiracular lobe not elongate. Mesoscutum: notauli and adlateral lines complete or nearly so. Mesopleuron with complete, crenulate episternal sulcus; and with anteriorly crenulate hypersternaulus. Metapleuron wide, crossed by subhorizontal sulcus. Other thoracic structures unrecognizable due to deformation. Forewing vein 2r-rs meeting pterostigma near the latter's midlength, meeting RS near 2rm (longer than costal margin of cell 2rm), 2rm weakly arching, 3r-m straight, anterior end of cu-a slightly closer to wing base than M+Cu fork. Hindwing vein cu-a meeting M relatively close to M+Cu fork. Midfemur: dorsal margin straight, ventral margin convex. Hindfemur about as long as head height, widest subbasally, attenuated apically, with dorsal margin concave in apical half and ventral margin straight except basally. Midtibia slightly shorter, hindtibia slightly longer, than respective femur. Mid- and hindtarsi longer than respective tibiae, respective basitarsi slightly shorter than following 3 tarsomeres combined. Metasoma somewhat attenuated basally, with apex missing, but probably shorter than head and thorax combined. Body length, as preserved, 10 mm, forewing length 7.0 mm

Material examined.—Holotype: Central Mongolia, Bon-Tsagan, bed 87/8 (PIN, 3559/4529, incomplete, rather poorly preserved specimen with somewhat crumpled thorax).

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