RESEARCH PAPER

Neurostigma (Psocodea: Psocomorpha: Epipsocidae) from Colombia: new species and an identification key

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Abstract. Upon examination of recently collected epipsocid barklice from natural areas of Colombia, five new species of *Neurostigma* Enderlein, 1900 were found: *N. lienhardi* sp. nov., *N. mockfordi* sp. nov., *N. newi* sp. nov., *N. thorntoni* sp. nov., and *N. valderramae* sp. nov. They are here described and illustrated. A cladistic analysis of 32 morphological characters indicates that *Neurostigma* is monophyletic. An updated key for the identification of males of the described species of the genus is presented.

Key words. Psocoptera, Epipsocetae, barklice, biodiversity, cladistics, morphology, phylogeny, taxonomy, Neotropics, South America

Introduction

'Psocoptera', non-parasitic members of the order Psocodea, grouped in its suborders Trogiomorpha, Troctomorpha and Psocomorpha (Yoshizawa & Johnson 2003) and also known as barklice or booklice, are small, soft-bodied insects with filiform antennae, a prominent postclypeus and free laciniae that serve the purpose of supporting the head while the insect feeds on the substrate (Badonnel 1951, Mockford 1993, Lienhard 1998, Yoshizawa 2005). They live in microecosystems of tree bark, rocky walls, plant remains, and occasionally inhabited places. They are generally herbivores or detritivores, feeding on carbohydrate-rich materials, including decomposing organic matter, but some species are partially predatory. Basic aspects of the biology of psocopterans can be found in New (1987) and Mockford (1993). Psocopterans are widely distributed, and recent studies in tropical areas have significantly increased the number of described species. Mockford (2018) estimated that there were 5941 species of extant Psocoptera in 485 genera (published until 2014). We have updated those numbers based on more recent literature (until 2020) and found that there are 6214 species in 492 genera.

With 1040 species in 161 genera and 34 families, South America is 2.6 times richer than North America (397 species in 90 genera and 27 families), as defined by Mockford (2012): Canada, USA and Nearctic Mexico, with the Tropic of Cancer as the southern boundary with the Neotropical Region. The South American psocopterans have been studied by a pleiad of researchers, beginning with Günther Enderlein (1900), and followed by Rudolf Roesler, André Badonnel, Edward L. Mockford, Longinos Navás, Tim R. New, Ian W. B. Thornton, Bryan D. Turner, G. J. Williner, Charles Lienhard, Rodrigo Lopes Ferreira, A. N. García Aldrete, Alberto Moreira Da Silva Neto, Ranulfo González, Nancy Carrejo, Oscar Saenz, Nadia Calderón, Cristian Román, Julián Mendivil, Stephania Sandoval, and others. The references are too numerous to be cited, but up to the year 2000, they can be found in Lienhard & Smithers (2002).

The present paper is part of an ongoing project to document the species richness of Psocoptera in Colombia, and, as such, it follows the tradition of psocid studies in South America. Until the year 2000, only 78 species of Psocoptera were known from Colombia, but in the last

ten years, as a result of collaboration of the Instituto de Biología, Universidad Nacional Autónoma de México, with the Group of Entomological Investigations, of the Universidad del Valle, Santiago de Cali, Colombia, that number has increased to 720 species, about 70% of them still undescribed.

The barklouse genus *Neurostigma* Enderlein, 1900 (Psocodea: Psocomorpha) was described based on a male of *N. chaetocephalum* Enderlein, 1900 from Callanga, Peru. Enderlein's (1900: Fig. 24) illustration of the whole specimen shows that the pterostigma of the forewings has ten slender crossveins, the areola postica (i.e. the cell delimited by the vein CuA_1) joins M, which is proximally deeply concave just before joining the areola postica, the proximal halves of the forewings are dark brown, and the proximal halves of the hindwings are light brown (Fig. 39). Enderlein (1900) placed this genus in the tribe Peripsocini and later he defined a monogeneric subfamily Neurostigmatinae in his family Caeciliidae (Enderlein 1903). Eertmoed (1973), in his review of the genera of Epipsocetae, placed *Neurostigma* in the monogeneric family Neurostigmatidae, and Casasola-González (2006) transferred it to Epipsocidae. Yoshizawa & Johnson (2014) considered Epipsocidae a senior synonym of Neurostigmatidae Enderlein, 1903, justified by the fact that Epipsocini Karny, 1930 takes precedence over Bertkauiini Kolbe, 1882, but the date of the latter is preserved (Lienhard & Yoshizawa 2019).

Neurostigma presently includes nine species (Mendivil-Nieto et al. 2020): *N. chaetocephalum* Enderlein, 1900; *N. dispositum* Roesler, 1940; *N. enderleini* New, 1980; *N. furcivenula* Badonnel, 1986; *N. garcialdretei* Mendivil et al., 2020; *N. paucivenosum* New, 1980; *N. radiatum* Mockford, 1991; *N. roesleri* New, 1980; and *N. xanthopterum* New, 1980, of which three present the forewing areola postica joined to M (*N. chaetocephalum*, *N. enderleini* and *N. xanthopterum*). As far as known, the genus is restricted to the Neotropical Realm. Three species have been known in Colombia (Badonnel 1986, Mendivil-Nieto et al. 2020): *N. furcivenula*, *N. xanthopterum*, and *N. garcialdretei*. Upon examination of epipsocid specimens recently collected in natural areas of Colombia, we have found 15 specimens of *Neurostigma*, in which five undescribed species are represented. The purpose of this paper is to describe and illustrate those species, and to provide an identification key to the males of the species of the genus.

Material and methods

The specimens were collected as part of the project "Revisión taxonómica y endemismo de los psócidos (Insecta: Psocodea: 'Psocoptera') de Parques Naturales de Colombia", conducted in 2013–2016. Specimens in the collection of the Alexander von Humboldt Institute (Boyacá, Colombia) were also examined. Fifteen specimens were available for study; they were dissected in 80% ethanol, and the head, right wings, legs, and genitalia were processed in 80–100% ethanol and clove oil, before mounting onto slides in Canada balsam. Type specimens are deposited in the Entomological Museum, Universidad Del Valle, San-

tiago de Cali, Colombia (MUSENUV) and the Alexander von Humboldt Institute, Boyacá, Colombia (IAVH).

Morphological terminology follows Yoshizawa (2005). Color was recorded from whole specimens preserved in ethanol prior to mounting, observed under a stereomicroscope illuminated with a cold white light at a magnification of 50×. Measurements of body parts (head, right wings and legs and genitalia) were taken from the slides with an ocular micrometer, mounted on a Nikon Eclipse Ci microscope. Abbreviations of the measurements and counts are as follows:

ah	areola postica height;
al	areola postica length;
ctt1	number of ctenidiobothria on t1 of right hind leg;
D	antero-posterior diameter of right compound eye (in dorsal view of head);
d	transverse diameter of right compound eye (in dorsal view of head);
F	length of femur of right hind leg;
f1–n	lengths of flagellomeres 1–n of right antenna;
FW	length of right forewing;
H	head median length (in dorsal view);
HW	length of right hindwing;
IO	minimum distance between compound eyes (in dorsal view of head);
lp	pterostigma length;
Mx2	length of second segment of right maxillary palpus;
Mx4	length of fourth segment of right maxillary palpus;
MxW	maximum width of head capsule;
T	length of tibia of right hind leg;
t1, t2	lengths of tarsomeres 1–2 of right hind leg;
W	forewing width;
w	hindwing width;
wp	pterostigma width.

Additionally, the following ratios were calculated for the head and wings: H/MxW; PO: d/D; IO/d; FW/W; HW/w; lp/wp; al/ah (González et al. 2011).

Illustrations are based on digital photographs, taken with a Canon T5i camera and Helicon Focus software, later processed in Clip Studio Paint vector graphics editor. The values given for the scale bars are in mm.

The phylogenetic analysis was conducted using the parsimony optimality criterion in TNT (Goloboff et al. 2008). Character states considered ambiguous or unobservable were coded as "?" in the matrix. All characters were treated as non-additive. The option "implicit enumeration" was utilized for the search of the most parsimonious tree(s) in TNT. Trees were collapsed after each search. The support for each node was calculated in TNT by means of bootstrap and symmetric resampling (Felsenstein 1985), with 1000 pseudoreplicates. *Loneura gorgonaensis* García Aldrete, Sarria & González, 2011 (Psocomorpha: Ptiloneuridae); *Ptiloneura columnaris* García Aldrete, González & Carrejo, 2020 (Psocomorpha: Ptiloneuridae), and *Cladiopsocus eertmoedi* González, García Aldrete & Carrejo, 2016 (Psocomorpha: Cladiopsocidae) were chosen as outgroups according to the analyses made by Casasola-González (2006), the first of these was used to root the tree. The following 12 species were included in the ingroup: *N. chaetocephalum*, *N. dispositum*, *N. enderleini*, *N. garcialdretei*, *N. paucivenosum*, *N. lienhardi* sp. nov., *N. mockfordi* sp. nov., *N. newi* sp. nov.,

N. radiatum, *N. thorntoni* sp. nov., *N. valderramae* sp. nov., and *N. xanthopterum*. *Neurostigma furcivenula* and *N. roesleri* were not included in the analysis, because they are known from females only. The characters of the species not examined were coded from their original descriptions (ENDERLEIN 1900, ROESLER 1940, NEW 1980, MOCKFORD 1991). The strict consensus tree generated in TNT was read with WinClada v. 1.00.08 (NIXON 2002), to be later exported and edited in CorelDraw X7.

Species descriptions

Neurostigma lienhardi sp. nov.
(Figs 1–6)

Type material. HOLOTYPE: ♂, **COLOMBIA:** Valle del Cauca, Santiago de Cali, La Buitrera, 3°32′14.1″N, 76°45′19.0″W, 1140 m, 23.vii.2011, R. González leg. (MUSENUV, slide no. 29870). PARATYPE: 1 ♂, same data as holotype (MUSENUV, slide no. 29871).

Description. *Measurements* (male holotype, in μm). FW: 3825, HW: 2725, F: 850, T: 1400, t1: 520, t2: 180, ctt1: 20, f1: 500, f2: 350, Mx4: 210, IO: 520, D: 290, d: 230, IO/d: 2.26, PO: 0.79, H/MxW: 1.41, H/D: 3.56, IO/MxW: 0.75, Mx4/Mx2: 1.55, FW/W: 2.38, lp/wp: 3.24, al/ah: 2.35, HW/w: 2.95.

Color. Body creamy, with brown spots. Head (Fig. 3): vertex, frons and postclypeus creamy; genae creamy, light brown close to lower edge of compound eyes; postgenae creamy; compound eyes black, ocelli hyaline, with pale brown centripetal crescents; anteclypeus and labrum creamy; labral sclerites pale brown. Antennae pale brown. Maxillary palps creamy to pale brown. Tergal lobes of mesothorax creamy, tergal lobes of metathorax brown; thoracic pleura creamy. Legs: coxae and trochanters creamy, apex blackish; femora creamy, with oval blackish spots, mainly on anterior side; tibiae creamy; tarsomeres 1 creamy; tarsomeres 2 light brown. Forewing membrane hyaline, light brown proximally (Fig. 1); crossveins of pterostigma dark brown to black; Rs, M and areola postica dark brown, other veins creamy; nodulus blackish. Hindwing membrane hyaline, with light brown spot near base of CuP; veins brown (Fig. 2). Abdomen creamy, tergum with irregular blackish spots. Clunium pale brown. Hypandrium light brown. Phallosome pale brown, radular sclerites light brown. Epiproct and paraprocts creamy.

Morphology. Head with abundant macrosetae, mainly on vertex (Fig. 3). Vertex convex, bilobed, clearly above upper border of compound eyes. Outer cusp of lacinial tips broad, with 6–7 denticles. Labrum with five distal sensilla: central placoid one, flanked by pair of trichoid–placoid sensilla. Forewings (Fig. 1): pterostigma long, much wider posteriorly, with five crossveins; Rs, proximal to transverse vein r–m, strongly concave; R_{2+3} sinuous, R_{4+5} less than three times the length of Rs section distal to r–m; M with three branches, M_3 forked or simple. Areola postica high, slanted posteriorly, apex rounded, separated from CuA_2 by about 0.25× its own length. Hindwings elongate (Fig. 2): M simple, unbranched; R_{2+3} and R_{4+5} longer than Rs; Cu angled in middle; Rs and M fused at a distance; Rs+M shorter than Rs section proximal. Legs: fore coxae with

rasp as long as tympanum; trochanters with two long setae dorsally; fore tarsi without ctenidobotria; mid- and hind tarsi with ctenidobotria. Abdominal tergum with tubercular lobes. Hypandrium membranous (Fig. 5), with dense field of long setae, posterior margin rounded. Phallosome (Fig. 6) open basally; side struts curved outwards; aedeagal arch robust, posterior process robust, truncated apically, with parallel sides; external parameres absent; radula with two groups of small sclerotized teeth separated by reticulated area. Paraprocts (Fig. 4) broad basally, short, posterior border rounded, with setae and macrosetae distally, sensory fields large, with 37–39 trichobothria on basal rosettes. Epiproct (Fig. 4) wide anteriorly, posterior border broadly rounded, with microsetae and setae; one seta mesally. Female unknown.

Diagnosis. *Neurostigma lienhardi* sp. nov. resembles *N. thorntoni* sp. nov. in head, wing and radular sclerites. It differs from the latter in the following characters: posterior process of aedeagus broad, with parallel sides and distally truncate; two groups of sclerotized teeth in radula separated by a reticulate area (Fig. 6); hindwing less widened basally, with Rs proximal to M interception basally inclined towards wing base (Fig. 2).

Etymology. This species is dedicated to Dr. Charles Lienhard, from the Museum of Natural History, Genéve, Switzerland, in recognition of his vast contributions to psocidology.

Distribution. Colombia (Valle del Cauca).

Neurostigma mockfordi sp. nov.
(Figs 7–12)

Type material. HOLOTYPE: ♂, **COLOMBIA:** Valle del Cauca, Santiago de Cali, Kilómetro 18, vía a Zingara, 3°30′38.3″N, 76°37′13.8″W, 1990 m, 17.vi.2010, R. González leg. (MUSENUV, slide no. 29872). PARATYPE: **COLOMBIA:** 1 ♂, Boyacá, Flora and Fauna Sanctuary Iguaqué, El Níspero, 5°38′N, 73°31′W, 2730 m, 28.x.–14.xi.2001, Malaise trap, P. Reina leg. (IAVH).

Description. *Measurements* (male holotype, in μm). FW: 4275, HW: 3125, F: 950, T: 1625, t1: 620, t2: 200, ctt1: 20, f1: 630, f2: 460, f3: 370, Mx4: 280, IO: 560, D: 240, d: 210, IO/d: 2.67, PO: 0.88, H/MxW: 1.41, H/D: 4.37, IO/MxW: 0.81, Mx4/Mx2: 1.73, FW/W: 2.47, lp/wp: 2.83, al/ah: 1.76, HW/w: 3.10.

Color. Body dark brown, with pale spots. Head (Fig. 9) with small pale brown spot between lower inner margin of compound eyes and antennal socket; vertex, frons, postclypeus, genae and postgenae creamy; compound eyes black; ocelli hyaline, ocellar triangle creamy; anteclypeus light brown; labrum pale brown; labral sclerites brown. Antennae pale brown. Maxillary palps light brown to creamy. Tergal lobes of meso- and metathorax dark brown; thoracic pleura brown. Legs: coxae and trochanters brown; femora brown, darker basally, with oval blackish spots; tibiae creamy, with contours blackish; tarsomeres 1 creamy; tarsomeres 2 pale brown. Forewing membrane brown proximally (Fig. 7), hyaline distally; crossveins of pterostigma dark brown; veins brown, Rs, M and areola postica dark brown; nodus and nodulus blackish. Hindwing membrane pale brown proximally, hyaline distally, veins

brown (Fig. 8). Abdomen brown, tergum dark brown. Clunium dark brown. Hypandrium brown, posterior edge darker. Phallosome dark brown, endophallus creamy. Epiproct and paraprocts dark brown.

Morphology. Head with abundant macrosetae, mainly on vertex (Fig. 9); compound eyes small, widely separated; vertex convex, bilobed, clearly above upper border of compound eyes. Outer cusp of lacinial tips broad, with eight denticles. Labrum with five distal sensilla: central placoid one, flanked by pair of trichoid–placoid sensilla. Forewings (Fig. 7): pterostigma triangular, long, wider medially, with 4–5 crossveins; M with three branches, strongly concave distal to transverse vein r–m; areola postica high, slanted posteriorly, rounded apically, separated from CuA_2 by about 0.28× its own length; R_{2+3} strongly sinuous, R_{4+5} almost five times the length of Rs section
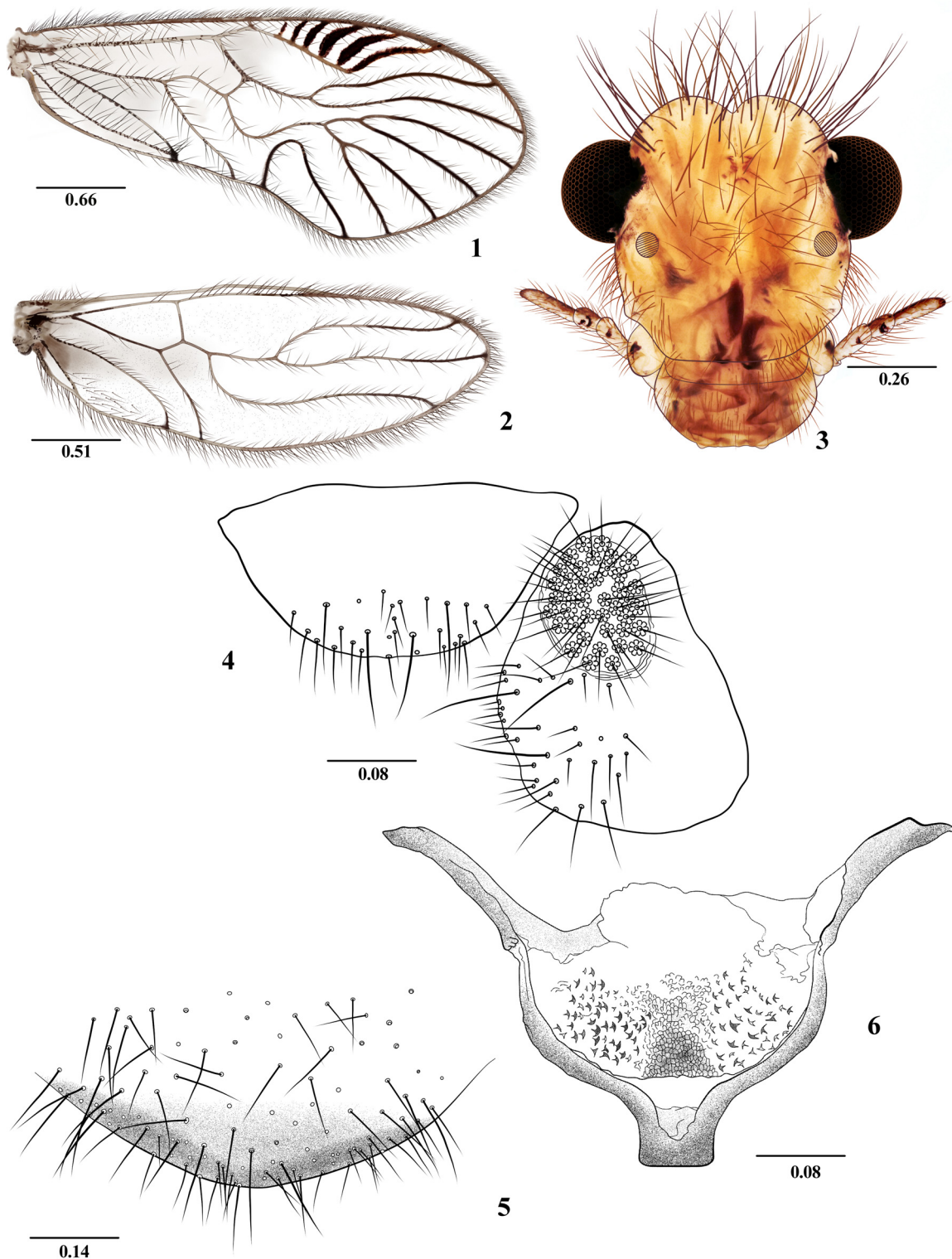

Figs 1–6. *Neurostigma lienhardi* sp. nov., male. 1 – forewing; 2 – hindwing; 3 – head, frontal view; 4 – epiproct and right paraproct; 5 – hypandrium; 6 – phallosome. Values for scale bars in mm.

proximal to transverse r–m. Hindwings elongate (Fig. 8): M unbranched; Rs+M much shorter than Rs section proximal to transverse rs–m. Legs: hind coxae with rasp smaller than tympanum; trochanters with two long setae dorsally; fore and mid-tarsi without ctenidobotria; hind tarsi with ctenidobotria. Hypandrium membranous (Fig. 11), with dense field of long setae, posterior border rounded, postero-lateral borders more sclerotized. Phallosome (Fig. 12) open basally; side struts short, wide basally, curved

outwards; aedeagal arch robust, posterior process rounded apically; external parameres absent; endophallus membranous, lacking sclerites. Paraprocts (Fig. 10) elongate, posterior border rounded, with setae, sensory fields large, with 26–28 trichobothria on basal rosettes. Epiproct broad basally, posterior margin truncate, setal field as illustrated in Fig. 10. Female unknown.

Diagnosis. *Neurostigma mockfordi* sp. nov. is similar to *N. valderramae* sp. nov. in the forewings and radula. It
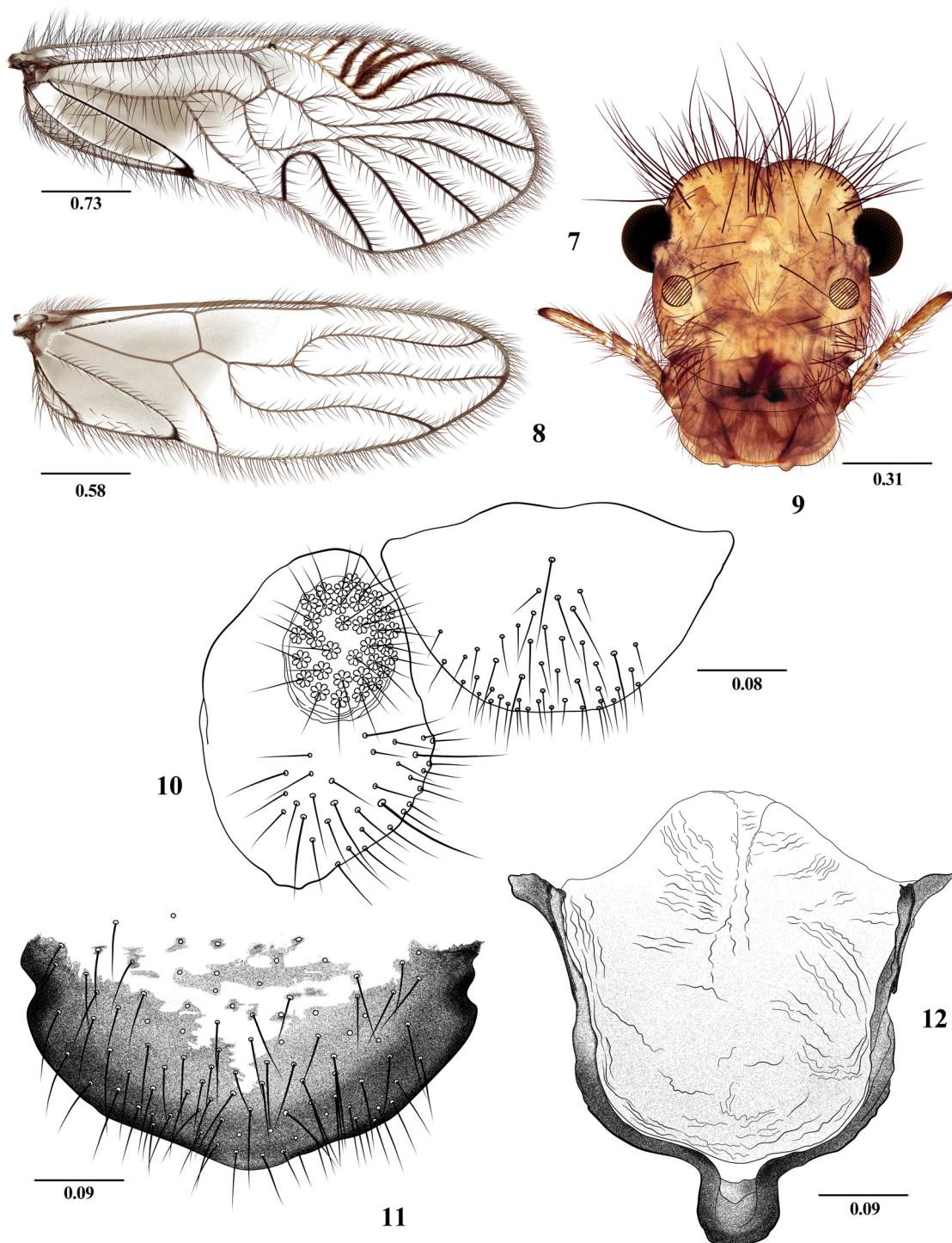
Figs 7–12. *Neurostigma mockfordi* sp. nov., male. 7 – forewing; 8 – hindwing; 9 – head, frontal view; 10 – left paraproct and epiproct; 11 – hypandrium; 12 – phallosome. Values for scale bars in mm.

differs from the latter in the following characters: posterior process of aedeagus broad, stout, and distally rounded; pterostigma with five crossveins; areola postica slanted posteriorly, with apex rounded.

Etymology. This species is dedicated to Dr. Edward L. Mockford, from the Illinois State University, an undisputed leader in psocidological studies worldwide.

Distribution. Colombia (Boyacá and Valle del Cauca).

Neurostigma newi sp. nov.
(Figs 13–18)

Type material. HOLOTYPE: ♂, **COLOMBIA**: Valle del Cauca, Dagua, Km 30, parcelación Plenitud, 3°34′19.8″N, 76°39′46.5″W, 1344 m, 29.iv.–1.v.2011, J. A. Mendivil leg. (MUSENUV, slide no. 29873). PARATYPE: **COLOMBIA**: 1 ♂, Magdalena, National Natural Park Tayrona, 11°19′N, 73°59′W, 600 m (IAVH, slide no. 3429).

Description. *Measurements* (male holotype, in μm). FW: 3200, HW: 2425, F: 700, T: 1150, t1: 510, t2: 150, ctt1: 20, f1: 400, f2: 300, f3: 260, f4: 270, Mx4: 180, IO: 440, D: 220, d: 180, IO/d: 2.44, PO: 0.82, H/MxW: 1.33, H/D: 3.51; IO/MxW: 0.77, Mx4/Mx2: 1.43, FW/W: 2.45, lp/wp: 2.85, al/ah: 1.85, HW/w: 2.91.

Color. Body creamy, with brown spots. Head (Fig. 15) with light brown band from inner margin of each compound eye to ocellar triangle and pale brown band around compound eyes; vertex, frons, postclypeus, anteclypeus and labrum creamy; labral sclerites pale brown; genae light brown; postgenae pale brown; compound eyes blackish; ocelli hyaline, with pale brown centripetal crescents. Antennae pale brown. Maxillary palps: segments 1–3 pale brown; segment 4 brown, apex darker. Tergal lobes of mesothorax creamy, posterior edge brown; tergal lobes of metathorax brown, creamy distally; thoracic pleura creamy. Legs: coxae and trochanters creamy, with blackish spot apically; femora creamy, with blackish spots; tibiae creamy; tarsi pale brown. Forewing membrane hyaline (Fig. 13); pterostigma crossveins brown; Rs, M and areola postica dark brown, other veins pale brown; nodulus blackish. Hindwing membrane hyaline, light brown basally; veins brown. Abdomen: tergum with blackish band, sternum creamy. Clunium light brown, anterior edge darker. Hypandrium light brown. Phallosome dark brown, radula with one group of sclerites on each side of longitudinal midline, on spinose matrix, each group with long, sclerotized black teeth. Epiproct and paraprocts light brown.

Morphology. Head with abundant macrosetae, mainly on vertex (Fig. 15). Vertex convex, bilobed, clearly above upper border of compound eyes. Outer cusp of lacinial tips broad, with five denticles. Labrum with five distal sensilla: central placoid one, flanked by pair of trichoid–placoid sensilla. Forewings (Fig. 13): pterostigma triangular, wider in middle, with four crossveins, third or fourth crossvein forked; R_{2+3} sinuous, R_{4+5} approximately three times the length of Rs section proximal to transverse r–m; M with three branches, strongly concave distal to r–m; areola postica high, rounded apically, slanted posteriorly, separated from CuA_2 by about 0.3× its own length. Hindwings elongate (Fig. 14): M simple, unbranched; Rs+M longer than Rs section proximal to transverse r–m; Cu angled in middle;

Rs and M fused at a distance. Legs: hind coxae with rasp slightly smaller than tympanum; trochanters with elongate setae dorsally; fore and mid-tarsi without ctenidobotria; hind tarsi with ctenidobotria. Hypandrium triangular, membranous (Fig. 17), with abundant setae. Phallosome (Fig. 18) open basally; side struts straight, somewhat wide basally and gently curved outwards; aedeagal arch robust, posterior process wide, short and rounded apically; external parameres absent; radula with two sclerites with numerous pointed teeth, immersed in spinose matrix. Paraprocts (Fig. 16) oval, short, with abundant setae distally, sensory fields large, with 32–36 trichobothria on basal rosettes. Epiproct broad basally, posterior margin rounded, with one macroseta mesally, other setae as illustrated in Fig. 16. Female unknown.

Diagnosis. *Neurostigma newi* sp. nov. is close to *N. garcialdretei* and *N. radiatum* in R_{4+5}/Rs length ratio, and the presence of spines in the radular sclerites. It differs from both species in the shape and length of the pterostigma and the posterior process of the aedeagus which is short, broad and rounded distally.

Etymology. This species is dedicated to Dr. Timothy Richard New, from La Trobe University, Victoria, Australia, in recognition of his studies on South American Psocoptera and insect conservation.

Distribution. Colombia (Magdalena and Valle del Cauca).

Neurostigma thorntoni sp. nov.
(Figs 19–24)

Type material. HOLOTYPE: ♂, **COLOMBIA**: Putumayo, Puerto Asís, El Horizonte, 0°22′58.37″N, 76°31′31.62″W, 264 m, 3–4.iii.2014, J. Panche leg. (MUSENUV, slide no. 29874). PARATYPE: 1 ♂, same data as holotype (MUSENUV, slide no. 29875).

Description. *Measurements* (male holotype, in μm). FW: 3350, HW: 2425, F: 625, T: 825, t1: 330, t2: 150, ctt1: 13, f1: 400, f2: 300, Mx4: 270, IO: 460, D: 300, d: 230, IO/d: 2.0, PO: 0.77, H/MxW: 1.40, H/D: 3.18, IO/MxW: 0.70, Mx4/Mx2: 1.67, FW/W: 2.48. lp/wp: 3.29, al/ah: 2.27, HW/w: 2.96.

Color. Body creamy, with brown spots. Head (Fig. 21): vertex creamy; frons, postclypeus, anteclypeus, genae and labrum light brown; postgenae creamy; compound eyes black, ocelli hyaline, with ochre centripetal crescents; labral sclerites brown. Antennae pale brown. Maxillary palps pale brown to creamy. Tergal lobes of mesothorax creamy; tergal lobes of metathorax brown; thoracic pleura creamy. Legs: fore and mid-coxae and trochanters pale brown; fore and mid-femora creamy, with oval blackish spots dorsally; fore and mid-tibiae creamy; fore and mid-tarsomeres 1 creamy to brown; fore and mid-tarsomeres 2 pale brown; hind legs missing in the material examined. Forewing membrane hyaline, brown basally, with small, oval brown spot near point of separation of CuA and M (Fig. 19); pterostigma crossveins dark brown; Rs, M and areola postica dark brown, other veins pale brown. Hindwing membrane hyaline, with large brown spot proximally (Fig. 20); veins brown. Abdomen creamy, tergum with irregular blackish spots. Hypandrium hyaline. Phallosome pale brown, radular sclerites pale brown. Epiproct and paraprocts missing.

Morphology. Head with abundant macrosetae, mainly on vertex (Fig. 21), vertex convex, bilobed, clearly above upper border of compound eyes. Outer cusp of lacinial tips broad, with 7–8 denticles. Labrum with five distal sensilla: central placoid one, flanked by pair of trichoid–placoid ones. Forewings (Fig. 19): pterostigma long, wider distally, with five crossveins; R_{2+3} sinuous, R_{4+5} less than three times the length of Rs section proximal to transverse r–m; M with three branches, strongly concave distal to r–m; areola postica tall, slanted posteriorly, rounded apically, separated from CuA_2 by about 0.3× its own length. Hindwings elongate (Fig. 20): M unbranched; Rs+M almost as long as or longer than Rs section proximal to r–m. Legs: trochanters with two long setae
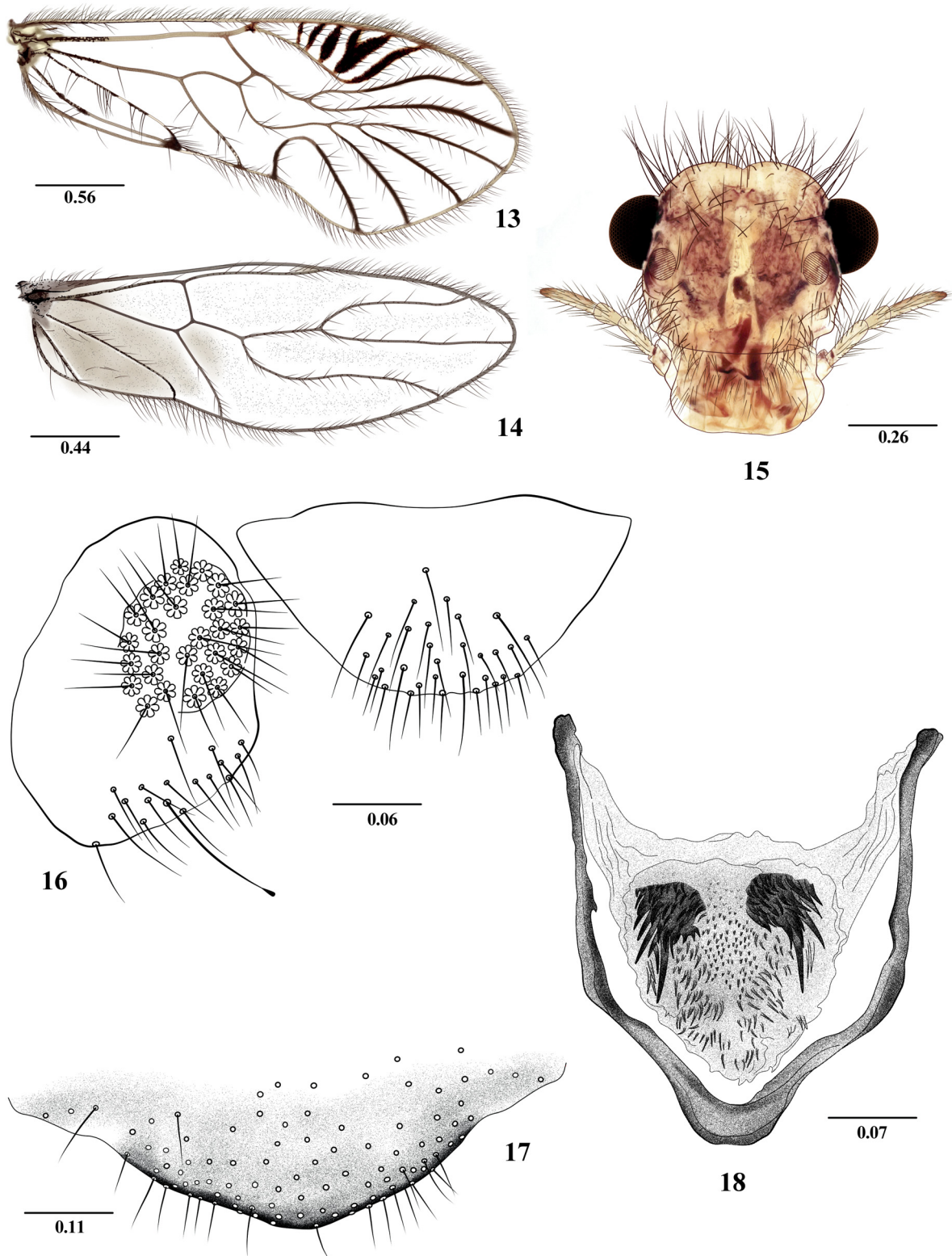

Figs 13–18. *Neurostigma newi* sp. nov., male. 13 – forewing; 14 – hindwing; 15 – head, frontal view; 16 – left paraproct and epiproct; 17 – hypandrium; 18 – phallosome. Values for scale bars in mm.

dorsally; fore tarsi without ctenidobotria; hind legs missing in the material examined. Hypandrium membranous (Fig. 23) with abundant setae, posterior border rounded. Abdomen: tergum with tubercles. Phallosome (Fig. 24) open basally; side struts curved outwards; aedeagal arch robust, posterior process robust, rounded apically, with sides converging to apex; external parameres absent;

radula with two groups of small sclerotized teeth. Paraprocts (Fig. 22) oval, with setae and macrosetae distally, sensory fields large, with 33 trichobothria on basal rosettes. Epiproct (Fig. 22) broad basally, posterior margin broadly rounded, with microsetae and setae distally. Female unknown.

**Diagnosis.** *Neurostigma thorntoni* sp. nov. is similar to
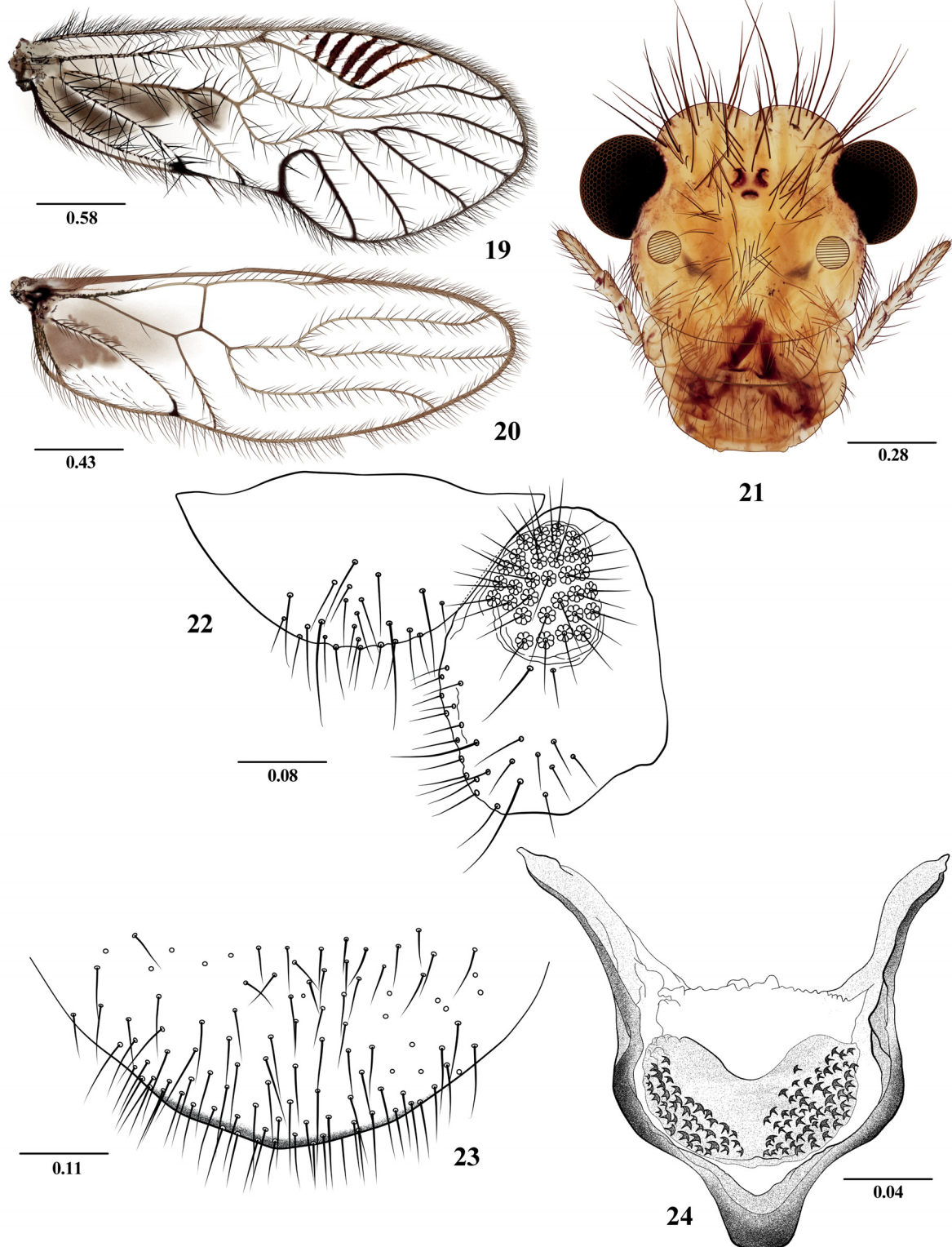
Figs 19–24. *Neurostigma thorntoni* sp. nov., male. 19 – forewing; 20 – hindwing; 21 – head, frontal view; 22 – epiproct and right paraproct; 23 – hypandrium; 24 – phallosome. Values for scale bars in mm.

N. lienhardi sp. nov. in the head, wings and radular sclerites. It differs from the latter in the following characters: posterior process of aedeagus distally rounded, with sides converging to the apex; two groups of sclerotized teeth of radula separated by a smooth membranous area (Fig. 24); hindwing Rs, proximal to M interception, basally inclined towards the wing apex (Fig. 20).

Etymology. This species is dedicated to Dr. Ian W. B. Thornton (1926–2002), professor of Zoology at the La Trobe University, Victoria, Australia. He greatly contributed to the knowledge of Psocoptera of Australia, Indonesia and New Guinea. His work on Krakatau provided seminal insights into the recolonization of islands.

Distribution. Colombia (Putumayo).
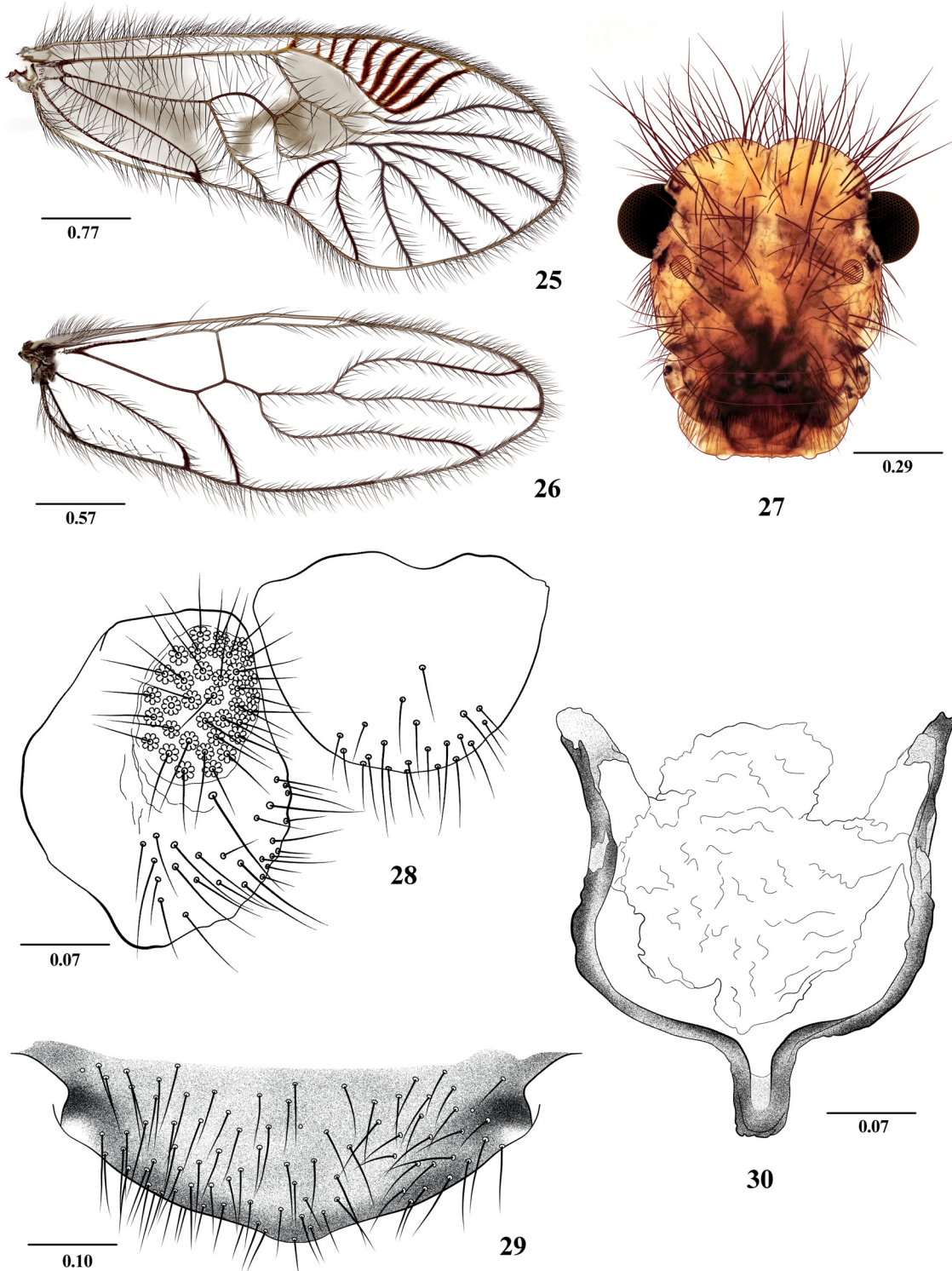
Figs 25–30. *Neurostigma valderramae* sp. nov., male. 25 – forewing; 26 – hindwing; 27 – head, frontal view; 28 – left paraproct and epiproct; 29 – hypandrium; 30 – phallosome. Values for scale bars in mm.

Neurostigma valderramae sp. nov.
(Figs 25–30)

Type material. HOLOTYPE: ♂, **COLOMBIA:** Huila, La Plata, Meremberg, 2°13′7.0″N, 76°7′0.9″W, 2118 m, 21.i.2015, R. González, O. Saenz & N. Calderón leg. (MUSENUV, slide no. 29876).

Description. *Measurements* (male holotype, in μm). FW: 4700, HW: 3325, F: 875, T: 1650, t1: 600, t2: 200, ctt1: 17, f1: 650, f2: 450, f3: 400, f4: 400, Mx4: 260, IO: 550, D: 230, d: 200, IO/d: 2.75, PO: 0.87, H/MxW: 1.36, H/D: 4.00, IO/MxW: 0.73, FW/W: 2.39, lp/wp: 2.45, al/ah: 1.13, HW/w: 2.92.

Color. Body dark brown, with pale spots. Head (Fig. 27) with dark brown spots around compound eyes; vertex, frons, postclypeus, genae and postgenae light brown; compound eyes black, with pale transverse bands; ocelli hyaline, ocellar triangle creamy; anteclypeus and labrum light brown; labral sclerites brown. Antennae pale brown. Maxillary palps brown to creamy. Tergal lobes of meso- and metathorax dark brown; thoracic pleura brown. Legs: coxae brown; trochanters creamy to brown; femora creamy, darker basally, with oval spots; tibiae creamy, with blackish lateral contours; tarsomeres 1 creamy; tarsomeres 2 pale brown. Forewing membrane (Fig. 25) hyaline, with pale brown spot extending from CuA to R_1; cell cua with pale brown spot in middle; pterostigma crossveins dark brown; veins brown, Rs, M and areola postica darker; nodulus dark brown. Hindwings hyaline; veins brown. Abdomen brown, tergum dark brown. Clunium dark brown. Hypandrium brown, posterior border darker. Phallosome dark brown. Epiproct and paraprocts dark brown.

Morphology. Head with abundant macrosetae, mainly on vertex (Fig. 27); compound eyes small, vertex convex, bilobed, above upper border of compound eyes. Outer cusp of lacinial tips broad, with 7–8 denticles. Labrum with five distal sensilla: central placoid one, flanked by pair of trichoid–placoid sensilla. Forewings (Fig. 25): pterostigma elongate, wider distally, with seven crossveins; R_{2+3} sinuous; R_{4+5} about five times as long as Rs section proximal to r–m; M with three branches; M_3 forked, strongly concave distal to r–m; areola postica high, almost as long as wide, angled apically, separated from CuA_2 by about 0.25× its

own length. Hindwings elongate (Fig. 26): M simple, unbranched; Rs+M shorter than Rs section proximal to r–m; Cu angled in middle. Legs: hind coxae with rasp as long as tympanum; trochanters with two long setae dorsally; fore and mid-tarsi without ctenidobotria; hindtarsi with ctenidobotria. Hypandrium membranous (Fig. 29), with abundant setae, posterior margin rounded and more sclerotized. Phallosome (Fig. 30) open basally; side struts short, straight; posterior process elongate, narrow and almost truncate apically; external parameres absent; endophallus membranous. Paraprocts (Fig. 28) oval, short, posterior border rounded, with long and short setae; sensory fields with 33–34 trichobothria on basal rosettes. Epiproct wide anteriorly, posterior border rounded, setal field as illustrated in Fig. 28. Female unknown.

Diagnosis. *Neurostigma valderramae* sp. nov. is similar to *N. mockfordi* sp. nov. in the absence of endophallic sclerites and the forewing vein R_{2+3} being longer than four times the length of Rs section distal to r–m. It differs from the latter in the following characters: posterior process of aedeagus long, narrow and distally truncate (Fig. 30); pterostigma with 7 crossveins; apex of areola postica angled (Fig. 25).

Etymology. This species is dedicated to Graciela Valderrama de Díaz, enthusiastic and dedicated professor (retired) of Animal Genetics, Biology Department, Universidad del Valle, Santiago de Cali, Colombia.

Distribution. Colombia (Huila).

Key to males of *Neurostigma*

Modified from MENDIVIL-NIETO et al. (2020). *Neurostigma chaetocephalum*, *N. furcivenula* and *N. roesleri* are not included because their male genitalia are unknown.

1   Forewing with areola postica fused with M; pterostigma with seven or more crossveins (Figs 31, 32). Distal process of the aedeagal arch very wide, trapezoidal (Fig. 38). 2

–   Forewing with areola postica free, not fused with M; pterostigma with 2–7 crossveins (Figs 1, 7, 13). Distal process of the aedeagal arch variable (Figs 6, 12, 18, 24, 30). 3

Table 1. Species of *Neurostigma* and their known distribution.

Species	Distribution	Reference
N. chaetocephalum Enderlein, 1900	Peru	ENDERLEIN (1900)
N. dispositum Roesler, 1940	Brazil, Mexico, Peru	ROESLER (1940), GARCIA ALDRETE (1988), NEW (1972, 1973), NEW & THORNTON (1988)
N. enderleini New, 1980	Brazil	New (1980)
N. furcivenula Badonnel, 1986	Colombia	BADONNEL (1986)
N. garcialdretei Mendivil, González & Carrejo, 2020	Colombia	MENDIVIL et al. (2020)
N. paucivenosum New, 1980	Brazil	NEW (1980)
N. lienhardi sp. nov.	Colombia	this paper
N. mockfordi sp. nov.	Colombia	this paper
N. newi sp. nov.	Colombia	this paper
N. radiatum Mockford, 1991	Brazil	MOCKFORD (1991)
N. roesleri New, 1980	Brazil	NEW (1980)
N. thorntoni sp. nov.	Colombia	this paper
N. valderramae sp. nov.	Colombia	this paper
N. xanthopterum New, 1980	Brazil, Colombia	NEW (1980), MENDIVIL et al. (2020)
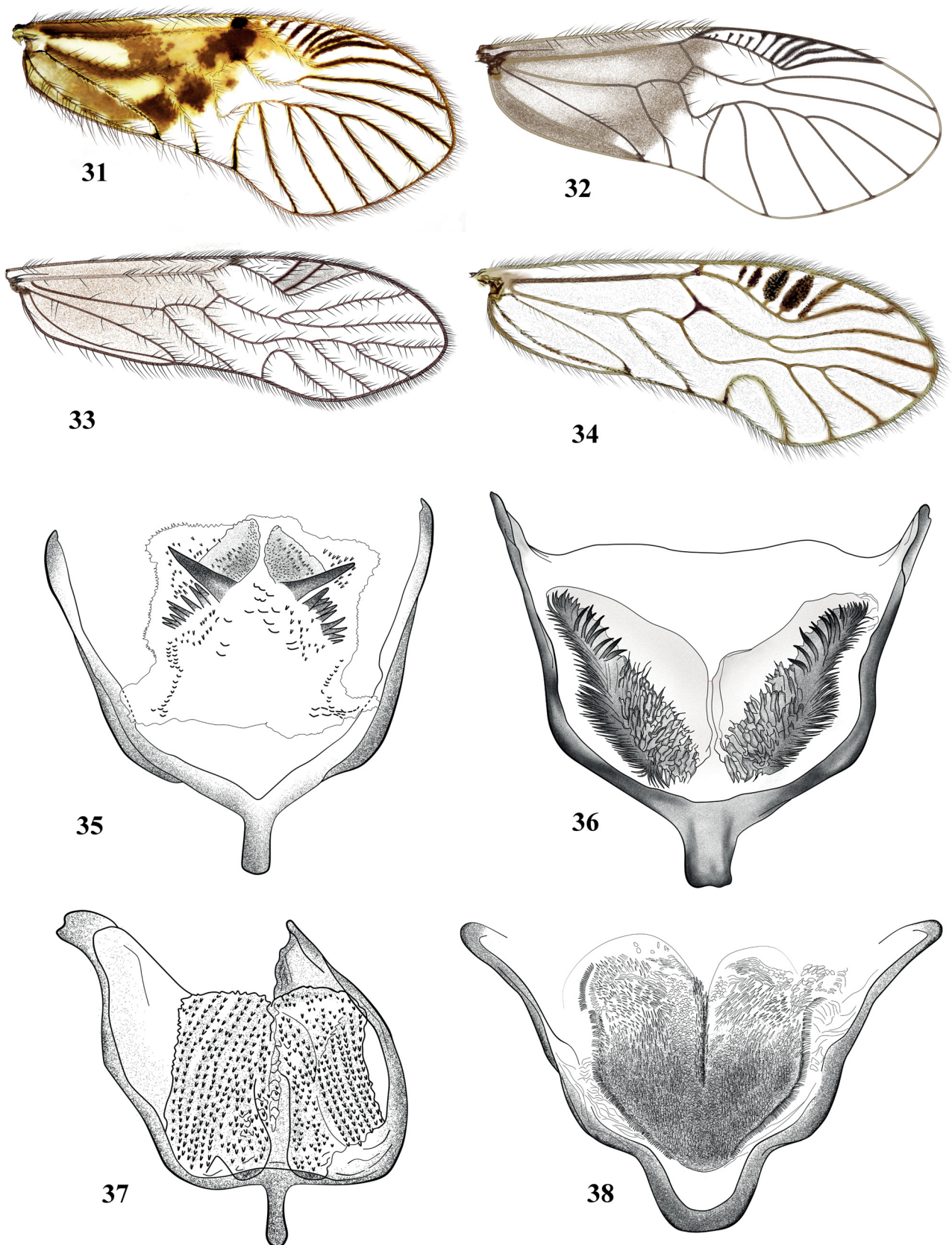
Figs 31–38. Forewings and phallosomes of *Neurostigma* spp. 31, 38 – *N. xanthopterum* New, 1980; 32 – *N. enderleini* New, 1980; 33, 37 – *N. paucivenosum* New, 1980 (redrawn from NEW 1980: figs 52, 53); 34, 36 – *N. garcialdretei* Mendivil et al., 2020; 35 – *N. radiatum* Mockford, 1991 (redrawn from MOCKFORD 1991: fig. 134).

Fig. 39. *Neurostigma chaetocephalum* Enderlein, 1900, male (redrawn from Enderlein 1900: fig. 24).
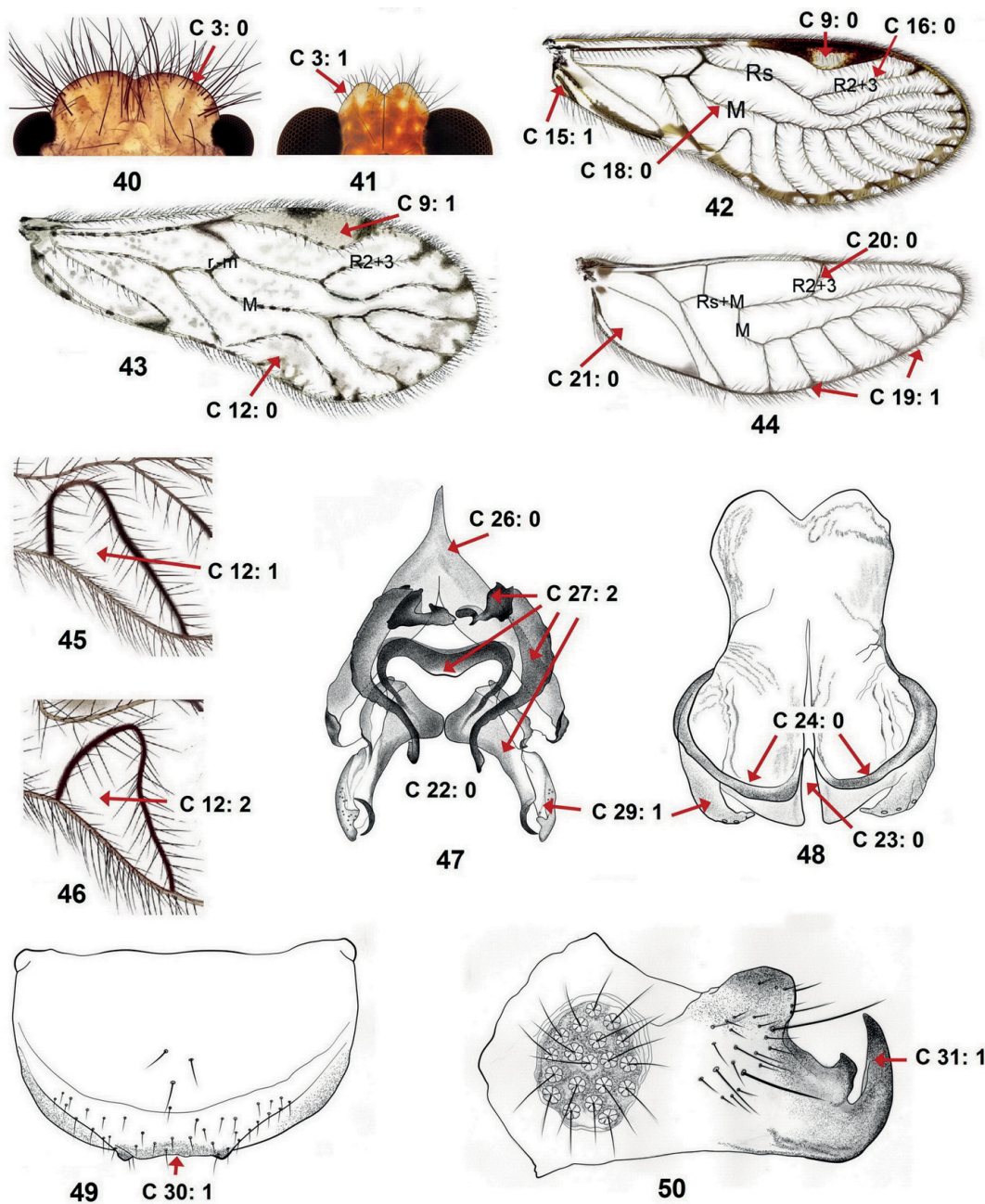
Figs 40–50. Structural characters of *Cladiopsocus* (taken with permission from González Obando et al. 2016: figs 15, 18, 19, 21), *Neurostigma* (taken with permission from Mendivil-Nieto et al. 2020: figs 7–9) and *Ptiloneura* (taken with permission from Garcia Aldrete et al. 2020: figs 2, 6). 40 – *Neurostigma mockfordi* sp. nov., vertex; 41 – *N. xanthopterum* New, 1980, vertex; 42, 44 – *Ptiloneura columnaris* García Aldrete et al., 2020, fore- and hindwing; 43 – *Cladiopsocus eertmoedi* González Obando et al., 2016, forewing; 45 – *N. mockfordi*, areola postica, type 2; 46 – *N. valderramae* sp. nov., areola postica, type 3; 47 – *P. columnaris*, phallosome; 48–50 – *C. eertmoedi*, phallosome, epiproct and paraproct, respectively.

2   Radular sclerites with small denticles, more pronoun-
ced in midline (Fig. 38). Vertex narrow, raised and
distinctly emarginate in the middle. Proximal half of
forewing yellowish to brown, with large dark brown
spots and hyaline basal area, basal crossveins of pte-
rostigma pigmented at the wing margin (Fig. 31). ......
.... ***N. xanthopterum*** New, 1980

–   Radular sclerites weakly developed. Vertex not as
above. Proximal half of forewing dark brown; basal
crossveins of pterostigma not pigmented at the wing
margin (Fig. 32). .... ***N. enderleini*** New, 1980

3   Forewing vein R_{2+3} strongly sinuous, more than four
times the length of Rs section distal to transverse vein
r–m (Figs 7, 25). 4

–   Forewing vein R_{2+3} weakly or strongly sinuous, but less
than four times the length of Rs section distal to r–m
(Figs 1, 13, 19). 5

4   Posterior process of aedeagus moderately broad, apex
rounded (Fig. 12). Pterostigma with five crossveins;
apex of areola postica rounded (Fig. 7). ....
.... ***N. mockfordi*** sp. nov.

–   Posterior process of aedeagus elongate, narrow, distally
truncate (Fig. 30). Pterostigma with seven crossveins;
areola postica slanted posteriorly, apex acute (Fig. 25).
.... ***N. valderramae*** sp. nov.

5   Distal process of the aedeagal arch wide, short, broadly
rounded apically. Radular sclerites well developed. ....
.... ***N. dispositum*** Roesler, 1940

–   Distal process of the aedeagal arch different. Radular
sclerites with spicules or spines. 6

6   Pterostigma with 2–3 crossveins (Fig. 33). Vertex al-
most at the same level as the upper border of com-
pound eyes. Aedeagus with elongate, slender, distally
rounded posterior process; radula with rows of sclero-
tized denticles (Fig. 37). ....
.... ***N. paucivenosum*** New, 1980

–   Pterostigma with 4–7 crossveins (Figs 1, 19). Vertex
above the upper border of compound eyes (Figs 3, 15,
21). Posterior process of the aedeagus variable, short
or long, slender or stout, distally round, truncate or
acuminate; radula with or without spicules or large
spines (Figs 6, 18, 24). 7

7   Radula with few to abundant small to large teeth or
spicules (Figs 18, 35, 36). 8

–   Radula with only small teeth or spicules (Figs 6, 24).
.... 10

8   Posterior process of aedeagus short, stout, distally
rounded (Fig. 18). .... ***N. newi*** sp. nov.

–   Posterior process of aedeagus longer and narrower
(Figs 35, 36). 9

9   Radular sclerites with two long, pointed spines direc-
ted antero-laterally, arising from a dense field of short-
er spines and spinose membrane (Fig. 35); posterior
process of aedeagus long, slender, distally round. ....
.... ***N. radiatum*** Mockford, 1991

–   Radular sclerites with pointed spines directed antero-
mesally, long spicules on external margin and a den-
se field of short spines and spicules latero-posteriorly
(Fig. 36); posterior process of aedeagus long, stout,
distally truncate. ....
.... ***N. garcialdretei*** Mendivil, González & Carrejo,
2020

10   Posterior process of aedeagus short, stout, with pa-
rallel sides, distally truncate; radula with two groups
of small sclerotized teeth separated by a reticulated
area (Fig. 6). .... ***N. lienhardi*** sp. nov.

–   Posterior process of aedeagus long, stout, with sides
converging to straight apex; radula with two groups of
small sclerotized teeth separated by a smooth mem-
branous area (Fig. 24). .... ***N. thorntoni*** sp. nov.

Phylogenetic analysis

To assess the phylogenetic relationships of the *Neu-rostigma* species, a cladistic analysis was conducted. A character matrix was built with 32 discrete morphological characters, scored for 15 taxa (Table 2):

Table 2. Data matrix of morphological characters used for the cladistic analysis of *Neurostigma*. Outgroup: *Loneura gorgonaensis* García Aldrete et al., 2011, *Ptiloneura columnaris* García Aldrete et al., 2020 and *Cladiopsocus eertmoedi* González Obando et al., 2016.

```
                                1111111111222222222233
                                1234567890123456789012345678901 2
        Loneura gorgonaensis    00000111100-00010-01000---02-100
        Ptiloneura columnaris   00000112200-00010-01000---02-100
        Cladiopsocus eertmoedi  00011000110-00010-0000100-10-111
        Neurostigma dispositum  ???110001011101010101?1112111010
        Neurostigma chaetocephalum 1???????10113110101011111????10
        Neurostigma enderleini  1??110002011311010101?1112110010
        Neurostigma garcialdretei 110110001011201010101111111111010
        Neurostigma paucivenosum ???110001010201010100?1?1110110010
        Neurostigma lienhardi   110110001011101010101111111110010
        Neurostigma mockfordi   11011000001110101101111110-010
        Neurostigma newi        110110000011101010101111112111010
        Neurostigma radiatum    ???110001011101010101?1110111010
        Neurostigma thorntoni   110110001011101010101111112110010
        Neurostigma valderramae 11011000001120101110111110-010
        Neurostigma xanthopterum 10111000101131101011111112110010
```

0. Vertex: at about the same level as the upper border of the compound eyes (0); clearly above the upper border of the compound eyes (1).
1. Separation of compound eyes (ratio IO/MxW): < 0.6 (0); > 0.6 (1).
2. Vertex lateral margins: convex (Fig. 40) (0); straight (Fig. 41) (1).
3 Labral sclerites anteriorly: membranous/separated (0); joined by a sclerotic strip (1).
4. Labral sclerites posteriorly: extended to posterior margin of labrum (0); curved towards the sides (1).
5. Dorsal end of epistomal suture: absent (0); present (1).
6. Number of tarsomeres: two (0); three (1).
7. Number of primary branches in vein M of forewing: 3–4 (0); 5 (1); > 5 (2).
8. Ratio pterostigma length/width: < 3.0 (0); 3.0–4.5 (1); > 4.5 (2).
9. Pterostigma: widest in the middle (Fig. 42) (0); widest distally (Fig. 43) (1).
10. Pterostigma crossveins: absent (0); present (1).
11. Number of pterostigma crossveins: < 4 (Fig. 33) (0); > 4 (Fig. 1) (1).
12. Shape of areola postica: type 1 (Fig. 43) (0); type 2 (Fig. 45); (1) type 3 (Fig. 46) (2); type 4 (Fig. 32) (3).
13. Areola postica and vein M: separated (0) (Fig. 1); fused (1) (Fig. 32).
14. Areola postica and CuA: joined (Fig. 43) (0); separated (1) (Fig. 1).
15. Vein A_2 in forewing: (0) absent (Fig. 1); present (1) (Fig. 42).
16. Forewing vein R_{2+3}: subequal or shorter than Rs section distal to r–m (Fig. 42) (0); longer than Rs section distal to r–m (Fig. 1) (1).
17. Forewing R_{2+3}: less than four times Rs section length distal to r–m (Fig. 1) (0); more than four times Rs section length distal to r–m (Fig. 7) (1).
18. Forewing vein M distal to r–m: slightly concave (Fig. 42) (0); strongly concave (Fig. 31) (1).
19. Hindwing vein M: not branched (Fig. 1) (0); branched (Fig. 44) (1).
20. Hindwing vein R_{2+3}: straight and directed towards costal margin (Fig. 44) (0); curved basally and directed towards apex (Fig. 1) (1).
21. Setae on membrane in hindwing cup: absent (Fig. 44) (0); present (Fig. 2) (1).
22. Aedeagal arch: absent (Fig. 47) (0); present (Fig. 6) (1).

23. Distal process of the aedeagal arch: absent (Fig. 48) (0); present (Fig. 12) (1).
24. Aedeagal arch present: interrupted in the middle (Fig. 48) (0); continuous (Fig. 6) (1).
25. Distal process of aedeagal arch: narrow (Fig. 37) (0); moderately wide (Fig. 36) (1); very wide (Fig. 38) (2).
26. Struts of phallobase: V-shaped (Fig. 47) (0); vertical (Fig. 36) (1).
27. Endophallus: membranous (Figs 12, 30) (0); with spines or denticles (Figs 6, 24, 35) (1); with large sclerites but not spines or denticles (Fig. 47) (2).
28. Radular sclerites: with small denticles (Fig. 6) (0); with medium to large spines (Figs 18, 35, 36) (1).
29. External parameres: absent (Fig. 6) (0); present (Fig. 47) (1).
30. Emargination of epiproct: absent (Fig. 4) (0); present (Fig. 49) (1).
31. Paraproctal prong: absent (Fig. 4) (0); present (Fig. 50) (1).

The cladistic analysis produced 34 most parsimonious trees with length (L) of 48 steps, consistency index (CI) of 0.79 and retention index (RI) of 0.82. The strict consensus tree (Fig. 51) has a length of 54 steps, consistency index of 0.70 and retention index of 0.72. The analysis indicates that *Neurostigma* is monophyletic, representing a clade supported by eleven unambiguous synapomorphies (characters 0, 1, 10, 12, 14, 15, 16, 18, 20, 21 and 29) (Fig. 51). Further, there is a clade supported by two unambiguous synapomorphies related to the shape and development of the areola postica (characters 12 and 13) that includes three species, *N. xanthopterum, N. enderleini* and *N. chaetocephalum*. Also *N. mockfordi* and *N. valderramae* appear to be closely related, as they form another clade supported by one unambiguous synapomorphy (character 17) and two homoplasies (characters 8 and 27) (Fig. 51).
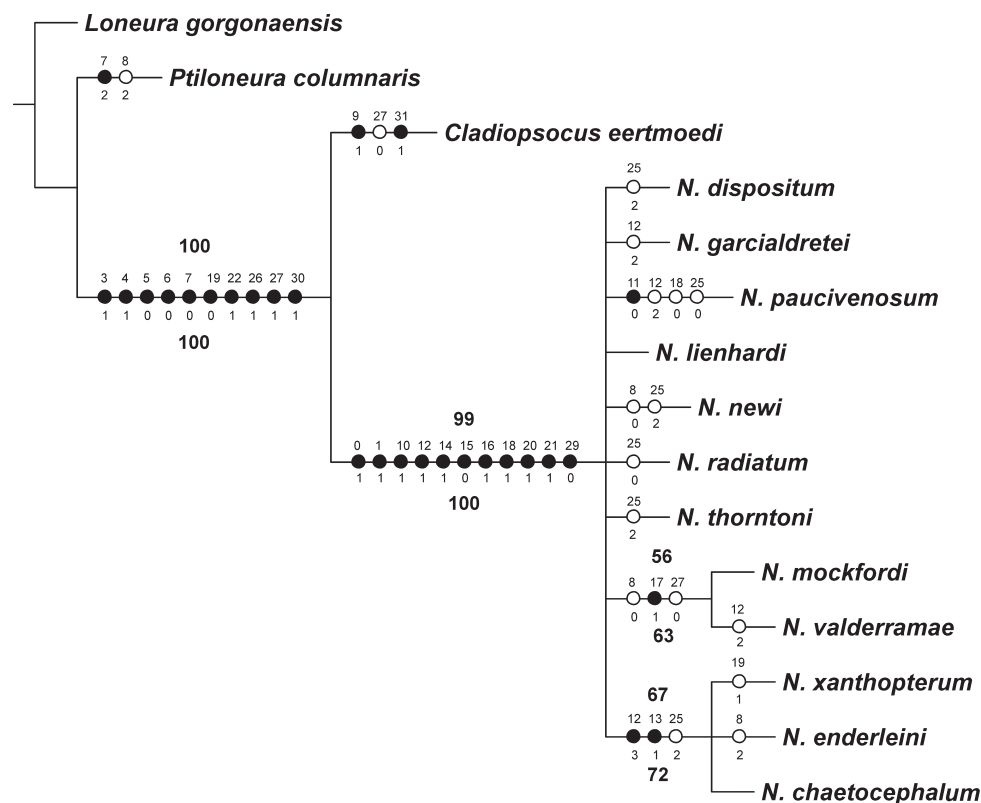

Fig. 51. Strict consensus cladogram for *Neurostigma* species (L = 54; CI = 0.70; RI = 0.72). *Cladiopsocus eertmoedi* González Obando et al., 2016, *Loneura gorgonaensis* García Aldrete et al., 2011 and *Ptiloneura columnaris* García Aldrete et al., 2020 were used as outgroups. Full circles (black) indicate unique (unambiguous) character state changes; empty circles indicate homoplasies (parallelisms or reversals). Character numbers are indicated above and character states below each circle. Bootstrap and symmetric resampling support values for nodes are given above and below the branches,

Discussion

The number of species in *Neurostigma* is raised to 14, which represents a significant increase in the known diversity of the genus. Most species (8) are known from Colombia, followed by Brazil (6) (Table 2).

According to Casasola-González (2006), Ptiloneuridae, *Spurostigma* Eertmoed, 1973, *Cladiopsocus* Eertmoed, 1986 (Cladiopsocidae) and Epipsocidae together form a monophyletic group, supported by five synapomorphies. In our analysis, a close relationship between *Cladiopsocus* and *Neurostigma* is also supported.

Mendivil-Nieto et al. (2020) recognized two species groups in *Neurostigma*, defined on the basis of the forewing areola postica which is either joined to M or free. Based on the cladistic analysis carried out here, their group II is not supported as monophyletic. The following classification based on the areola postica, updated with the species newly described in the present paper, should thus only be maintained for a practical taxonomic purpose:

Species group I. Forewing areola postica joined to M. Species included: *N. chaetocephalum*, *N. enderleini*, and *N. xanthopterum*.

Species group II. Forewing areola postica free. Species included: *N. dispositum*, *N. furcivenula*, *N. garcialdretei*, *N. lienhardi* sp. nov., *N. mockfordi* sp. nov., *N. newi* sp. nov., *N. paucivenosum*, *N. radiatum* Mockford, *N. roesleri*, *N. thorntoni* sp. nov., and *N. valderramae* sp. nov.

The three species in the group I, which is monophyletic, present the same pattern of wing pigmentation: the proximal half of forewing dark brown, and the proximal half of hindwing light brown. In the two Colombian specimens of *N. xanthopterum* examined by us (Mendivil-Nieto et al. 2020), the hindwing presents M with two to three branches, sometimes with M_3 forked; in the other two species, M is simple, according to the original descriptions. *Neurostigma xanthopterum* and *N. enderleini* also differ in the shape of the posterior process of the aedeagus, which is apically rounded in *N. xanthopterum*, and apically straight in *N. enderleini*, and in the endophallus, with a well-developed radula in the former, and a less developed radula in the latter. Based on the cladistic analysis (Fig. 51), and also according to New (1980), *N. enderleini* differs from *N. chaetocephalum* in (a) a smaller size, (b) the basal forewing pigmentation being more pronounced, and (c) the basal pterostigmal crossveins unpigmented at the wing margin (Figs 31, 32). Since a considerable variation has been observed in the number of pterostigmal crossveins, there is a possibility that *N. enderleini* could be conspecific with *N. chaetocephalum*, but as the specimens studied by Enderlein (1900) seem to be lost (García Aldrete et al. 2020), their identity cannot be checked.

In the heterogeneous species group II, *N. paucivenosum* differs from the other species based on a relatively narrow forewing with only a few pterostigmal crossveins, and a more pronounced apical projection of the phallosome, as already indicated by New (1980). On the other hand, *N. mockfordi* and *N. valderramae* form a clade supported by three synapomorphies (Fig. 51). However, in neither of these cases, nor for the species of group I, the data support the splitting of *Neurostigma* into several genera.

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