

RESEARCH PAPER

The genus *Pteremis* (Diptera: Sphaeroceridae) in the West Palaearctic area, with description of four new species

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Abstract. The West Palaearctic species of the genus *Pteremis* Rondani, 1856 (Diptera: Sphaeroceridae) are revised, including the type species of the genus and its synonyms. A total of six species are recognized, four of them new – *Pteremis fenestralis* (Fallén, 1820) (type species, wing polymorphic), *P. apterina* sp. nov. (apterous, Portugal: Azores), *P. canaria* (Papp, 1977), *P. ferreus* sp. nov. (Spain: Canary Is.: El Hierro I.), *P. pulliceps* sp. nov. (Portugal: Madeira) and *P. tenebricus* sp. nov. (Spain, male only). In addition, *Paraspelobia vlasovi* (Duda, 1938) from Turkmenistan is re-examined and transferred to the genus *Pteremis* as *Pteremis vlasovi* (Duda, 1938), comb. nov., and the genus *Paraspelobia* Duda, 1938, syn. nov., is synonymized with *Pteremis*. All these species are described or redescribed in detail including illustrations of their male and female terminalia. Lectotypes of *Borborus nivalis* Haliday, 1833 and *Pteremis subapterus* Frey, 1947 (both being brachypterous forms of *P. fenestralis*) are designated. The genus *Pteremis* is newly taxonomically delimited, redefined and redescribed, with discussion of its relationships. A new key to West Palaearctic species of *Pteremis* is constructed and their relationships, biology and distribution are discussed.

Key words. Diptera, Sphaeroceridae, Limosininae, *Pteremis*, biology, distribution, key, new combination, new species, new synonym, relationships, taxonomy, Palaearctic Region

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Introduction

The genus *Pteremis* Rondani, 1856 is one of the few groups of the subfamily Limosininae (Sphaeroceridae) hitherto unrevised in the western part of the Palaearctic Region. Only two species have been recognized in this area, the widespread *Pteremis fenestralis* (Fallén, 1820) and *P. canaria* (Papp, 1977) only known from the Canary Islands (ROHÁČEK et al. 2001, MARSHALL et al. 2011). The taxonomic history of *Pteremis* is somewhat intricate. It was originally established by RONDANI (1856: 124) as a monotypic genus for a brachypterous species *Borborus nivalis* Haliday, 1833 (now a synonym of *P. fenestralis*). Eight years later, LIOY (1864) designated the macropterous *Copromyza fenestralis* Fallén, 1820 as type species of a new genus *Coprobria*. DUDA (1918: 28), not knowing of LIOY (1864), described *Stenhammaria* (as a monotypic subgenus of *Limosina* Macquart, 1835) to include the same type species and classified *B. nivalis* in a separate subgenus *Pteremis* of the genus *Limosina*. RICHARDS

(1930) synonymized both *Coprobria* and *Stenhammaria* with *Pteremis* (as a subgenus of *Leptocera* Olivier, 1813) but treated both brachypterous *Leptocera* (*Pteremis*) *nivalis* and macropterous *L. (P.) fenestralis* as separate species, see also RICHARDS (1951). However, DUDA (1938) had not accepted this synonymy and continued his (DUDA 1918) classification of both these forms in the subgenera *Stenhammaria* and *Pteremis*. COLLIN (1956: 178) was the first to recognize that *nivalis* is only a brachypterous form of *fenestralis* and suggested their synonymy but, for unknown reasons, treated them as species of the genus *Stenhammaria*. HACKMAN (1964) accepted this synonymy and added to it also *Pteremis subapterus* Frey, 1947 as another, strongly wing-reduced, form from Finland. Except for FREY (1947), who treated *Pteremis* as a genus when describing *P. subapterus*, all other authors classified it as a subgenus of *Leptocera*, including HACKMAN (1969) who, however, restricted the former giant genus *Leptocera* to



a group of only a few subgenera (roughly corresponding to the group ‘Hygrophilae’ of DUDA 1918, 1938). PAPP (1984) elevated *Pteremis* to genus although earlier (PAPP 1973a, 1977) he also described three new species (two from Mongolia, one from Canary Is.) in *Leptocera* (*Pteremis*). ROHÁČEK et al. (2001) catalogued the world fauna of *Pteremis*, comprising six species, four in the Palaearctic, and two in the Nearctic Region.

I began to revise West Palaearctic material of *Pteremis* 13 years ago due to a suspicion that there are more species mixed under the most widespread species, *P. fenestralis*. However, this task proved to be very complicated and time consuming not only because of intricate structures of the male external genitalia (gonostylus in particular) but mainly owing to difficulties with revision of old type material. The study of all preserved putative type specimens of *Copromyza fenestralis* Fallén resulted in the surprising finding that none of them belongs to *P. fenestralis* as interpreted since STENHAMMAR (1855) and DUDA (1918) but to 5 (or 6) other species of four different genera, see ROHÁČEK (2012a). Because designation of any of them as lectotype would destabilise generic classification and nomenclature of Limosiniinae, ROHÁČEK (2012a) asked the International Commission on Zoological Nomenclature to use its plenary power to set aside this series of syntypes and to designate as neotype a male newly collected in Sweden, so that the specific name *Pteremis fenestralis* is conserved in its current usage. This request was positively granted by Opinion 2341 (Case 3578) published by ICZN (2014). Because it was also necessary to verify the synonymy of *Borborus nivalis* with *P. fenestralis*, I have made several attempts to find syntypes of *B. nivalis*. COLLIN (1914), who was first to revise the collection of A. H. Haliday in Dublin, had not located any specimen of this species there and considered syntypes to be lost. However, during a thorough review of the Haliday collection (for its history see O’CONNOR & NASH 1982), one putative syntype of *B. nivalis* was found and I was able to examine it in 2022.

The discovery of the first fully apterous *Pteremis* species (herein described from the Azores) with (for the genus) unusual modifications of mid leg chaetotaxy and of female postabdomen led to a reassessment of the taxonomic limits of the genus, and, particularly, to a reconsideration of the generic classification of *Paraspelobia vlasovi* (Duda, 1938). Although ROHÁČEK (1983) revised this unusual subterranean species and recognized its close resemblance and affinity to *Pteremis*, he retained it in the monotypic genus *Paraspelobia* Duda, 1938 owing to several distinct dissimilarities, particularly in wing venation, mid leg chaetotaxy and modifications of the female postabdomen. Inasmuch as the above wingless *Pteremis* species from Azores proved to be in some features intermediate between typical *Pteremis* spp. and *Paraspelobia vlasovi* (see below) the concept and taxonomic limits of the genus *Pteremis* are here broadened to include both above mentioned enigmatic taxa. This action resulted in the necessity to synonymize *Paraspelobia* under *Pteremis* and to redescribe the more broadly defined genus *Pteremis*.

Material and methods

Material. The material listed in this paper is deposited in collections as follows:

CTB	Collection of Dr. Miguel Carles-Tolrà, Barcelona, Spain;
DEBU	University of Guelph Insect Collection, School of Environmental Sciences, University of Guelph, Guelph, Ontario, Canada;
DTP	Dalberto Teixeira Pombo Collection, University of Azores, Angra do Heroísmo, Terceira, Azores, Portugal;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
IZUI	Institut für Zoologie, Universität Innsbruck, Austria;
IZS	Institute of Zoology, Sofia, Bulgaria;
JRO	Collection of Jindřich Roháček, Opava, Czech Republic;
MBP	Collection of Miroslav Barták, Praha, Czech Republic;
MCNV	Museo Civico di Storia Naturale, Venezia, Italy;
MMBC	Moravian Museum, Brno, Czech Republic;
MZHF	Finnish Museum of Natural History, Helsinki, Finland;
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden;
NMID	National Museum of Ireland, Dublin, Ireland;
NMPC	National Museum of the Czech Republic, Praha, Czech Republic;
SMOC	Silesian Museum, Opava, Czech Republic;
ULCI	Universidad de La Laguna, Departamento de Zoología, La Laguna, Tenerife, Canary Is., Spain;
ZISP	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia;
ZMHB	Museum für Naturkunde, Berlin, Germany;
ZMUC	Zoology Section of the Natural History Museum of Denmark, København, Denmark.

Methods. Specimens were examined, drawn and measured using two types of binocular stereoscopic microscopes (Reichert, Leica Sterozoom S9i). Detailed examinations were performed with a compound microscope (Jenaval). Abdomens of a number of specimens were detached and boiled in 10% solution of KOH in water for several minutes. KOH was neutralized in 10% solution of acetic acid and abdomen washed in water and transferred to glycerine. Terminalia were dissected and studied in a drop of glycerine under a binocular microscope. After examination all parts of the abdomen were transferred to glycerine in a coalesced plastic tube or microvial and pinned below the respective specimen.

Drawing techniques and photography. Genital structures were drawn by means of Abbe’s drawing apparatus on a compound microscope at a higher magnification (130–350×). For more detail see ROHÁČEK (2006). Living *Pteremis* specimens were photographed in special boxes by means of a digital camera Canon EOS 60D with a macro lens (Canon MP-E 65 mm 1–5×) and ring macro flash (Canon MR-14EX). Dry-mounted adult specimens or their parts were photographed by means of a digital camera Canon EOS 5D Mark III with a Nikon CFI Plan 4×/0.10NA 30 mm WD objective and/or with a Nikon CFI Plan 10×/0.25NA 10.5mm WD objective attached to Canon EF 70–200mm f/4L USM zoom lens. The specimen photographed by means of the latter equipment was repositioned upwards between each exposure using a Cognisys StackShot Macro Rail and the final photograph was compiled from about 40 layers using Helicon Focus Pro 7.0.2. The final images were edited in Adobe Photoshop CS6. Wings were photographed on a compound microscope Olympus BX51 with an attached digital camera (Canon EOS 1200D).

Measurements. Six main characteristics of the new species were measured: body length (measured from anterior margin of head to end of cercus, thus excluding the antenna), index $t_2 : mt_2$ (= ratio of length of mid tibia : length of mid basitarsus), wing length (from wing base to wing tip), wing width (maximum width), *C-index* ($Cs_2 : Cs_3$) (= ratio of length of 2nd costal sector : length of 3rd costal sector) and index $r-m \setminus dm-cu : dm-cu$ (= ratio of length of section between *rm* and *dm-cu* on discal cell : length of *dm-cu*). If available, a total of 10 males and 10 females (3 smallest, 4 medium, 3 largest examined specimens of each sex) of each species were measured; in species with fewer specimens available, all were measured.

Presentation of faunistic data. Label data of primary-type specimens are presented strictly verbatim including information on colour of all associated labels. Data from other material examined are standardized and presented in full. Phenological and other biological information obtained from the material examined and literature are given in the Biology paragraph; data on occurrence are summarized in the Distribution paragraph.

Morphological terminology follows that used for Sphaeroceridae by ROHÁČEK (1998) in the Manual of Palaearctic Diptera and, most recently, in ROHÁČEK (2016) including terms of the male hypopygium. The ‘hinge’ hypothesis of the origin of the eremoneuran hypopygium, re-discovered and documented by ZATWARNICKI (1996), has been accepted and, therefore, the following synonymous terms of the male genitalia (emanating from other hypotheses) need to be listed (terms used first): aedeagus (= phallus), ejacapodeme (= ejaculatory apodeme), epandrium (= perianthrium), gonostylus (= surstylus, telomere), medandrium (= bacilliform sclerite, intraepandrial or intraperianthrial sclerite), phallapodeme (= aedeagal apodeme), phallophore (= basiphallus), postgonite (= gonite, paramere). Morphological terms of the male postabdomen and genitalia are depicted in Figs 25–32, those of the female postabdomen in Figs 34–36.

Abbreviations of morphological terms used in text and illustrations are listed below:

*A*₁ – anal vein
ac – acrostichal (seta)
ads – additional (setulae) on frons
av – anteroventral (seta)
C – costa
ce – cercus
*Cs*₁, *Cs*₂, *Cs*₃ – 1st, 2nd, 3rd costal sector
*CuA*₁ – cubitus
dc – dorsocentral (seta)
dm – discal medial cell
dm-cu – discal medial-cubital (= posterior, tp) cross-vein
dp – distiphallus
ea – ejacapodeme
ep – epandrium
*f*₁, *f*₂, *f*₃ – fore, mid, hind femur
g – genal (seta)
gs – gonostylus
hap – hypandrial apodeme
hu – humeral (= postpronotal) (seta)
hy – hypandrium
ifr – interfrontal (seta)
M – media
*mt*₂ – mid basitarsus

npl – notopleural (seta)
oc – ocellar (seta)
occe – outer occipital (seta)
occi – inner occipital (seta)
ors – fronto-orbital (seta)
pa – postalar (seta)
pg – postgonite
pha – phallapodeme
pp – phallophore
prs – presutural (= posthumeral) (seta)
pvt – postvertical (seta)
*R*₁ – 1st branch of radius
*R*₂₊₃ – 2nd branch of radius
*R*₄₊₅ – 3rd branch of radius
r-m – radial-medial (= anterior, ta) cross-vein
rs – 6th right spiracle
S1–S10 – abdominal sterna
sa – supra-alar (seta)
sc – scutellar (seta)
stpl – sternopleural (= katepisternal) (seta)
T1–T10 – abdominal terga
*t*₁, *t*₂, *t*₃ – fore, mid, hind tibia
va – ventroapical seta on *t*₂
vi – vibrissa
vpa – ventropreapical (seta)
vte – outer vertical (seta)
vti – inner vertical (seta)

Results

Genus *Pteremis* Rondani, 1856

Pteremis Rondani, 1856: 124 (gender: masculine). Type species: *Borborus nivalis* Haliday, 1833 [= *Pteremis fenestralis* (Fallén, 1820)], original designation.

Pteremis: DUDA (1918): 28 (as subgenus of *Limosina* Macquart, 1835; diagnosis in key); SPULER (1924): 375 (as subgenus of *Leptocera* Olivier, 1813); RICHARDS (1930): 288 (as subgenus of *Leptocera*; diagnosis); HACKMAN (1969): 204, 208 (as subgenus of *Leptocera*; phylogenetic notes, biogeography); PAPP (1984): 87 (as genus; Palaearctic catalog); MARSHALL & RICHARDS (1987): 999 (as subgenus of *Leptocera*; diagnosis in key, illustr.); ROHÁČEK (1998): 479 (diagnosis in key, illustr.); ROHÁČEK et al. (2001): 210 (as genus, world catalog).

Pteremis (incorrect subsequent spelling): SCHINER (1864a): 334 (misspelling).

Pterennis (incorrect subsequent spelling): SCHINER (1864b): 49 (catalog, misspelling); SCHINER (1868): 228 (list of genera), see also O'HARA et al. (2011): 154.

Coprobria Lioy, 1864: 1116 (gender: feminine). Type species: *Copromyza fenestralis* Fallén, 1820, monotypy.

Coprobria: RICHARDS (1930): 265 (synonymy).

Stenhammaria Duda, 1918: 28 (gender: feminine) (as subgenus of *Limosina* Macquart, 1835). Type species: *Copromyza fenestralis* Fallén, 1820, monotypy.

Stenhammaria: RICHARDS (1930): 266 (synonymy).

Paraspelobia Duda, 1938: 96 (gender: feminine) (as subgenus of *Limosina* Macquart, 1835). Type species: *Limosina (Paraspelobia) Vlasovi* Duda, 1938, original designation. **New junior subjective synonym.**

Paraspelobia: HACKMAN (1969): 208 (as genus; list, biogeography); ROHÁČEK (1983): 227–232 (as genus, redescription, phylogenetic notes, illustr.); PAPP (1984): 87 (Palaearctic catalog); ROHÁČEK (1998): 485 (as genus; diagnosis in key, illustr.); ROHÁČEK et al. (2001): 189 (as genus, World catalog).

Note on gender. Because the gender of the name *Pteremis* was not given in the original description (RONDANI 1856: 124) the Art. 30.2.4. of the Code is to be applied saying: ‘If no gender was specified or indicated, the name is to be treated as masculine, except that, if the name ends in -a the gender is feminine, and if it ends in -um, -on, or -u the

gender is neuter.' Formerly, judging on ends of names of species listed in *Pteremis* by PAPP (1984: 87), this generic name was incorrectly treated as feminine, which was followed also in the World Catalog of Sphaeroceridae (ROHÁČEK et al. 2001). However, based on the above statement of the Code the gender of *Pteremis* is masculine as already recognized by FREY (1947) when describing *Pteremis subapterus* Frey, 1947 (a synonym of *P. fenestralis*) from Finland.

Redescription. (1) *pvt* present but small to hair-like and convergent to crossed, rarely absent;

(2) *occe* and *occi* of medium length; *vte*, *vti* (usually longest cephalic seta), *oc*, posterior *ors* and *vi* long and robust;

(3) 4, rarely 3 or 5 *ifr*, middle pair(s) longer and robust, often cruciate;

(4) 2–9 minute (posterior 2 often longer) *ads* inside and below *ors*;

(5) *g* short, as long as or slightly longer than anterior peristomal setula;

(6) frons with dark stripes between orbits, interfrontalia and frontal triangle almost forming M-shaped mark (Fig. 101);

(7) medial carina slightly developed;

(8) 2 *hu*, but the internal reduced to microseta;

(9) 1 long *dc* in prescutellar position but *dc* microsetae in front of it more or less enlarged;

(10) *ac* microsetae in 6–8 rows on suture, the medial prescutellar *ac* not or very slightly enlarged;

(11) 2 *sc*, also laterobasal *sc* long and robust, sometimes longer than apical *sc*;

(12) 2 or only 1 *stpl* but only the posterior strong, the anterior reduced, hair-like or absent;

(13) scutellum relatively large, rounded subtriangular to subcircular, flat to slightly convex;

(14) mid trochanter with only short setae

(15) t_2 chaetotaxy (Figs 55–57) dorsally with proximal and distal pair of strong setae and several short setulae;

(16) t_2 chaetotaxy ventrally variable, always with 1 short *av* seta below middle (Figs 23, 57, 140, 153) but distally with both *va* and *vpa* strong (Figs 23, 57), or *va* reduced and *vpa* strong (Figs 97, 116) or with only 1 long subterminal seta looking like *va* (Figs 140, 153) but probably homologous with *vpa* shifted more distally;

(17) mt_2 ventrally sometimes with 1 enlarged ventral setula (Figs 57, 97, 154);

Wing (if present) with

(18) Cs_1 with distinctly (Fig. 78) to slightly (Fig. 156) longer setulae than on rest of *C* but never as strong as those in *Leptocera* or *Rachispoda* Liroy, 1864 species;

(19) *C* distinctly (Fig. 16) to hardly (Fig. 156) extended beyond apex of R_{4+5} ;

(20) C-index slightly less to more than 1.0;

(21) R_{4+5} slightly sinuate, with apex more (Figs 16, 102) or less (Fig. 156) upcurved, in brachypterous forms slightly curved (Figs 17–21);

(22) *dm* cell of medium length, with distinct but short processes of *M* and CuA_1 beyond *dm-cu* (Figs 16, 156), in brachypterous forms short, with *dm-cu* often absent (Figs 17–21);

(23) A_1 sinuate, only basal part well developed, distally formed by venal fold (Fig. 53);

(24) alula relatively small and narrow, with tapered to acute apex;

(25) abdomen with preabdomen relatively broad, with wide terga; female postabdomen relatively narrow (Figs 34–36) to very narrow (Figs 132, 135–136, 162, 163) and telescopically retractile into preabdomen;

(26) male *S5* broad and relatively large, always with posteromedial comb of spines (Figs 26, 131, 157) and usually also with a pale-pigmented micropubescent area in front of it (Figs 26, 74, 108);

(27) male postabdomen relatively small (compared to preabdomen), with *S6*, *S7* and *S8* fused and forming strongly asymmetrical synsclerite (Figs 25, 27); near right end of *S6*, there is an enlarged annular sclerite (= modified 6th right spiracle, Fig. 27, *rs*);

(28) *S6+7* with transverse dark-pigmented ledge and 1+1 to 2+3 setae; *S7* with irregular posteroventral projection bent inside postabdomen (Fig. 27);

(29) male *S8* saddle-shaped and almost bare, at most with a pair of small setulae (Fig. 25);

(30) epandrium small, uniformly setose, without markedly enlarged setae (Figs 29, 126, 158);

(31) male cerci large, far produced ventrally, with variously modified (usually flattened) apex; and ventromedially separated by narrow incision (Figs 28, 104, 125, 159), each with 1 long seta and a few shorter setae;

(32) medandrium low (short) and broad, with long lateral arms, each connected with posterior part of gonostylus and posteromedially with narrow, dark-pigmented and ventrally usually split keel (Figs 28, 125);

(33) hypandrium genus-specific, short, with very short and strongly asymmetrical (right directed) anteromedial apodeme (Figs 29, 31, *hap*);

(34) gonostylus (Figs 28–30) of complex bilobed structure, composed of larger anterior (more lateral) lobe and of smaller (shorter and more medial) posterior lobe;

(35) anterior lobe of gonostylus characterized by 3 or 4 strong curved ventral setae, a distinct ventral (posteriorly or posteromedially directed and variously modified) projection and an oblique spinulose posterolateral ledge (Figs 30, 85, 127, 160);

(36) posterior lobe of gonostylus with robust terminal spine and posteriorly with subconical process armed by a robust seta on apex (Figs 30, 86, 128, 160);

(37) aedeagal complex with phallophore, distiphallus and postgonite subequal in length (Figs 32, 87, 130, 161);

(38) phallophore short (Figs 107, 130, 161) to very short (Fig. 50), laterally somewhat flattened, ventrally more or less pointed, epiphallus never developed;

(39) distiphallus of simple and relatively uniform construction: weakly sclerotized mainly proximoventrally and dorsally, always with a pair of band-like and pale lateral sclerites and dorsal sclerite subapically forked and bent laterally; middle part of dorsal side of distiphallus finely haired (Figs 32, 107, 161);

(40) postgonite relatively large, more or less sinuate in lateral view, with tapered distal third to half but with apex always dilated and usually rounded (Figs 32, 87, 107, 161), almost bare;

(41) ejacapodeme present but small to very small (Figs 32, 130, 161);

(42) female postabdomen narrow to very narrow, gradually tapered (Figs 34–36) or suddenly narrowed and subparallel (Figs 135–137) from preabdomen, always telescopically retractile;

(43) female *T7* usually simple (Fig. 35), rarely modified (Fig. 165);

(44) female *T8* with tripartite pigmentation composed of a pale tongue-shaped medial part and larger darker lateral parts (Fig. 35, 135, 165), with a few setae only laterally (Figs 34, 35, 135, 136);

(45) female *T10* simply plate-shaped (Fig. 35) to somewhat elongate (Fig. 135), with 1 pair, rarely 2 pairs (Fig. 165) of short medial setae;

(46) female *S7* normally simple (Fig. 36), rarely posteromedially emarginate (Fig. 167);

(47) female *S8* smaller than *S7*, more or less modified, posteromedially always with a group of setae (all short or 2 long) on elevated sockets (Figs 38, 59, 91, 112, 142, 167);

(48) female *S10* relatively large (about as *S8*), with anterolateral corners more or less projecting (thus anteromedially emarginate, Figs 39, 60, 141, 167), rarely also with elongate medial structure (Fig. 167);

(49) female genital chamber largely membranous, with spectacles-shaped sclerite (Fig. 27) represented only by pale-pigmented submembranous rings (Figs 58, 113, 143);

(50) spermathecae (2+1) subovoid to pyriform, with some surface sculptures (tubercles, spines, rings); terminal parts of ducts long, strongly sclerotized (Figs 37, 61, 115, 134) and sometimes curved (Fig. 164) and those of paired spermathecae connected far from their bodies;

(51) female cerci free, relatively robust, subconical (Fig. 89) or dorsoventrally flattened (Fig. 35), rarely shortened (Fig. 165), each usually with 2 long (apical and dorsopreapical) sinuate setae and a few shorter setae.

Discussion. Because the morphology (particularly of the male and female terminalia) of *Pteremis* has hitherto not been studied in a sufficient detail its relationships to other genera of Limosiniinae remains poorly understood. DUDA (1918) classified this group (as subgenera *Pteremis* and *Stenhammaria*) within his informal group ‘Hygrophilae’ comprising otherwise the subgenera *Collinella* Duda, 1918 (= now genus *Rachispoda* Lioy, 1864 + genus *Leptocera* Olivier, 1813) and *Opacifrons* Duda, 1918 (comprising also species now in *Pseudocollinella* Duda, 1924). DUDA (1925, 1938, as tribe Hygrophilae) also maintained this grouping of subgenera and characterized this assemblage by a strong *vpa* on *t*₂ and a distinct (reduced only in *Pteremis*) ventral seta on mid basitarsus (called by him ‘Metatarsalborste’). Interestingly, HACKMAN (1969: 204) also considered these subgenera (although also erroneously including *Archicollinella* Duda, 1925) to form a natural group and classified them as subgenera of the restricted genus *Leptocera*. Subsequently, only ROHÁČEK (1991), when discussing relationships of *Leptocera* (including *Rachispoda* as a subgenus), listed *Pteremis* together with *Paraspelobia*, *Opacifrons*, *Pseudocollinella* and also *Phthitia* Enderlein, 1938 as groups with more or less distinct affinities

to *Leptocera*. On the other hand, revisionary studies on *Leptocera* relatives, viz., *Phthitia* (see MARSHALL & SMITH 1992), *Pseudocollinella* (by MARSHALL & SMITH 1993) and *Opacifrons* (see MARSHALL & LANGSTAFF 1998) have not indicated *Pteremis* as a probable close relative of these genera. OKELY (1974: 49) described and illustrated the puparium of *Pteremis fenestralis* – not surprisingly it closely resembles those of the two *Leptocera* species she also studied (OKELY 1974: 45) including small, shortly palmate anterior spiracles. Moreover, very similarly formed anterior spiracles are also known in the puparium of *Rachispoda* species (ROHÁČEK 1991: Fig. 18).

The genus *Pteremis* (in the extended concept as delimited above) seems to be a monophyletic group supported by the following characters (those considered autapomorphic are marked AA, others also apomorphic A), numbered as above: (16) mid tibia with both *vpa* and *va* setae (the latter sometimes secondarily reduced or absent) (AA); (26) male *S5* with posteromedial comb of spines and with a pale-pigmented micropubescent area in front of it (A); (31) male cerci large, far produced ventrally, and ventromedially separated by narrow incision (A); (33) hypandrium short, with very short asymmetrical (right directed) anteromedial apodeme (AA); (34) gonostylus of bilobed structure, composed of larger complex anterior lobe and of smaller, simpler, posterior lobe (A); (35) anterior lobe of gonostylus characterized by 3 or 4 strong curved ventral setae, a distinct ventral (posteriorly, posteromedially or posteroventrally directed and variously modified) projection and an oblique spinulose posterolateral ledge (AA); (36) posterior lobe of gonostylus with robust terminal spine and posteriorly with subconical process armed by a robust seta on apex (A); (39) distiphallus of simple and relatively uniform construction but always with a pair of band-like lateral sclerites and dorsal sclerite subapically forked and bent laterally (AA); (40) postgonite sinuate in lateral view, tapered distally but with apex always dilated (A); (47) female *S8* more or less modified, posteromedially with a group of setae on elevated sockets (A); (50) spermathecae (2+1) subovoid to pyriform, with terminal parts of ducts long, strongly sclerotized, in paired spermathecae connected far from their bodies (AA).

The presence of both *va* (directed with axis of tibia) and *vpa* setae on mid tibia in *Pteremis* is unique within the Limosiniinae (see below) irrespective of the fact that *va* can be reduced and/or *vpa* shifted distally in aberrant species. The form and structure of hypandrium (33) and the anterior lobe of gonostylus (35), the lateral band-like sclerites of distiphallus (39) and long sclerotized distal parts of spermathecal ducts (50) are also important apomorphies of the genus that separate it clearly from related genera. The armature of male *S5*, with a posteromedial comb of spines (26) also distinguishes *Pteremis* from allied genera although a similar comb of spines occurs as homoplasy in several unrelated genera of Limosiniinae (e.g. *Spelobia* Spuler, 1924, *Minilimosina* Roháček, 1983).

The dorsal mid tibial chaetotaxy, general construction of the bilobed gonostylus (34) and shape and armature of its posterior lobe (36), enlarged male cercus and weakly

sclerotized distiphallus suggest that *Pteremis* is related to the genera *Phthitia*, *Pseudocollinella*, *Rachispoda* and *Leptocera*, as in the original 'Hygrophilae' of DUDA (1918). This could also be true for the sinuate postgonite, although its dilated to clubbed apex only occurs in some *Pseudocollinella* species (MARSHALL & SMITH 1993). However, the sister-group of *Pteremis* remains in question. Because in *Pteremis* a number of distinctly plesiomorphic features is retained (e.g. only single postsutural *dc* seta, setulae on *Cs*₁ slightly enlarged; the elongate telescopic female postabdomen with a little reduced and/or modified sterna and terga; unmodified female cerci) it perhaps represents a sister-group to a clade including *Leptocera*, *Rachispoda*, *Pseudocollinella*, *Opacifrons* and *Phthitia* although the position of *Opacifrons* as a member of this group is only likely if its gonostylus is secondarily simplified (simply bilobed only in *O. maculifrons* group, otherwise unilobate, see MARSHALL & LANGSTAFF 1998).

Distribution. The genus is only known from the Holarctic Region.

Species included. *Pteremis fenestralis* (Fallén, 1820) (type species), *P. apterina* sp. nov., *P. canaria* (Papp, 1977), *P. ferreus* sp. nov., *P. kaszabi* (Papp, 1973), *P. mongolicus* (Papp, 1973), *P. pulliceps* sp. nov., *P. tenebricus* sp. nov., *P. vlasovi* (Duda, 1938) comb. nov. (all Palaearctic), *P. unicus* (Spuler, 1924), *P. wirthi* (Marshall, 1984) (both Nearctic).

Pteremis fenestralis (Fallén, 1820)

(Figs 1–4, 7–39)

Copromyza fenestralis Fallén, 1820: 8 (both sexes). Type locality (by neotype designation): Sweden, Huddinge, Gömmaren lake res. Neotype (designated by ICZN 2014: Opinion 2341, see also ROHÁČEK 2012a: 102): ♂ (NHRS).

Limosina fenestralis: ZETTERSTEDT (1847): 2504 (generic combination).

Limosina (Stenhammaria) fenestralis: DUDA (1918): 88–90 (subgeneric combination, redescription, illustr.); DUDA (1938): 90–91 (redescription, illustr.).

Leptocera (Stenhammaria) fenestralis: DUDA (1925): 73 (generic combination).

Leptocera (Pteremis) fenestralis: RICHARDS (1930): 845 (subgeneric combination); PAPP (1973b): 66 (key, illustr.); OKELY (1974): 49 (puparium, illustr.).

Pteremis fenestralis: HACKMAN (1963): 59 (generic combination); PAPP (1984): 87 (Palaearctic catalog); PITKIN (1988): 39, 103, 111, 123, 135, 149, 167 (key, genitalia, illustr.); ROHÁČEK et al. (2001): 211 (world catalog); MARSHALL et al. (2011): 265 (world catalog update); ROHÁČEK (2012b): 540 (wing polymorphism).

Borborus nivalis Haliday, 1833: 178 (both sexes?). Type locality: Ireland, Downshire, Hollywood. Lectotype (designated here): ♀ (NMID).

Borborus nivalis: COLLIN (1956): 178 (synonymy).

Limosina nivalis: HALIDAY (1836): 330 (generic combination).

Pteremis nivalis: RONDANI (1856): 124 (generic combination).

Limosina (Pteremis) nivalis: DUDA (1918): 90–92 (subgeneric combination, redescription); DUDA (1938): 89–90 (redescription, illustr.).

Leptocera (Pteremis) nivalis: DUDA (1925): 73 (generic combination).

Stenhammaria nivalis: COLLIN (1956): 178 (generic combination).

Limosina erratica Haliday, 1836: 330 (both sexes?). Type locality: not given. Syntypes (not found in NMID, cf. COLLIN 1914: 244, probably lost).

Limosina erratica: COLLIN (1914): 244 (synonymy).

Limosina paradoxa Stenhammar, 1855: 399 (female). Type locality: Sweden, 'Ostrogothia parocia Wärna'. Holotype: ♀ (not located in UZIU, cf. KIM 1972: 205–207, probably lost).

Limosina paradoxa: DUDA (1918): 90 (synonymy).

Pteremis subapterus: FREY (1941): 26 (nomen nudum).

Pteremis subapterus Frey, 1947: 68 (both sexes, illustr.). Type locality (by lectotype designation): Finland, Suomussalmi. Lectotype (designated here): ♂ (MZHF)

Pteremis subapterus: HACKMAN (1964): 75, 84 (synonymy).

Type material examined. *Copromyza fenestralis* Fallén: NEOTYPE (designated by ICZN 2014: Opinion 2341, see also ROHÁČEK 2012a: 102): ♂ (NHRS), labelled: 'SWEDEN: Huddinge, Gömmaren lake res., 59°15'15"N, 17°55'40"E, 58 m, J. Roháček leg.', '7.7.2011, peat-bog, sifting *Sphagnum*, moss and grass', 'NEOTYPUS ♂, *Copromyza fenestralis* Fallén, 1820, J. Roháček des. 2011' (red label) and '*Pteremis fenestralis* (Fallén) ♂, J. Roháček det. 2011' (see Figs 8, 9). The specimen is intact, glued onto pinned triangular card (Fig. 7).

Borborus nivalis Haliday: LECTOTYPE (designated here): ♀ (NMID), labelled: 'Hollywood' (green label), 'Haliday 20. 2. '82' (registration number of museum), 'Named by J. E. Collin, *Limosina nivalis*' (pencil handwritten), 'LECTOTYPUS ♀ *Borborus nivalis* Haliday, 1833, J. Roháček des. 2022' (red label), '*Pteremis fenestralis* (Fallén, 1920) ♀, J. Roháček det. 2022' (Fig. 12). The specimen is intact (Fig. 10), mounted in Haliday's style, glued on pinned quadrangular card (Fig. 12).

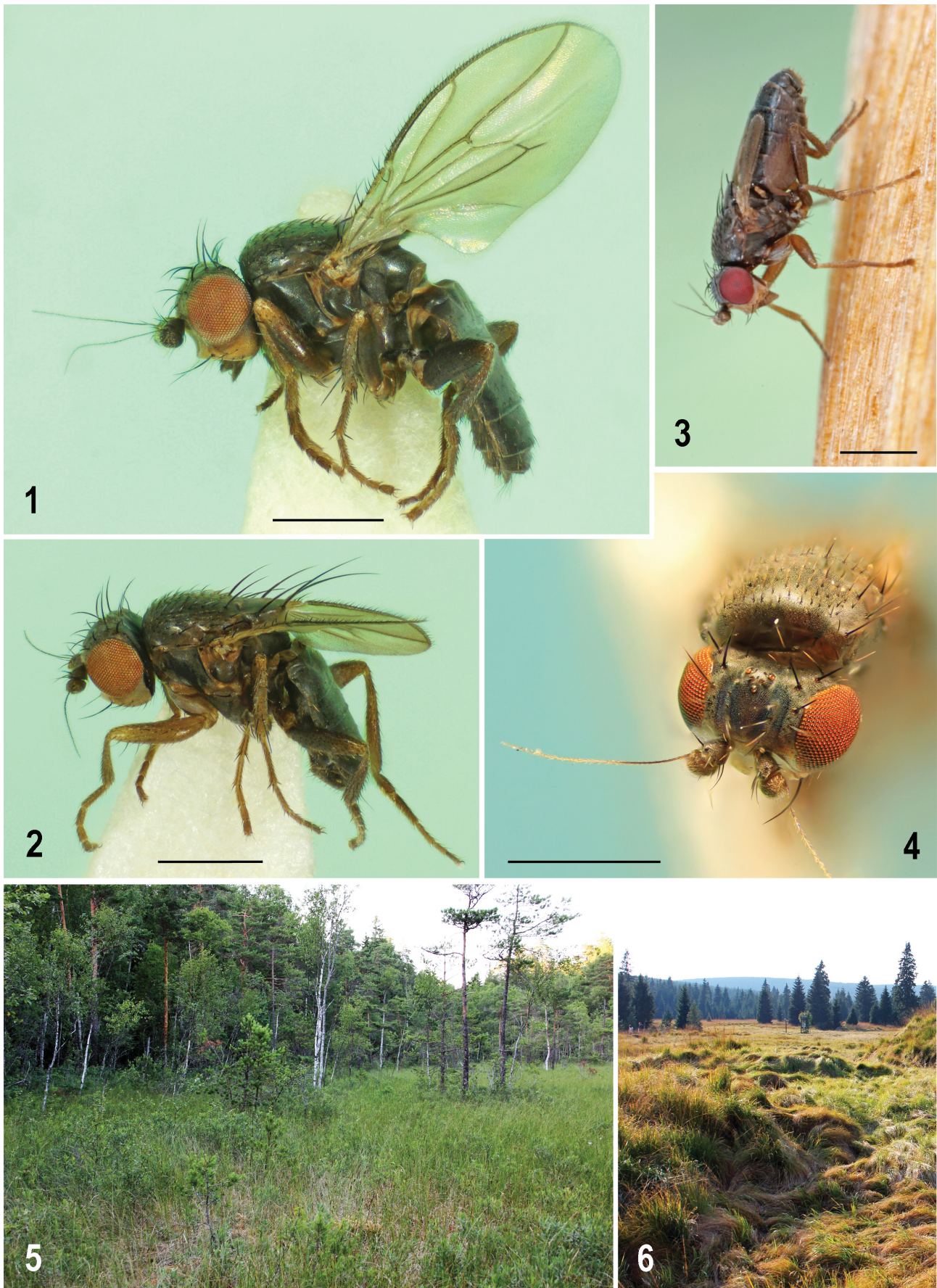
Pteremis subapterus Frey: LECTOTYPE (designated here): ♂ (MZHF), labelled: 'Suomussalmi', 'Hellén', '553', 'Mus. Zool. H:fors, Spec. typ No. 8182, *Pteremis subapterus* Frey' (faded green label, partly handwritten), '*Pteremis* ♂ *fenestralis* (Fall.) f. *subapterus*', 'J. ROHÁČEK det. 1985' (partly handwritten), 'Mus. Zool. Helsinki, Loan No. DIP 2010–17' (yellow label) and 'LECTOTYPUS ♂ *Pteremis subapterus* Frey, 1947, J. Roháček des. 2023' (red label) (see Fig. 15). The specimen is intact (Figs 13, 14), minutia pinned and mounted on pinned polyporus bricket. PARALECTOTYPE: ♀, labelled as lectotype, except for sex symbols and '516', 'Spec. typ No. 8182' and 'PARALECTOTYPUS ♀' (MZHF). **Note.** These two specimens are listed as 'Typen Nr. 8181–8182' in FREY (1947: 68). However, FREY (1947) listed a total of 1 ♂ 4 ♀♀, i.e. also 3 additional females from localities N. Finland: Om. Brahestad (G. Wuorentaus leg.), Ok. Kajana, 29.v.1917 (W. Hellén leg.) and Ok. Suomussalmi, 26.vi.1917, gesiebt (W. Hellén leg.). All these specimens are preserved in MZHF (J. Kahanpaa, pers. communication, 2023) but only the last one has been examined. According to article 72.4.6 of the Code (ICZN 1999) these three females do not belong to the type series and, consequently, cannot be designated as paralectotypes.

Additional material examined. **AUSTRIA:** Ebensee (am Traunsee), ~50 km E Salzburg, grass roots nr. River, 26.viii.1986, 2 ♂♂ 1 ♀ f. brach., S. A Marshall leg. (DEBU, 1 ♀ genit. prep.); Tirol: Igls, 900 m, 12.vii.1953, 1 ♂, J. R. Vockeroth leg. (HNHM); Obergurgl Mt., 1950 m, 4.vii.1975, 1 ♂, 2.x.1975, 1 ♂, H. Troger leg.; Badgastein, 16.vi.1977, 2 ♂♂ (f. brach.), H. Stockner leg. (IZIU). **BULGARIA:** Geleznitza nr. Sofia, 13.vii.1974, 1 ♂, 24.vii.1977, 1 ♂, P. Snejanka leg.; Zlatni piaszti, 23.viii.1974, 1 ♂; Drangovo-Petrtsch, 12.iv.1973, 1 ♂ 1 ♀; Papaz Tchair, 16.vi.1975, 1 ♀; Pirdop, 12.v.1973, 1 ♀, 1.vi.1977, 1 ♀; Rila-hut Musala, 2200 m, 2.x.1973, 1 ♀; Sandanski, 11.iv.1973, 1 ♀; Bistritza, vodopada, 24.ix.1972, 1 ♀, all V. Beschovski leg. (ZS). **CZECH REPUBLIC** (more than 1000 specimens, deposited in JRO, MBP, MMBC, NMPC, SMOC, many genit. prep.), examples of localities: **BOHEMIA:** W Bohemia: Doupovské hory Mts-Lochotín, Jelení nr. Karlovy Vary (Škaloudová leg.), Čistá nr. Sokolov (Dlabola leg.), Bílina-Chloumek, Bílina Štěpánov, Duchcov env. (M. Barták leg.); S Bohemia: Lipno nad Vltavou, Šumava Mts-Zhůřské slatě, Šumava Mts-Horská Kvilda, Šumava Mts-Pěkná (J. Roháček leg.), Šumava Mts-Rakouská louka, Šumava-Horská Kvilda, Vlkov nad Lužnicí (M. Barták leg.), České Budějovice-Švábův Hrádek (J. Olejníček leg.), Hluboká (I. Kovář leg.), Filipov, Žišov-Doubí (J. Máca leg.), Palupín nr. Strmilov, Dačice-Malý Pěčín (J. Roháček leg.); C Bohemia: Srbsko (J. Zuska leg.), Břežany, Lešany nr. Benešov (I. Kovář leg.), Ondřejov (M. Chvála leg.), Praha-Holešovice, Praha-Bohnice, Praha-Trója, Praha-Šárka, Třebotov, Úvaly nr. Praha, Srbsko-Koda, Jiloviště, Kunice, Kunice-Hůra, Velké Popovice, Struhařov, Sokoleč, Veltrusy-deer park (M. Barták leg.); N Bohemia: Holany 2.1 km NW-Dolské údolí valley, Hradčany 1.5–2 km W-Ploučnice valley, Mimoň 6 km E-Novodvorský rybník 5, Staré Splavy 1.2 km NE nr. Máchovo jezero, Doksy 4.3 km NE-Břežňanský rybník res., Obora nr. Doksy 0.6 km SE-Poselský pond, Jestřebí 1.7 km SE-Jestřebské slatiny

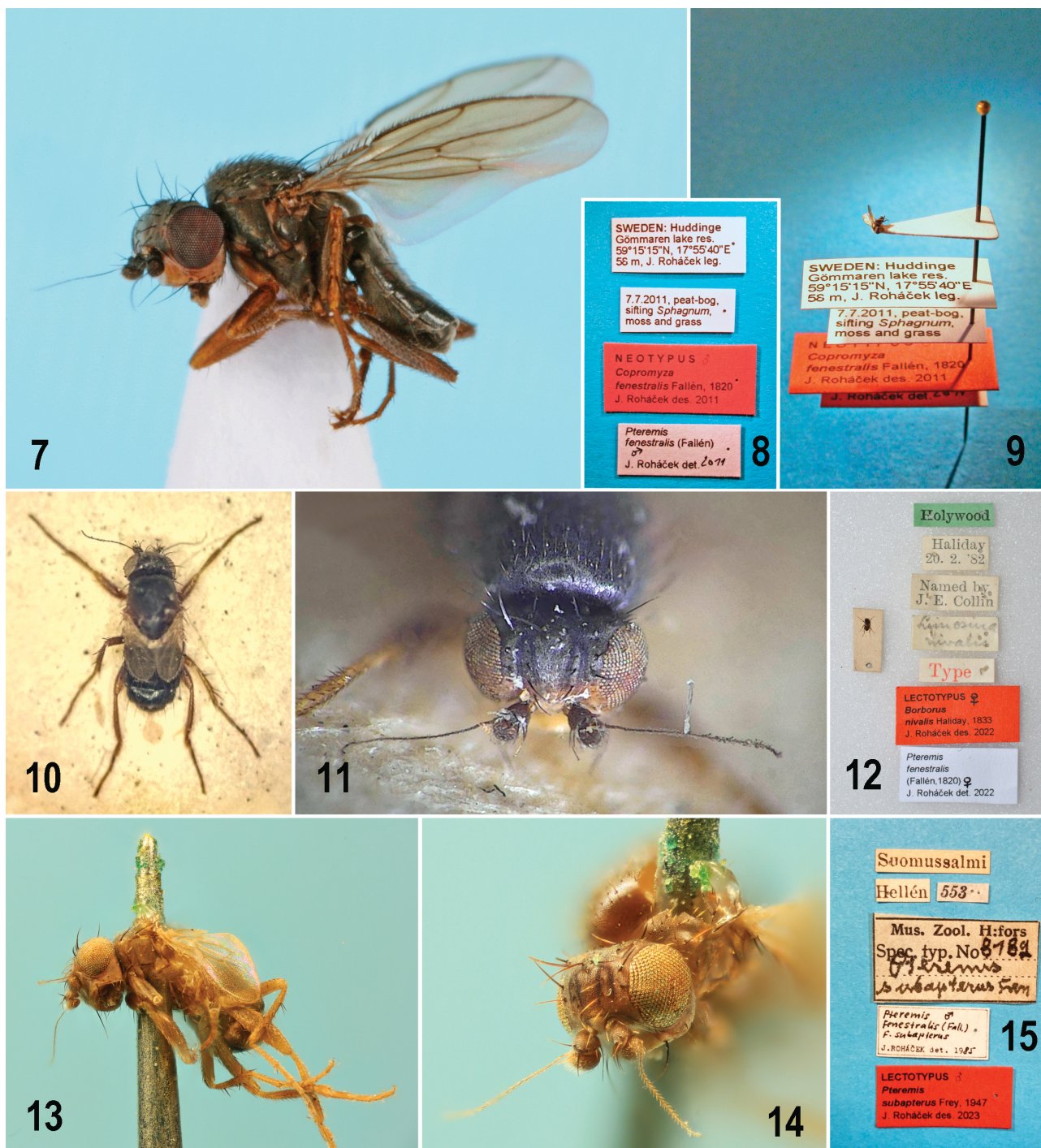
res., Jizerské hory Mts.-Jizerka (all J. Roháček leg.), Krkonoše Mts-Vitkovice (Zuska leg.); E Bohemia: Jilemnice (Dlabola leg.), Bohdaneč, Černá u Bohdanče (B. Mocek leg.). **MORAVIA:** W Moravia: Třešť-Kaz, Třešť-Jelenice, Třešť-Zákotský rybník (pond), Třešť-Otov, Třešť-Loučky, Řásná nr. Telč-Pařezitý rybník (pond) (J. Roháček leg.); S Moravia: Havraníky-Havranické vřesoviště, Lednice, Pouzdřany-Kolby (B. Mocek leg.), Lednice-park, Pálava Mts, Nejdek nr. Lednice, Sedlec u Míkulova-Skalky, Sedlec-Slanisko nr. Nesyt pond, Vranovská přehrada-Cornštejn, Bílé Karpaty-Radějov (J. Roháček leg.), Moravský Krumlov (M. Barták leg.), Havraníky, Hnanice, Horní Břečkov, Čížovský rybník (pond), Liščí skála nr. Podmolí, Zadní Hamry, Braitava, Široká pole, Hardegg vyhlídka, Fládnická chata (M. Barták et al. leg.); C Moravia: Nedvědice-Chlébské, Moravský kras-Líšeň, Moravský kras-Mariánské údolí, Brno-Lesná, Brno-Obřany, Dolní Loučky nr. Tišnov (B. Mocek leg.), Ohrozim (M. Vála leg.), Moravičany nr. Mohelnice, Hostýnské vrchy Mts-Rajnochovice (J. Roháček leg.); N Moravia: Rychlebské hory Mts-Nýznerov, Vidnavské louky res. nr. Vidnava, Supkovice 1.1 km NE-sand-pit, Kolnovice 1 km SW-sand-pit, Bohušov nr. Osoblaha 0.7 km S-sand-pit, Hrubý Jeseník Mts-Kouty n. Desnou, Hrubý Jeseník Mts-Skrátek peat-bog, Hrubý Jeseník Mts-Keprník-Vozka peat-bog, Hrubý Jeseník Mts-Rejvíz peat-bog, Bělá pod Pradědem, Hrubý Jeseník Mts-Vleká kotlina, Nízký Jeseník Mts-Slunečná Mt., Spálené-Sokolí důl, Horní Benešov, Hanušovická vrchovina-Jeřáb Mt., Karlova Pláň-Volárenský potok, Karlova Pláň-Karlovec, Klokočov nr. Vítkov, Úvalenské louky res. nr. Krmov, Hradec nad Moravicí-Pálles, Vršovice nr. Opava, Chvalíkovice nr. Opava, Opava, Hněvošice, Bělá nr. Chuchelná, Závada 1.8 km SE-sand-pit, Moravskoslezské Beskydy Mts-Tanečná Mt. (J. Roháček leg.), Moravskoslezské Beskydy Mts-Muřínkový vrch Mt., Trinec-Tyra (M. Barták leg.). **DENMARK:** Lyngbymoer, 15.ix.1912, 1 ♂, no collector (ZMHB); NEJ: Frederikshavn, 15.vi.1919, 1 ♂, T. Mortensen leg.; LFM: Radsted, 17.vii.1964, 1 ♀, N. M. Anderssen leg. (both ZMUC). **FINLAND:** Helsinki, 11.iv.1952, 1 ♀, L. Tiensuu leg.; 1 ♂ 3 ♀♀ (f. *nivalis*), 1 ♀, R. Frey leg.; Helsinki, 111, 1 ♂ (genit. prep.), R. Frey leg.; Kyrkslätt, 5341, 2 ♀♀, R. Frey leg.; Muonio, 2 ♂♂ 1 ♀ (f. *subapterus*), J. Sahlberg leg.; 2 ♀♀ (f. *subapterus*), Palmén leg.; Suomussalmi, 538, 1 ♀ (f. *subapterus*, genit. prep.), Hellén leg.; Kajana, 29.v, 1 ♀ (f. *subapterus*), Hellén leg.; Esbo, Westend, Sorkhäll, falla nr 4, 10.viii.1957, 1 ♀, W. Hackman leg. (all MZHF); Ab. Kaarina Järvelä, 67145:32457, pitfall, 17.v.-3.vi.2017, 1 ♀ (genit. prep.). 3.vi.-10.vii.2017, 1 ♀♀, V.-M. Mukkala leg. (SMOC). **FRANCE:** Arc, 30.viii.1986, 1 ♂ (f. *brach.*); 9 km S Chambéry, 1000 m, grass roots, 31.viii.1986, 1 ♂ 1 ♀, all S. A. Marshall leg. (DEBU, 1 ♂ genit. prep.); Hte Savoie, Le Môle, mousses, 1800 m, 17.vii.1979, 1 ♂, Besuchet leg. (HNHM). **GERMANY:** Westfalen: Herten, 18.iii.1916, 1 ♀, 20.iii.1916, 1 ♀; S. Harz: Ilfeld, 18.iv.1915, 1 ♀, 25.iv.1915, 1 ♀, 28.iv.1915, 1 ♂, all O. Duda leg. (ZMHB); Frankfurt an Oder, 30.x.1927, 1 ♂; Frankfurt an Oder-F See, 10.iv.1935, 1 ♂; Frankfurt an Oder-Eichwald, horse excrement, 21.iii.1935, 1 ♀, all M. P. Riedel leg. (ZMHB). **GREAT BRITAIN: ENGLAND:** Oxon: Bagley Wood nr. Oxford, nest of *Evolotomys*, 9.xii.1925, 1 ♀ f. *brach.*, O. W. Richards leg. (ZMHB); Oxford, University Park env., sifting grass and *Carex* tufts, 10.viii.1998, 2 ♀♀ (1 ♀ genit. prep.), J. Roháček leg. (SMOC); Suffolk: Lakenheath warren, breck grass & heather heath, suction sampler, 13.vii.2003, 2 ♂♂ 3 ♀♀ (1 ♂ 3 ♀♀ f. *brach.*); Suffolk: Madserscross Hill, acid grassland, 13.vii.2003, 2 ♂♂ 2 ♀♀, all P. Gatt leg. (SMOC). **GREECE:** Pieria: Olympos Mts, Karyá 5 km E, 39°59'N, 22°26'E, 750 m, sweeping undergrowth of mixed forest, 3.vi.2007, 2 ♂♂ 1 ♀ (1 ♂ genit. prep.); Karyá 3 km E, 39°59'N, 22°25'E, 800 m, under tufts of grass in damp meadow, 3.vi.2007, 6 ♀♀; NW Peloponnese: Ano Vlasia 2.9 km S, 37°58'32"N, 21°54'10"E, 1020 m, sifting leaf litter under *Platanus*, 29.v.2015, 1 ♂ (genit. prep.), all J. Roháček leg. (SMOC); Viotia, Parnassos, Ski Centre, 1900 m, 6.vi.1982, 1 ♂, R. Danielsson leg. (HNHM). **HUNGARY:** Kiskunsági N.P., Fülöpháza, homokbuckás, 26.vii.1978, 1 ♂; Kiskunsági N.P., Ágasegyháza, homokbuckás, 27.vii.1978, 1 ♂; Hortobágy N.P., Egyek, Ohati erdő, 17.vii.1978, 1 ♂, all L. Papp leg. (HNHM); Bátorliget, talajcsapda, iii.1990, 1 ♂, I. Loksa leg. (HNHM); Csik Szépvir, 9.v.1917, Fodor leg. (ZMHB). **ICELAND:** S. Iceland: Seljalandsfoss, Water falls, stream, 7.v.2013, 1 ex (sex unknown, abdomen damaged), P. Gatt leg. (SMOC). **ITALY:** N. Italy: Bibione env., seashore wrack, 16.vi.1994, 1 ♀ (genit. prep.), J. Roháček leg. (JRO); Volano, Strada spiaggia, aeroplancton, 5.x.1983, 17:30, 2 ♀♀, no collector; Volano, oRe 12, *Tamarix*, 12.xi.1972,

1 ♀, no collector; Arta Fornaci, prato umido, 22.iii.1964, 3 ♀♀, no collector; Vatte[s] Bur[gusio], 29.iv.1967, 1 ♂, no collector; Padova: Luvigliano, 22.vi.1988, 1 ♀, Scarpa leg.; Venezia: Mestre, S. Giuliano Terriccio, 20.ii.1988, 1 ♀; Monti Lessini: NE di Cortiolo, 897 m, stagno, 28.vi.1989, 1 ♂, L. Munari leg. (all MCNV); Abruzzo: (AQ), Monte Velino, Fontecchia, 1250 m, 17.v.2006, G. Lo Giudice leg. (SMOC); Puglia: Gargano, S. Giov. Rotondo, Coppa di Mezzo, 850 m, *Fagus* and *Quercus* grazed forest, 4.vii.2005, 1 ♂ (genit. prep.), P. Gatt leg. (SMOC); Calabria: Serre Calabresi Mts, Mongiana 2.4 km N, 38°32'05"N, 16°19'06"E, 1000 m, in tufts of *Juncus* in alder forest, 25.v.2018, 4 ♂♂ 4 ♀♀ (1 ♂ 1 ♀ genit. prep.); same, sweeping in alder forest and over meadow nr. brook, 25.v.2018, 1 ♂; Mongiana 2.5 km NNE, 38°32'09"N, 16°19'33"E, 1035 m, sweeping vegetation along brook in alder forest, 22.v.2018, 1 ♀, all J. Roháček leg. (SMOC). **SARDINIA:** Pattada 2.6 km SE, 40°34'12"N, 9°08'17"E, 575 m, aspirated from tufts of grass, 10.v.2014, 1 ♀ (genit. prep.), J. Roháček leg. (SMOC). **SICILY:** Messina: Nebrodi, Monte Sorro, 1700 m, *Fagus*, *Quercus*, 7.vi.1999, 1 ♀ (genit. prep.), P. Gatt leg. (SMOC); Parco di Nebrodi, Lago Pisciotto, 37°58'48"N, 14°50'49"E, 1240 m, sweeping swampy shores of lake, 21.iv.2016, 2 ♂♂ (1 ♂ genit. prep.), J. Roháček leg. (SMOC). **POLAND:** W. Poland: Gleiwitz, 21.iii.1934, 1 ♀; Wustung bei Habelschwerdt, 6.iv.1925-11.iv.1929, ca 40 specimens, all O. Duda leg. (ZMHB); E. Poland: Bondary, Narew river shore, under tufts of grass, 26.vi.2005, 1 ♂ 2 ♀♀ (1 ♀ genit. prep.); Białowieża-Budy 2 km NE, under tufts of grass in damp meadow, 24.vi.2005, 1 ♀; Białowieża-Budy 4 km S, Czerlon, on carrion of *Bison bonasus*, 25.vi.2005, 2 ♀♀, all J. Roháček leg. (SMOC). **POR-TUGAL:** Algarve: Tavira 3 km N, 37°08'52"N, 7°39'12"W, 24 m, sweeping over boggy meadow, 1.iv.2009, 1 ♂ (genit. prep.), J. Roháček leg. (SMOC); Manteigas, Serra de Estrela, 40°19'23"N, 7°36'09"W, 1860 m, grazed bog, steppe, stream, 29.ix.2014, 1 ♂ 1 ♀; Seia, Aldeia da Serra, 40°25'03"N, 7°40'38"W, 893 m, grasses & scrub, 28.ix.2014, 1 ♀, P. Gatt leg. (SMOC). **ROMANIA:** Banat: Sfânta Elena 2.5 km NE, 44°41'44"N, 21°43'10"E, 420 m, sweeping over meadow, 1.vi.2008, 1 ♀ (genit. prep.), J. Roháček leg. (SMOC). **SLOVAKIA** (about 400 specimens, deposited in JRO, MBP, SMOC, many genit. prep.), examples of localities: S Slovakia: Patince nr. Komárno, Búč nr. Komárno, Kamenín nr. Štúrovo, Nová Vieska nr. Štúrovo (J. Roháček leg.), Hegyfárok, Štúrovo, Biel, Pribylina (M. Barták leg.); C Slovakia: Kremnické pohorie Mts-Turček, Detva-Horná Chrapková, Hrochofská dolina-Hrochof 3 km E., Kyslinky-Dolná Zálomská, Kyslinky-Hrochofská dolina, Kyslinky-Majerová, Predná Poľana Mt.-Žliebky, Sihla env., Sihla-Kamenistý potok, Zákľuky Mt., Stankovany nr. Kraľovany, Chočské vrchy Mts-Škútova dolina, Muránska Huta-Šiance res., Muránska planina NP-Šiance res. top plateau, Pohronská Polhora 5.3 km SE-Rosiarka res., Tisovec 3.9 km NW-Trstie res., Jestice-Hradisko Mt. (all J. Roháček leg.); N Slovakia: Tatranská Lomnica (M. Barták leg.), Vysoké Tatry Mts-Batizovská dolina, Vysoké Tatry Mts-Velické pleso, Vysoké Tatry Mts-Štrbské pleso, Belianske Tatry Mts-Tatranská Kotlina, Tatranská Kotlina-Šarpanec res., Regetovka res. peat-bog (J. Roháček leg.); E Slovakia: Levočské pohorie Mts-Branisko Mt., Boľ nr. Král. Chlmec, Boľany nr. Latorica, Stakčín, Vihorlat Mts-Sninský kameň Mt., Hostovce-Hostovické lúky res., Nová Sedlica-Stužica res. (J. Roháček leg.). **SPAIN:** S. Spain: Sierra Nevada Mts, Llano Prado, 2200 m, on decayed grass, 14.v.1979, 2 ♂♂ 3 ♀♀ (1 ♂ 1 ♀ genit. prep.), in runs of *Pitymys* and *Arvicola* sp., 14.v.1979, 1 ♂ 1 ♀; Grazalema nr. Ronda, 1000 m, 16.-17.v.1979, sifting moss, 1 ♂ (genit. prep.), sweeping over meadow, 1 ♀, sweeping by stream, 1 ♀, all J. Roháček leg. (JRO); Sierra Nevada, Hwya, 1860 m, edge of small, cold stream, 7.viii.1986, 1 ♂ 1 ♀; Sierra Nevada, Hwy, 2100 m, along small stream, 9.viii.1986, 1 ♂ 3 ♀♀ (1 ♀ genit. prep.); Sierra Nevada, Hwy, 2270 m, grass of dry stream, 11.viii.1986, 2 ♂♂ 2 ♀♀ (1 ♂ 1 ♀ genit. prep.), J. R. Vockeroth leg. (DEBU). **SWEDEN:** Huddinge, Gömmaren lake res., 59°15'15"N, 17°55'40"E, 58 m, peat-bog, sifting *Sphagnum*, moss and grass, 7.vii.2011, 3 ♂♂ 1 ♀ (2 ♂♂ 1 ♀ genit. prep.), all collected together with the male neotype, J. Roháček leg. (SMOC). **SWITZERLAND:** Delémont, 500 m, conifer slash (fresh), 28.viii.1986, 1 ♂ 3 ♀♀ (1 ♀ genit. prep.), S. A. Marshall leg. (DEBU); ZH: Unterengstringen, 15.ix.1997, 1 ♂, G. Bächli leg. (HNHM).

Redescription. Male (Figs 2, 3, 7). Total body length 1.38–1.98 mm; general colour brown to dark brown with greyish brown to grey microtomentum, subshining dorsally



Figs 1–6. *Pteremis fenestralis* (Fallén, 1820) and its habitats. 1 – female, f. macropt., laterally (Czech Republic); 2 – male, f. brach., laterally (Czech Republic); 3 – male, f. brach., living specimen on grass stem (Czech Republic); 4 – male (topotypic specimen, Sweden), head dorsofrontally; 5 – peat-bog meadow, habitat in the (neo)type locality (Sweden: Huddinge, Gömmaren lake reserve); 6 – montane meadow with tufts of grasses, habitat near Jizerka in the Jizerské hory Mts (Czech Republic). Scales = 0.5 mm. Photo by M. Deml (1, 2) and J. Roháček (others).

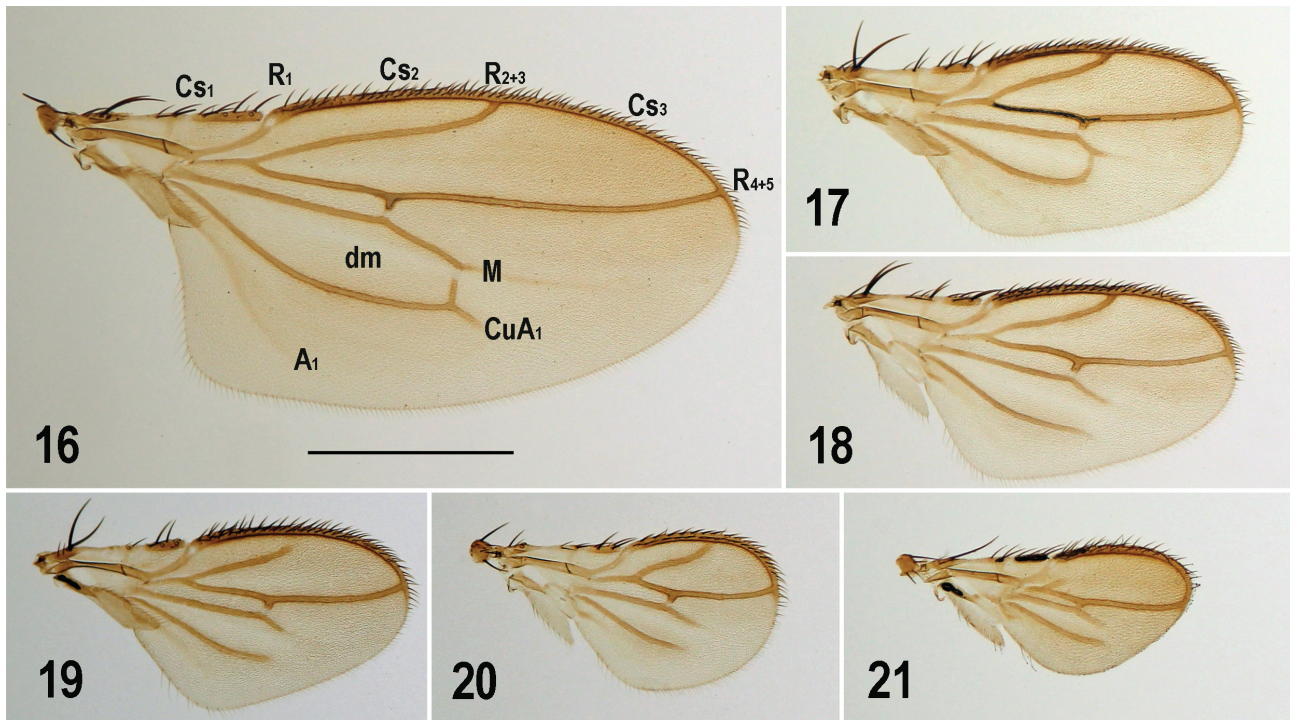


Figs 7–15. *Pteremis fenestralis* (Fallén, 1820), type specimens. 7 – neotype male of *Copromyza fenestralis* Fallén, laterally; 8 – labels of the neotype; 9 – neotype mounted and pinned, with all labels; 10 – lectotype female of *Borborus nivalis* Haliday, 1833, dorsally; 11 – ditto, head dorsofrontally; 12 – lectotype mounted on card and all its labels; 13 – lectotype male of *Pteremis subapterus* Frey, 1947, laterally; 14 – ditto, head laterofrontally; 15 – all labels of this lectotype. Photo by A. O’Hanlon (10–12) and J. Roháček (others).

on thorax and abdomen), duller on head, thoracic pleuron and ventral abdominal sterna.

Head (Figs 4, 11, 14) about 1.4× higher than long, blackish posterodorsally, orange to yellow anteroventrally. Frons dark brown to blackish except for orange-brown anterior margin, distinctly microtomentose; occiput almost black, with dark grey microtomentum. Orbits, interfrontalia (very narrow) and frontal (including ocellar) triangle with silvery grey glittering microtomentum and all separated by dull blackish (often with some bluish tinge) stripes

almost forming M-shaped mark; frontal triangle distinctly delimited and reaching to anterior third of frons; anterior margin of frons orange to orange-brown, wider laterally. Frontal lunule relatively long (although shorter than wide), yellow, whitish microtomentose, distinctly lighter than anterior margin of frons. Face normally yellow (darkened in some specimens, for detail see Variability below), whitish microtomentose including facial cavities below antennae; medial carina slightly developed, distinct only dorsally, below frontal lunule. Gena yellow to ochreous,



Figs 16–21. *Pteremis fenestralis* (Fallén, 1820), wings. 16 – f. macropt., male; 17–21 – f. brach.; 17 – female with *dm-cu* preserved; 18 – female (f. *nivalis*); 19 – male (f. *subapterus*); 20 – female (f. *nivalis*); 21 – male (f. *subapterus*). Figs 16–20 are based on specimens from Rejvíz, peat-bog meadow (Czech Republic); Fig. 21 on specimen from Muonio (Finland). Scale = 0.5 mm. Photo by J. Roháček.

paler anteriorly, all greyish microtomentose and sharply separated from dark occiput by dark and shining perpendicular stripe on postgena. Cephalic chaetotaxy (Fig. 4): *pvt* small and weak but strongly convergent or crossed; a pair of minute convergent postocellar setulae between *pvt* and posterior ocelli also present; *occe* and *occi* subequal (or *occi* slightly longer) and about two-thirds of *vti*; *vti* and *vte* subequal, robust and longest of frontal bristles; *oc* distinctly shorter than *vti*; 2 *ors*, posterior as long as *oc* and about 1.4 times as long as anterior *ors*; 4 (more rarely only 3) *ifr*, two middle pairs usually longer and more robust, sometimes with 1 microseta in front of anterior *ifr* in addition; 2 or 3 very minute *ads* inside and below *ors*; *g* and 1 or 2 setae behind it weak, hardly longer than anterior peristomal setula; *vi* very long and robust, about as long as *vti*; peristomal setulae sparse (only 4 or 5) and about as long as 2 weak postgenal setae; postocular setulae shorter than peristomals, in single long row. Eye subcircular (19:17), of moderate size, with longest diameter about 4 times as long as smallest genal height. Antenna with scape ochreous to yellow, pedicel blackish and 1st flagellomere dark brown, the latter relatively short (as long as pedicel), suboval to ovoid, with whitish ciliation on apex distinctly longer than cilia on arista. Arista relatively long, about 4.2 times as long as antenna, with short dense ciliation.

Thorax dark brown to brown (ventral part of pleuron palest) and dark grey microtomentose; mesonotum subshining, pleuron and scutellum duller. Sutures between pleural sclerites pale brown to ochreous. Scutellum large and relatively long, flat on disc, little transversely (3:2), rounded subtriangular. Thoracic chaetotaxy: mesonotal macrosetae relatively long and robust; 1 *hu* (as long as

anterior *npl*) and 1 microseta on humeral callus; 2 relatively short *npl* (posterior shorter); 1 *prs* (= posthumeral) and 1 *sa*, both short; 2 *pa*, the outer very long, longer than *dc*, the inner small; only 1 robust (but shorter than laterobasal *sc*) *dc* in prescutellar position; *dc* microsetae (in front of *dc*) somewhat longer than *ac* microsetae; 8 rows of *ac* microsetae on suture but only 4 in front of scutellum; medial prescutellar *ac* pair small, hardly or only slightly longer than other *ac* microsetae; 2 very long and robust *sc*, laterobasal longer than scutellum, apical (longest thoracic seta) 1.5–1.6 times as long as laterobasal; 2 *stpl* but only posterior long (as long as laterobasal *sc* but finer), anterior reduced to microseta.

Legs brown or dark brown (femora, coxae, *t*₃) to ochreous or dirty yellow (trochanters, tibiae, tarsi) but colouration is variable, generally darker in montane and boreal specimens and more yellow in brachypterous forms. *f*₁ with base and apex usually yellow; also *f*₂ and *f*₃ with apex (knee) often ochreous, and *t*₃ with both ends ochreous to yellow. On the contrary, the largely yellow *t*₁ and *t*₂ can be darkened about middle as is also hind tarsus or its basal segments. Pedal chaetotaxies: *f*₁ with 2 rows of setae: a short posterodorsal row with 3 or 4 setae in the middle of femur, and a longer row of posteroventral setae, 3 of which in distal half of femur are enlarged. *f*₂ anteriorly with 1 robust subapical seta and 1 short in front of it, and posteriorly with 1 shorter posteroapical seta. *t*₂ ventrally (see Fig. 23) with 3 setae, viz. 1 long robust *va* (directed in axis of tibia), 1 similarly long and strong *vpa* and 1 short *av* near middle; dorsally (Fig. 22) there are two groups of setae: proximal group, with 1 longer anterodorsal seta + 1 shorter above it and 1 shorter posterodorsal seta in about

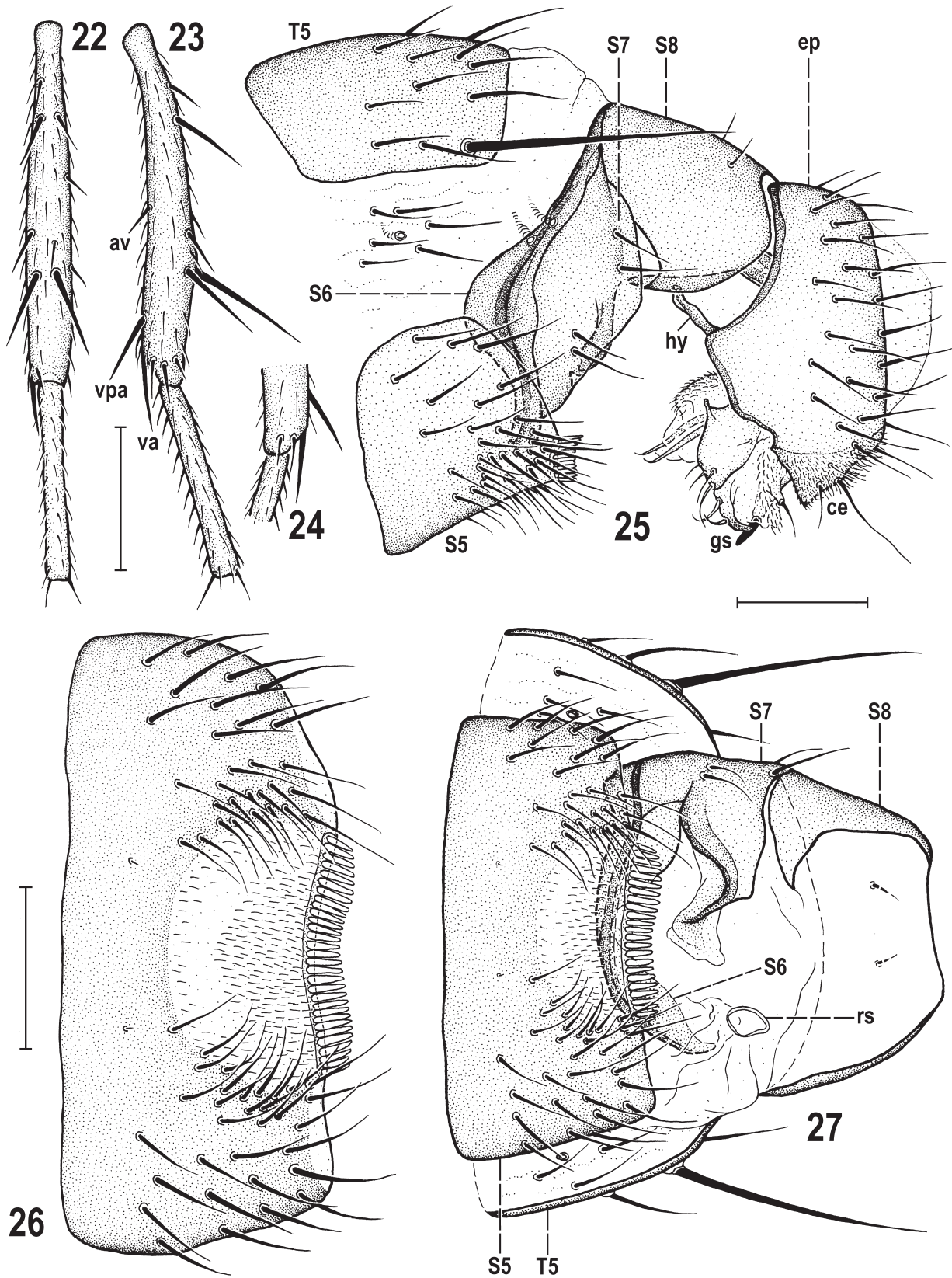
proximal fourth; distal group with 1 shorter anterodorsal and 1 very long posterodorsal (rather subdorsal) seta in about distal fourth, each surmounted with a short seta (that subdorsal can be reduced); in addition there are 2 small posterior setae in proximal third and above distal fourth (Fig. 22); apex of tibia provided with 3 short (1 or 2 longer) subapical setae anteriorly (Fig. 23) and 2 posteriorly (Fig. 24). f_3 with 1 short and weak anterior subapical seta. Other parts of femora and tibiae uniformly finely setulose. Mid basitarsus (mt_2) sometimes with 1 enlarged ventral (or anteroventral) setula (similarly as in Fig. 57). Ratio $t_2 : mt_2 = 1.81-1.94$.

Wing normal (macropterous form, Fig. 1) or reduced (brachypterous form, Figs 2, 3). Membrane distinctly brownish fumose, veins brown to dark brown. Macropterous form: wing (Fig. 16) relatively broad; C distinctly produced beyond apex of R_{4+5} . Cs_1 with markedly longer setulae than rest of C . R_{2+3} very slightly sinuate but apically distinctly upcurved to C ; R_{4+5} distinctly sinuate, distally upcurved to C and diverging from and ending about as far from apex of wing as venal fold of M . Discal cell (dm) of moderate length, relatively broad but distally tapered, with small process of M and longer one of CuA_1 beyond $dm-cu$; that of M continued by venal fold; both outer corners of cell dm normally obtuse-angled. A_1 relatively long but only small basal part fully developed, more distally formed by brownish coloured fold not reaching wing margin. Anal lobe large, well developed; alula relatively small and narrow. Wing measurements: length 1.19–1.71 mm, width 0.50–0.78 mm, $C-index = 0.80-0.96$, $r-m\backslash dm-cu : dm-cu = 1.64-2.09$. Brachypterous form: wing size and venation variously reduced (Figs 17–21). C shortly produced beyond apex of R_{4+5} . R_{4+5} rather curved (slightly to distinctly) than sinuate. Discal cell (dm) very shortened beyond $r-m$, usually with cross-vein $dm-cu$ absent (f. *nivalis*, Figs 18, 20), more rarely with it present and posterior outer corner of dm cell rounded (Fig. 17); also R_{2+3} can sometimes be more or less shortened (f. *subapterus*, Figs 19, 21) or apex of wing reduced and rounded (Fig. 20). A_1 always with coloured distal venal fold shortened or discoloured and hardly visible. Wing measurements: length 0.75–1.03 mm, width 0.37–0.49 mm, $C-index = 0.80-0.95$. Haltere bicolorous, with ochreous-yellow stem and dark brown knob.

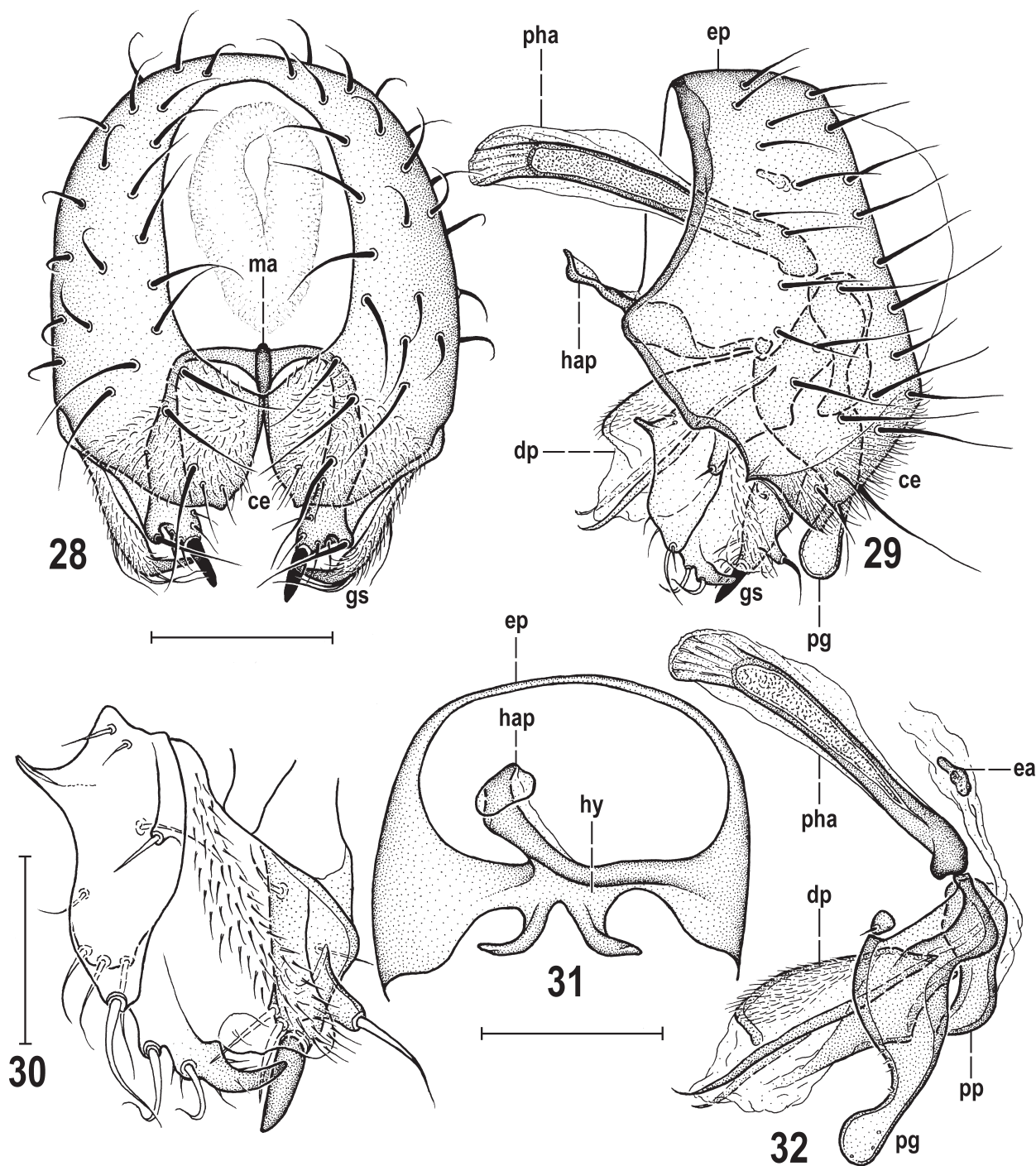
Abdomen blackish brown, dorsally (particularly medially) less microtomentose and more shining than ventrally. Basal preabdominal terga relatively broad (as wide as thorax) and sparsely dark grey microtomentose; $T2-T5$ sparsely and relatively shortly setose, with only setae in posterior corners long and robust (cf. Fig. 25). $T1+2$ largest tergum (about 1.4 times as long as $T4$ or $T5$), narrower anteriorly, widest at posterior margin; with pale brown base (on original $T1$) and the rest blackish brown. $T3$ widest tergum but clearly shorter than $T4$ (thus most transverse), the latter slightly narrowed posteriorly and about as long as $T5$; $T5$ markedly narrower than $T4$ and posteriorly more distinctly tapered. Preabdominal sterna: $S1+2$ (or $S2$) smallest, transversely trapezoidal (narrowed anteriorly), pale brown to pale ochreous (lightest anteriorly), contrasting with dark brown $S3-S5$ and sparsely shortly setose;

$S3$ and, particularly, $S4$ large, broad, blackish brown and strongly sclerotized; $S3$ only slightly narrower anteriorly, shorter than $S4$, the latter largest sternum, transversely suboblong and distinctly longer than (equally broad) $S5$. $S2-S4$ with sparse, short setae, finer than those on adjacent terga; also setae in their posterior corners short and weak. $S5$ (Figs 26, 27) shorter and, hence more transverse than $S4$, very slightly asymmetrical, with relatively large, (usually) pale-pigmented and finely micropubescent semicircular area in front of simple posteromedial comb of spines (this extended over about medial third of posterior margin of $S5$); lateral setae of $S5$ more robust and more or less separated from two groups of finer setae surrounding lateral margins of posteromedial semicircular area. $S6+7$ strongly asymmetrical, situated left ventro- to dorsolaterally (Figs 25, 27) and dorsally fused with $S8$; the latter less asymmetrical and situated dorsally. $S6+7$ with transverse dark-pigmented ledge and $S7$ with irregular posteroventral projection bent inside postabdomen; right laterally, near right end of $S6$, there is an enlarged, annular, 6th right spiracle (Fig. 27, *rs*). $S6+7$ with 2 pairs of setae (Fig. 25) and $S8$ with only a pair of small dorsal setae near middle (Figs 25, 27).

Genitalia. Epandrium (Figs 28, 29) of medium length and width, almost symmetrical in caudal view (Fig. 28), with rather uniform setosity, longest setae posteroventrally near margin of anal fissure. Anal fissure relatively high and narrow, elongately suboval. Cerci large but completely fused with epandrium and ventromedially separated by acute incision; each cercus ventrally terminated by a small subtriangular tubercle (Fig. 28) and with 1 long sinuate seta and 2 small setae. Medandrium low (short) and broad, with long lateral arms, each connected with posterior part of gonostylus (Fig. 28). Hypandrium genus-characteristic, short, laterally fused with epandrium, posteroventrally projecting on each side to connect with postgonites and medially with very short, strongly asymmetrical (right directed) flattened apodeme (Fig. 31). Gonostylus (Figs 28–30) of complex structure, composed of larger anterior (more lateral) lobe and of smaller (shorter and more medial) posterior lobe. Anterior lobe (Fig. 30) with short pointed anterodorsal process, 3 robust curved setae anteroventrally, 1 robust darkened ventral, posteriorly directed projection (finely spinose subapically but with simple apex) and posterolaterally with oblique longitudinal spinulose ledge; a single short external seta on small process in front of proximal end of this ledge is also characteristic. Posterior lobe (dotted in Fig. 30) terminated by very robust spine and 2 subapical setae and posteriorly with subconical process having a robust, medially bent seta on apex (see Fig. 28). Aedeagal complex (Fig. 32) of relatively simple construction. Phallopodeme rod-like, about as long as aedeagus, with moderate, pale-pigmented, dorsal keel. Aedeagus proximally with short but compact, laterally somewhat flattened, phallopore (Fig. 32) having simply pointed but not acute (ventral) apex. Distiphallus relatively weakly sclerotized and pale-pigmented, basally narrow, widened laterally (but hardly so dorsoventrally) towards apex, proximoventrally and dorsally more sclerotized,



Figs 22–27. *Pteremis fenestralis* (Fallén, 1820), topotypic male (Sweden: Huddinge). 22 – left t_2 and mt_2 dorsally; 23 – ditto, anteriorly; 24 – apex of left t_2 posteriorly; 25 – male 5th abdominal segment and postabdomen, left laterally; 26 – male S_5 , ventrally; 27 – 5th abdominal segment and postabdomen (genitalia omitted), ventrally. Scales = 0.2 mm (Figs 22–24), 0.1 mm (others). For abbreviations see Material and methods.



Figs 28–32. *Pteremis fenestralis* (Fallén, 1820), topotypic male (Sweden: Huddinge). 28 – external genitalia, caudally (aedeagal complex omitted); 29 – ditto, left laterally; 30 – gonostylus, laterally; 31 – epandrium and hypandrium (setosity omitted), anteriorly; 32 – aedeagal complex, laterally. Scales = 0.05 mm (Fig. 30), 0.1 mm (others). For abbreviations see Material and methods.

and with a pair of slender band-like lateral sclerites, each with thinly pointed apex. Middle part of dorsal side of distiphallus finely haired and its dorsal sclerite subapically forked and bent laterally on side of distiphallus (Fig. 32). Postgonite relatively large (as long as distiphallus), sinuate in lateral view, broader proximally, strongly tapered distally but with apex knob-like dilated, with 2–3 microsetae anteriorly in distal third, some minute sensilla on apex, and with minute sclerite (= remnant of pregonite)

with 1 or 2 setulae, inserted in anterodorsal emargination of postgonite (Fig. 32). Ejacapodeme small, having short distal digitiform process on a wider proximal part (see Fig. 32) attached to ejaculatory duct.

Female (Fig. 1). Head, thorax, legs and wings very similar to those of male unless mentioned otherwise below. Total body length 1.43–2.10 mm. t_2 often with anterior subapical setae (or one of them) longer; mt_2 slightly longer on the average and with more frequent presence of 1 enlarged

ventral setula in proximal third. Ratio $t_2 : mt_2 = 1.78\text{--}1.94$. Wing measurements: macropterous form: length 1.38–1.79 mm, width 0.64–0.81 mm, $C\text{-index} = 0.78\text{--}1.01$, $r\text{-m}\backslash dm\text{-cu} : dm\text{-cu} = 1.67\text{--}2.00$; brachypterous form: length 0.59–0.99 mm, width 0.29–0.50 mm, $C\text{-index} = 0.84\text{--}1.08$. Abdomen more ovoid in dorsal view, basally broadest. $T1+2$ largest and widest tergum; other preabdominal terga ($T3\text{--}T5$) distinctly shorter and more transverse than in male, becoming narrower posteriorly, subequal in length or $T5$ slightly longer. Preabdominal sterna: $S1+2$ formed and pale as in male but with only a few short setae; $S3\text{--}S5$ dark brown as in male but $S3$ shorter and also narrower than $S4$ (largest sternum, slightly trapezoidal, wider posteriorly) and $S5$ almost as long as $S4$ but distinctly narrower (as wide as $S3$), unmodified, transversely suboblong, with rounded corners.

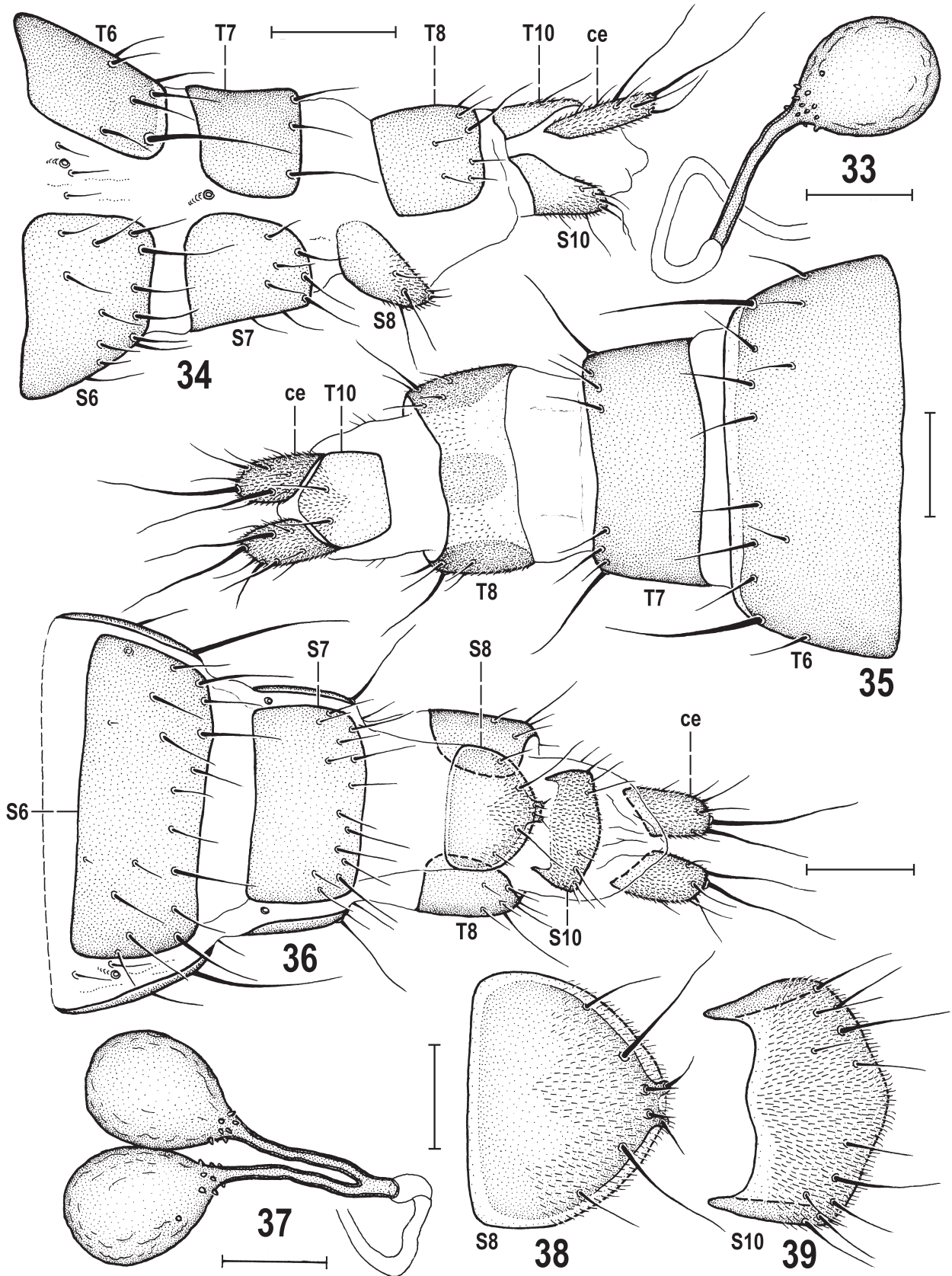
Postabdomen (Figs 34–36) relatively long when exposed, telescopic and retractible into preabdomen, basally (base of 6th abdominal segment) 0.7–0.8× as wide as 5th segment posteriorly, with subsequent segments becoming narrower (cf. Figs 35, 36). $T6$ transversely subtrapezoidal to suboblong, much narrower than $T5$ but wider and longer than $S6$, with posterior margin pale and sparse setae in posterior two-fifths, those in posterior corners long and robust (Fig. 35); $T7$ markedly shorter and narrower than $T6$ and bent farther laterally (see Fig. 34), with single row of sparse posterior setae on each side. $T8$ dorsally with tripartite pigmentation composed of a paler brown tongue-shaped medial part and larger darker lateral parts (Fig. 35), micropubescent in only posterior half, with a few setae (one longer) laterally (Figs 34, 35). $T10$ about as long as wide, roughly pentagonal, micropubescent only posteromedially and with a pair of relatively short setae in the middle (Fig. 35). $S6$ transversely trapezoidal (Fig. 36), narrower, and shorter but with more setae than $T6$. $S7$ simple, transversely suboblong, much narrower than $S6$ and also $T7$, with more setae than on $T7$, all in posterior half. $S8$ (Figs 36, 38) relatively narrow, slightly wider than long, rounded pentagonal to subtriangular (largest extension view, see Fig. 38), rather convex, with 2 or only 1 lateral setae in posterior half, and posteromedially with a group of (usually) 4 short setae on elevated sockets, which can also be situated in membranous part of sclerite; disc of sclerite micropubescent in posterior two-thirds (Fig. 38). $S10$ (in largest extension) only slightly shorter and as wide as $S8$, transversely subpentagonal, but anteriorly broadly emarginate, largely micropubescent (only anteriorly projecting corners and anterior margin bare) and relatively long setose in front of posterior margin (Fig. 39). Spectacles-shaped sclerite (= sclerotization of female genital chamber) poorly developed as a pair of ovoid rings, almost invisible because unpigmented and membranous. Spermathecae 2+1 (Figs 33, 37) blackish, each ovoid, with somewhat wrinkled surface and a group of spine-like tubercles on tapered base; terminal parts of ducts long, slender, well-sclerotized and dark-pigmented, those of paired spermathecae connected far from their bodies (Fig. 37). Cerci (Figs 34, 35) relatively broad but dorsoventrally flattened (see Fig. 34), micropubescent, each with 2 long sinuate setae (dorsopreapical and apical) and several short fine setae.

Variability. Body of brachypterous form is on average distinctly smaller, particularly so in specimens with wings most reduced (form *subapterus*). In smallest specimens also *ifr* setae are weaker and in only 3 pairs. Male $S5$ is also somewhat variable depending on body size of specimens. Smallest flies (usually brachypterous form) have posterior comb with spines less numerous and, consequently, the comb is narrower than in large specimens. Female $S8$ sometimes (in largest specimens) with an additional pair of setae near middle. Two pairs of short posteromedial setae can often be situated in membrane just behind posterior margin of pigmented part of $S8$.

Comments. *Pteremis fenestralis* (Fallén, 1820) is a wing polymorphic (for detail see ROHÁČEK 2012b), externally seemingly variable species. Its brachypterous form, having besides the shortened wing also a narrowed thorax (caused by reduction of wing musculature) and, hence, relatively large head and generally smaller body, has long been considered a separate species, even placed in a different (sub)genus than was the fully winged form. Due to its striking appearance and variable wing venation (cf. Figs 17–21), the brachypterous form was described three times, as *Borborus nivalis* Haliday, 1833, *Limosina paradoxa* Stenhammar, 1855 and *Pteremis subapterus* Frey, 1947. However, the chaetotaxy and structures of the male $S5$, male terminalia and female postabdomen of the brachypterous form are practically identical to those of the more common macropterous form regardless of some size variability of setae. Although this fact was first recognized already by COLLIN (1956) and HACKMAN (1964) terminalia of numerous specimens of both forms (including topotypic specimens) have been checked during this revision to confirm their conspecificity. Moreover, the barcoding region of COI of both forms from the Czech Republic have been compared with no difference recognized (see ID record DNMPC020-17 = f. brach. and DNMPC023-17 = f. *macropt.* in the BOLD database).

Pteremis fenestralis is readily distinguished from all similar relatives by the shape and armature of the male cercus (with only a small apical tubercle, Fig. 28), the gonostylus (with an apically simple ventral process on the anterior lobe and a robust terminal spine on the posterior lobe), the distiphallus (not dorsoventrally dilated in the middle) and the postgonite (with a knob-like apex, Fig. 32). In the female sex, it distinctly differs from all relatives by the spermathecae (ovoid rather than pyriform, with minute tubercle-like spines basally and sclerotized ducts connected far from bodies of paired spermathecae, Fig. 37) and $S8$ (of characteristic shape and posteromedially having only two pairs of small setae, Fig. 38). The armature and setosity of male $S5$ (Fig. 26) and the somewhat dorsoventrally flattened female cerci (see Figs 34–36) are also different from those of its congeners. For other diagnostic characters of the species see the key below.

The relationships of *P. fenestralis* have not been unambiguously recognized. Judging from the chaetotaxy of the mid tibia (with both *va* and *vpa* setae developed), similar short anterodorsal of anterior lobe of distiphallus and chaetotaxy of male $S5$ *P. fenestralis* seems to be more



Figs 33–39. *Pteremis fenestralis* (Fallén, 1820), female. 33 – spermatheca; 34 – postabdomen, laterally; 35 – ditto, dorsally; 36 – ditto, ventrally; 37 – paired spermathecae; 38 – S8, ventrally; 39 – S10, ventrally. Scales = 0.05 mm (Figs 33, 37–39), 0.1 mm (others). For abbreviations see Material and methods.

closely allied to *P. pulliceps* sp. nov. and (perhaps) also to *P. tenebricus* sp. nov. than to other species treated here. However, the presence of both *va* and *vpa* setae on t_2 seems to be a ground-plan character of the whole genus, not a synapomorphy of the above three species, and also the other two features can be plesiomorphic within the genus. On the other hand, the pyriform shape and ringed surface of spermathecae seems to be a synapomorphy of *P. pulliceps* sp. nov., *P. canaria*, *P. ferreus* sp. nov. and possibly also *P. apterina* sp. nov. If so, this assemblage can be a sister group to *P. fenestralis* + *P. wirthi* (see below). The female is unknown in *P. tenebricus*, and, consequently, its position in this group is uncertain.

The Nearctic, also wing-polymorphic, *P. wirthi* (Marshall, 1984) obviously is currently the closest relative or even sister-species of *P. fenestralis*. Examination of several specimens (1 ♂ and 1 ♀ dissected) from Canada (Ontario), identified by S. A. Marshall, resulted in finding that both species share several features, some probably synapomorphic, e.g. the very similar male *S5*, almost identical ventral process of anterior lobe of gonostylus, relatively short (not ventrally prolonged and flattened) male cercus with an apical tubercle (although being wider in *P. wirthi*), similarly armed spermathecae (basally with small surface tubercles) and broad, dorsoventrally flattened female cerci. For differences between *P. fenestralis* and *P. wirthi* see comments under the latter species below.

Biology. The species is mainly associated with wet grassy and mossy sites, both in open (meadows, fens, peat-bogs, see DAHL 1909, RICHARDS 1930, DUDA 1938, BÄHRMANN 1984, ROHÁČEK 1984, FLORÉN 1989, NOWAKOWSKI 1989) but also in woodland (ROHÁČEK 2012b) habitats. Adults live terricolously near the ground among tufts of graminoid plants or in moss, *Sphagnum*, leaf litter, and often also in runs and nests of various small mammals (RICHARDS 1930; HACKMAN 1963, 1964, 1967; ISMAY 1978; ROHÁČEK 1984, 2019a) and can be easily collected by means of soil traps (ROHÁČEK 1980, 1984; PERSSON 1983; BÄHRMANN 1987). Adults are attracted to various rotting matter, including wet excrement, particularly in runs of small mammals and the microsaprophagous larvae surely develop in these substrates. *Pteremis fenestralis* occurs regularly in various types of peat-bogs, often in *Sphagnum*, and, therefore, ROHÁČEK (1984) and ROHÁČEK & BARTÁK (1999) classified it as a tytrrophilous species. OKELY (1974) reared both macropterous and brachypterous specimens from puparia obtained from bait (boiled grass cuttings) exposed in burrow tunnels of the rabbit.

ROHÁČEK (2012b) found that wing polymorphic populations are only known from North and Central Europe (here usually at higher altitudes) while in southern areas only macropterous specimens occur. Thus the presence of brachypterous forms in populations seems to be geographically dependent, inasmuch as the percentage of short-winged specimens increases in more northern latitudes and at higher altitudes (ROHÁČEK 1975). Macropterous specimens, particularly gravid females, serve as the main agent for dispersal of the species because they are (more or exclusively) represented in samples obtained by sweet-

ping, Malaise and light traps (PITKIN 1986) or car-netting (MUNARI & SCARPA 1989). Adults were recorded in all months of the year (in winter in mainly subterranean microhabitats), most commonly in spring (combined published data and material examined).

Distribution. Widespread in Europe: Andorra, Austria, Belgium, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Ireland, Italy (incl. Sardinia, new, and Sicily), Latvia, Netherlands, Norway, Poland, Portugal, Russia (Central European territory), Slovakia, Spain, Sweden, Switzerland (records summarized by ROHÁČEK et al. 2001, MARSHALL et al. 2011). Additional country records are as follows: Belarus (several records in BOLD System, e.g. https://www.boldsystems.org/index.php/Public_RecordView?processid=GMBMA074-17), Greece (new), Iceland (new), and Romania (new).

Note. The records of *P. fenestralis* from Madeira (ROHÁČEK 2007, MARSHALL et al. 2011) are erroneous because they are based on misidentification of *P. pulliceps* sp. nov. (described below). Also the record from the Far East of Russia, listed by ROHÁČEK et al. (2001) and MARSHALL et al. (2011), is probably a mistake.

Pteremis pulliceps sp. nov.

(Figs 40–43, 46–61)

Pteremis fenestralis (misidentification): ROHÁČEK (2003): 110 (Madeira).

Type locality. Madeira, close to the forest house Rabaçal, about 32°45'43" N, 17°08'01" W (Fig. 44, for habitat see Fig. 45).

Type material. HOLOTYPE: ♂ (SMOC), labelled: 'C. MADEIRA: Rabaçal env., 950 m, 5.9.2003, J. Roháček leg.', 'sifting leaves in laurel forest', 'Mus. Silesiae Opava, Inv. č. d 097 4-2003' and 'Holotypus ♂ *Pteremis pulliceps* sp. n., J. Roháček des. 2023' (red label) (Fig. 41). The specimen (see Fig. 40) is intact, dry mounted on triangular pinned card. PARATYPES: **PORTUGAL: MADEIRA:** 4 ♂♂ (1 ♂ genit. prep.), with same data as for holotype (SMOC); Eira do Serrado, N slope, 1000 m, sweeping vegetation along spring, 13.ix.2003, 7 ♂♂ 4 ♀♀ (1 ♂ 1 ♀ genit. prep.), J. Roháček leg.; Eira do Serrado 1 km E, 1100 m, sweeping vegetation along levada, 12.ix.2003, 1 ♀, M. Vála leg.; Curral des Freiras-Murteiras, 650 m, sweeping vegetation along small creek, 650 m, 4.ix.2003, 1 ♂ 1 ♀; Cumeal nr. Curral des Freiras, 600 m, sweeping riverside vegetation, 4.ix.2003, 2 ♀♀; Funchal-Corujeira 1 km N, 600 m, sweeping riverside vegetation, 11.ix.2003, 1 ♂, all J. Roháček leg.; Terreiro da Luta nr. Funchal, 800 m, sweeping vegetation along levada, 14.ix.2003, 1 ♂, M. Vála leg.; Ribeira da Janela, 3 km S, 850 m, sweeping vegetation along levada, 10.ix.2003, 1 ♀; Achadas da Cruz 1.5 km S, 800 m, sifting leaves in laurel forest, 10.ix.2003, 4 ♂♂ 6 ♀♀ (1 ♂ 1 ♀ genit. prep.), all J. Roháček leg. (all SMOC).

Description. Male (Fig. 40). Total body length 1.53–2.16 mm; generally darker than *P. fenestralis*, blackish brown, with greyish brown or dark grey microtomentum.

Head (Fig. 42) about 1.5× higher than long, reddish brown to dark brown (darkest in dorsal half of occiput); frons not darker than face or gena. Frons lighter brown to reddish brown in anterior half, dark brown more posteriorly (from ocellar triangle). Orbits, interfrontalia (very narrowly) and frontal (including ocellar) triangle silvery grey microtomentose and somewhat glittering, all separated by dull brown or reddish brown stripes, but M-shaped mark usually not distinctly developed (Fig. 42); frontal triangle narrow, well delimited (reddish brown up to dark ocellar triangle and almost reaching anterior margin of

frons; the latter above lunule slightly darker than anterior corner of frontal triangle (cf. Fig. 42). Frontal lunule rather dark, hardly or very slightly lighter than anterior margin of frons. Face also relatively dark, brown to reddish brown, usually darker than anterior half of frons in contrast to that of *P. fenestralis*. Gena reddish brown to brown, concolorous with face, all distinctly greyish microtomentose and posteriorly contrasting with shining perpendicular stripe on postgena; the latter hardly darker than gena. Cephalic chaetotaxy (Fig. 42) similar to that of *P. fenestralis* but differing as follows: *pvt* reduced to microsetae, convergent but not meeting with apices medially; *occi* usually longer than *occe*; *vti* longest cephalic seta, slightly to distinctly longer than *vte*; 4 (rarely 3) *ifr*, all relatively robust and subequal, or two middle pairs slightly longer; 2–4 minute *ads* inside and below *ors*; *g* well developed, longer than peristomals, and 1 or 2 setae behind it shorter; *vi* very long and robust, about as long as *vti*; peristomal setulae sparse (usually 5) and short, as long as or slightly shorter than 2 (both short) postgenal setae. Eye subcircular (7:6), with longest diameter about 4.5 times as long as smallest genal height. Antenna uniformly brown, thus scape hardly lighter than other segments. Arista about 3.8 times as long as antenna, with short and dense ciliation, cilia about as long as those on apex of 1st flagellomere.

Thorax closely resembling that of *P. fenestralis* but notopleural area (partly also humeral callus) reddish brown to ochreous. Scutellum large, flat on disc but its apex more broadly circular. Thoracic chaetotaxy as in *P. fenestralis* but with 2 microsetae (internal larger) on humeral callus; *prs* (= posthumeral) as long as *hu* and *sa* distinctly shorter; *dc* (in prescutellar position) only slightly shorter than *pa*; *sc* (particularly laterobasal) longer than in *P. fenestralis* and apical (longest thoracic seta) only about 1.25 times as long as laterobasal; only 1 long *stpl* because anterior reduced to a hardly discernible microseta or absent.

Legs relatively uniformly brown to dark brown (hind femora darkest), tibiae slightly or distinctly paler than femora but not distinctly variegated, knees of fore leg and apex of t_2 usually lightest, and tarsus normally as dark as relevant tibia (Figs 40, 42). Chaetotaxy of legs generally as in *P. fenestralis* including that of t_2 (see Figs 55–57) but the latter often with *va* seta (directed in axis of tibia) more or less shorter than the strong *vpa* seta (Figs 56, 57) and, particularly, in having 1 long (much longer than in *P. fenestralis*) and 2 small subapical setae posteriorly (Fig. 56). Mid basitarsus (mt_2) often with 1 somewhat enlarged ventral setula (Fig. 57) in proximal fourth. Ratio $t_2 : mt_2 = 1.81–1.97$.

Wing always normally developed (Fig. 43), closely resembling in shape and venation that of *P. fenestralis* but membrane somewhat darker fumose and with darker brown veins. R_{4+5} sinuate but distally often straightened (Fig. 43) and A_1 darker and well visible also distally, as a darkened fold. Wing measurements: length 1.47–1.82 mm, width 0.65–0.85 mm, *C-index* = 0.82–1.01, $r-m/dm-cu : dm-cu = 1.64–2.31$. Haltere with ochreous-yellow stem (being only basally very shortly dark brown) and brown knob.

Abdomen as in *P. fenestralis* but preabdominal terga

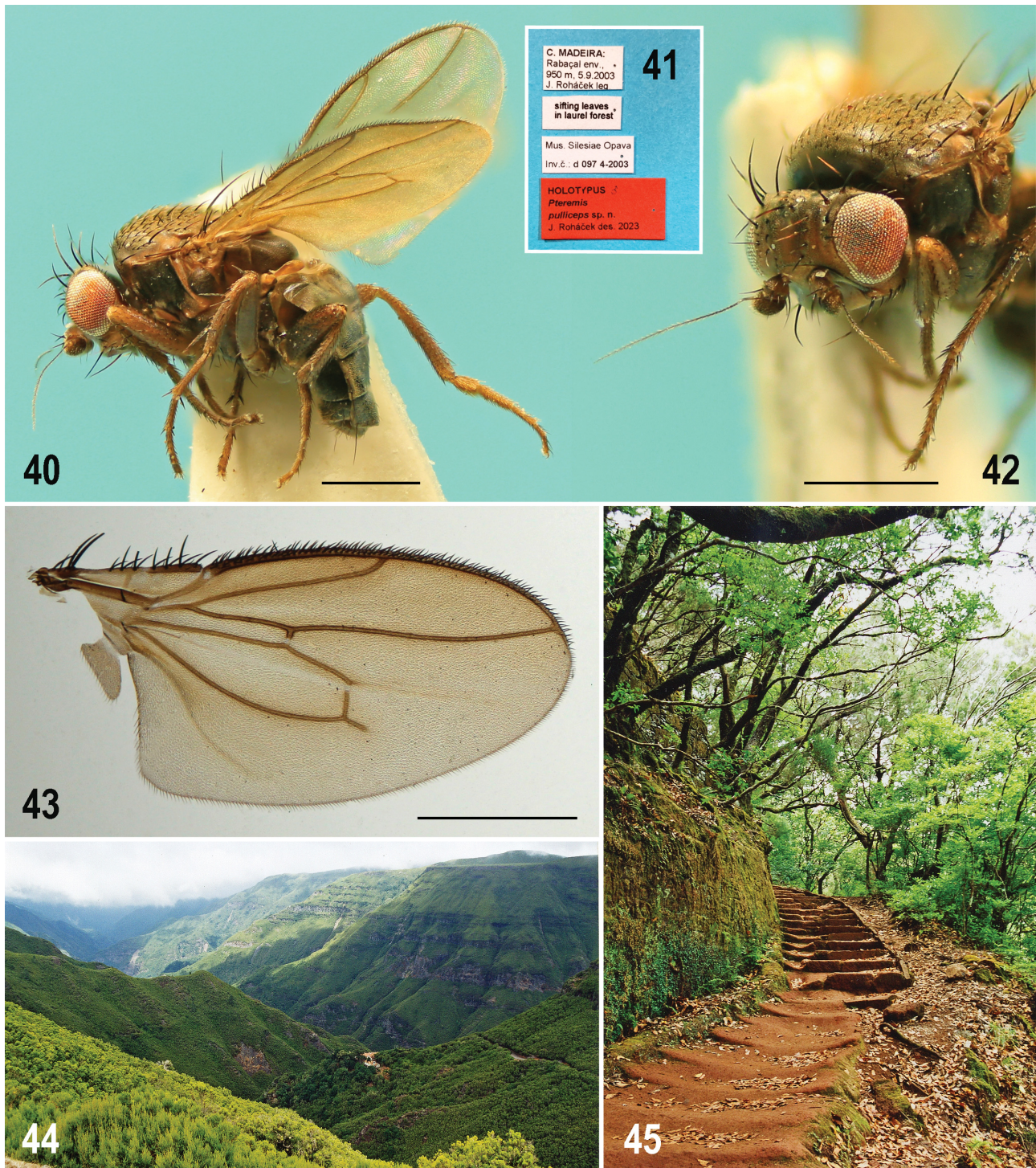
becoming narrower posteriorly, thus $T1+2$ largest and widest tergum and $T3$ slightly narrower (at most as wide as $T1+2$); $S1+2$ as that of *P. fenestralis* pale ochreous, lightest anteriorly but darkened posterolaterally; $S3$ distinctly tapered, broad posteriorly and as long as or slightly longer than $S4$, the latter widest sternum, distinctly longer and slightly wider than $S5$. $S5$ (Fig. 51) most similar to that of *P. fenestralis* but with (similarly large) posteromedial semicircular pale-pigmented area more densely and more finely micropubescent, posteromedial comb with spines finer and more dense and also all setae on lateral thirds of $S5$ much thinner. $S6+7$ and $S8$ as in *P. fenestralis* but $S6+7$ with only 1 + 1 or 1 + 2 fine setae.

Genitalia. Epandrium (Figs 46, 47) relatively short but distinctly wider than that of *P. fenestralis*, clearly widened ventrally (see Fig. 47) and with anal fissure large, broadly oval. Cerci large, dorsolaterally bulging (Fig. 47), distinctively micropubescent both laterally and medially but ventrally bare and each provided with subapical protruding curved ledge (with 2 setulae) and flattened apex (see also Fig. 49). Medandrium very low (short) with slender lateral arms (Fig. 47). Hypandrium small, with short, similarly asymmetrical apodeme (Fig. 46) as that of *P. fenestralis*. Gonostylus (Figs 46–48) also resembling that of *P. fenestralis*, with similarly pointed anterodorsal short process of anterior lobe and one short external seta on small process dorsally but with 4 (not 3) robust curved setae anteroventrally, robust ventral darkened projection slender, directed posteroventrally and with finely trifurcate apex (Fig. 48). Posterior lobe (dotted in Fig. 48) also characteristic, with robust spine unusually long and slender. Aedeagal complex (Fig. 50) of the same construction as that of *P. fenestralis* but aedeagus with much shorter (more slender) phallosophore (Fig. 50) having particularly slender and acute anteroventrally directed apex. Distiphallus differing from that of *P. fenestralis* by more dilated (also dorsoventrally) distal half (Fig. 50). Postgonite also similar to that of *P. fenestralis* but less sinuate in lateral view, and with more elongate and, hence, less clubbed apical part; minute sclerite (= remnant of pregonite) in anterodorsal emargination of postgonite with 2 longer setulae (Fig. 50). Ejacapodeme very small (not illustrated).

Female. Similar to that of *P. fenestralis* unless mentioned otherwise. Total body length 1.90–2.26 mm. t_2 with *va* seta distinctly shorter than *vpa* seta and usually with one anterior subapical seta enlarged, as long as that long on posterior side. Ratio $t_2 : mt_2 = 1.79–1.92$. Wing measurements: length 1.54–1.95 mm, width 0.69–0.93 mm, *C-index* = 0.94–1.06, $r-m/dm-cu : dm-cu = 1.79–1.90$.

Abdomen very similar to that of *P. fenestralis*, particularly as to preabdominal terga. Preabdominal sterna differing from those of *P. fenestralis* as follows: $S3$ as long as but narrower than $S4$ (largest sternum, transversely oblong) and (unmodified) $S5$ shorter than $S4$ but distinctly narrower (slightly narrower than $S3$), somewhat tapered posteriorly, with posterior corners rounded.

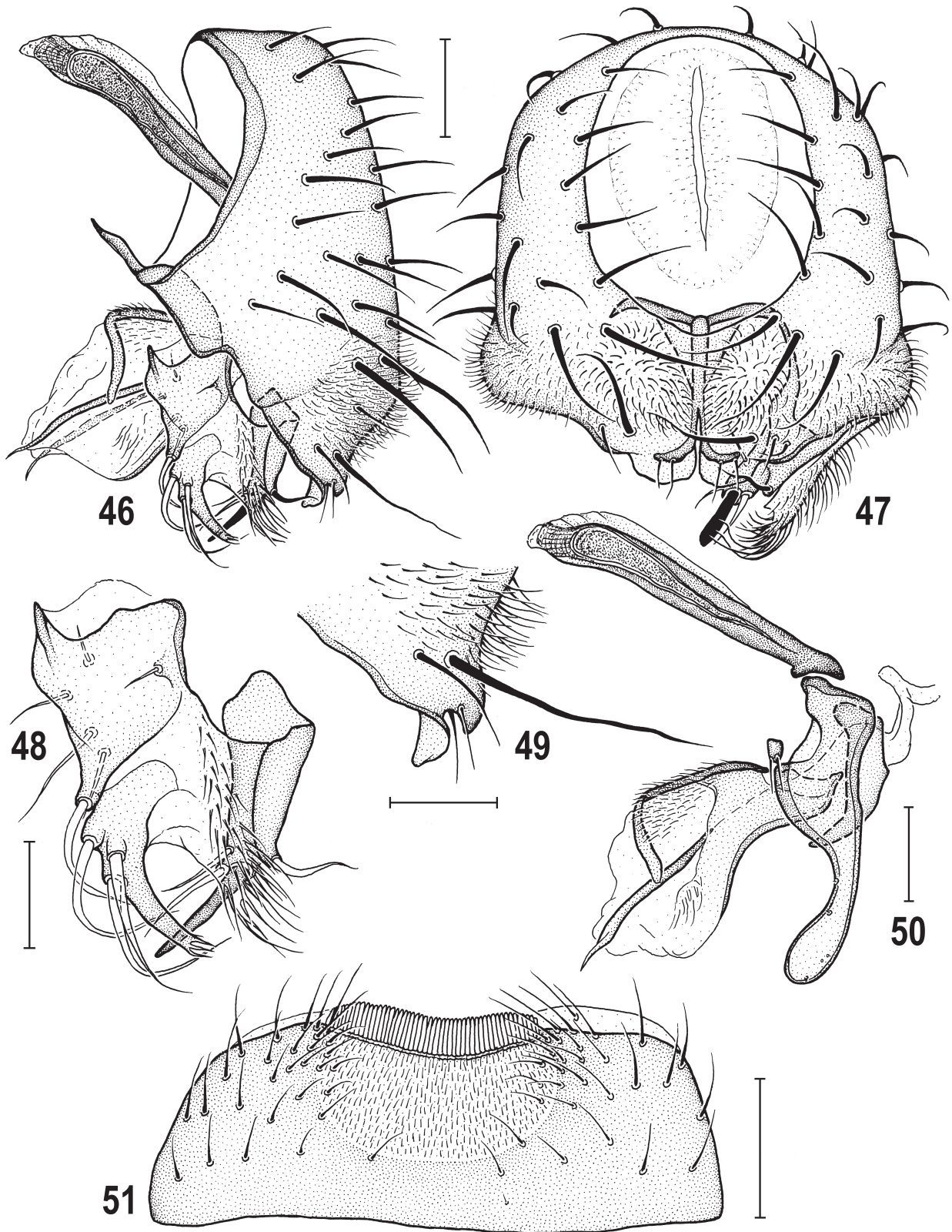
Postabdomen (Figs 52–54) resembling that of *P. fenestralis* but differing as follows: $T6$ and $T7$ less transverse and with shorter and weaker setae in posterior corners (Fig.



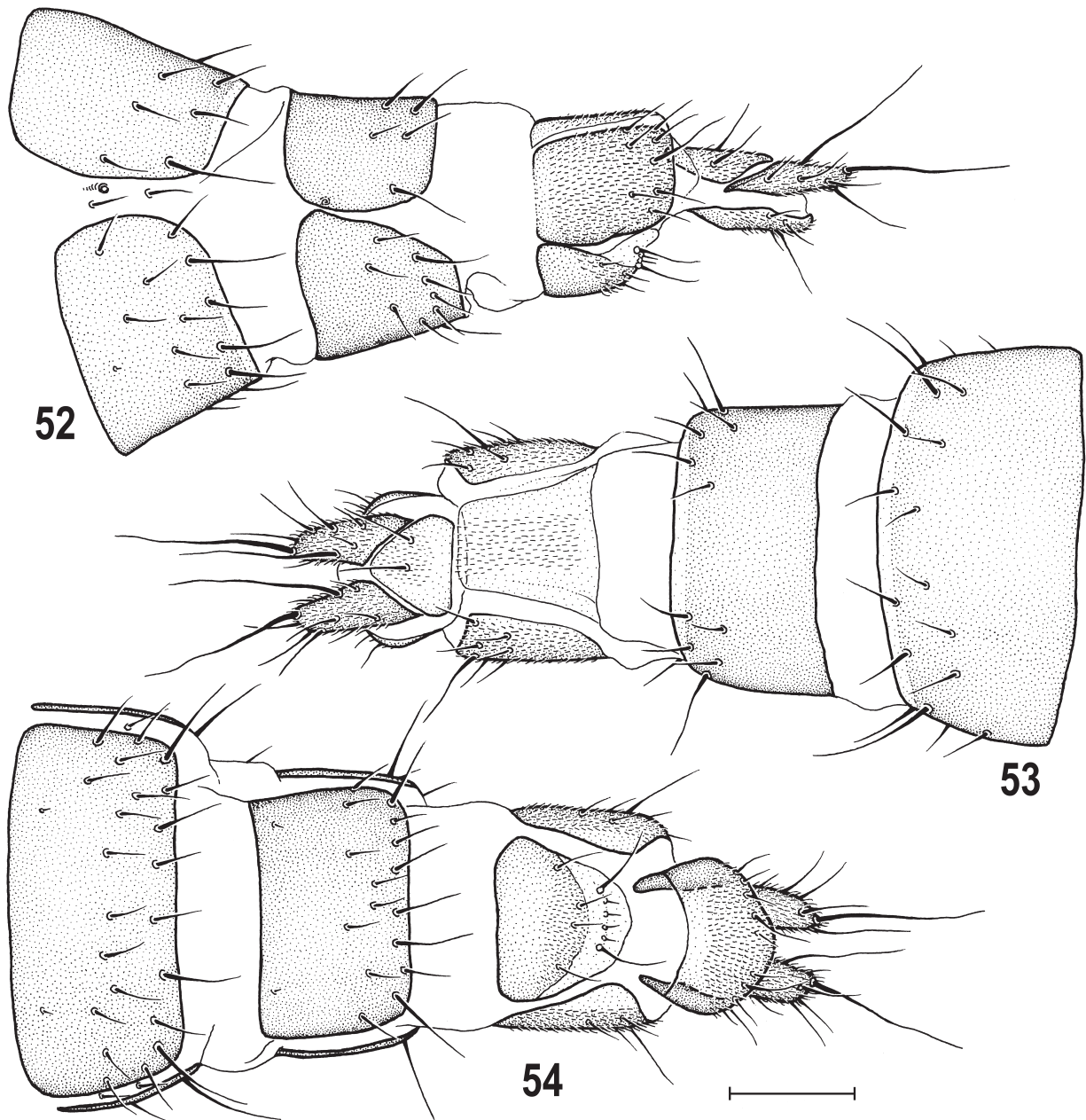
Figs 40–45. *Pteremis pulliceps* sp. nov. and its habitats. 40 – male, holotype, left laterofrontally; 41 – labels of the holotype; 42 – holotype, head and thorax, left laterofrontally; 43 – right wing, male paratype; 44 – type locality: upper part of valley of Ribeira de Janella nr. Rabaçal, Madeira; 45 – microhabitat of the species, leaf litter in laurel forest nr. Rabaçal. Scales = 0.5 mm. Photo by J. Roháček.

53); *T8* markedly longer, with distinctive pale-pigmented dorsomedial part being more or less distinctly separated from dark lateral parts, posteriorly tapered and only medially micropubescent (Fig. 53). *T10* subtriangular rather than pentagonal and shorter than cercus (Fig. 53). Both *S6* and *S7* relatively longer (less transverse) than in *P. fenestralis* (Fig. 54). *S8* (Figs 54, 59) distinctly longer, elongately trapezoidal, with pigmented anterior part provided with 2 pairs of short and weak setae; its posterior submembranous part relatively long, posteriorly tapered and rounded, and

having 2 long (lateral) setae and 4 more medial setulae (all on elevated sockets) arranged in a transverse row (Fig. 59). *S10* (in largest extension, Fig. 60) relatively longer (less transverse), with shorter setae, and lateral parts more projecting anteriorly than in *P. fenestralis*. Spectacles-shaped sclerite represented by a pair of unusually small ovoid rings (Fig. 58). Spermathecae 2+1 (Fig. 61) clearly different from those of *P. fenestralis* and more resembling those of *P. canaria*, particularly by wider basal conical part being separated from distal subcircular part by 3 or



Figs 46–51. *Pteremis pulliceps* sp. nov., male, paratype. 46 – external genitalia, left laterally; 47 – ditto, caudally (aedeagal complex and left gonostylus omitted); 48 – gonostylus, laterally; 49 – apex of cercus, left laterally; 50 – aedeagal complex, laterally; 51 – male S5, ventrally. Scales = 0.05 mm (Figs 46, 47, 50), 0.03 mm (Figs 48, 49), 0.1 mm (Fig. 51).



Figs 52–54. *Pteremis pulliceus* sp. nov., female, paratype. 52 – postabdomen, laterally; 53 – ditto, dorsally; 54 – ditto, ventrally. Scale = 0.1 mm.

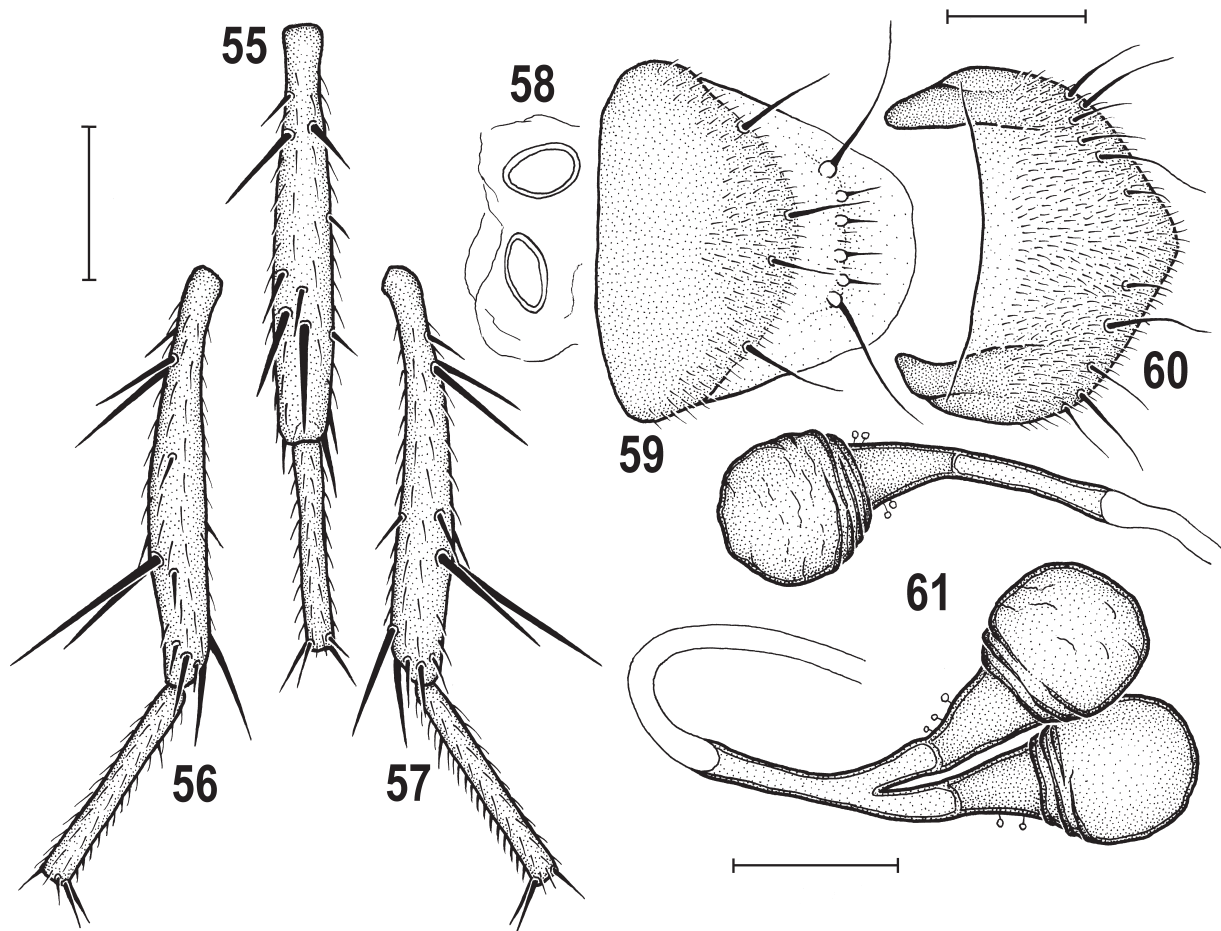
4 (some incomplete) rings and by dark terminal parts of ducts thicker and those of paired spermathecae joined near conical parts of spermathecae (Fig. 61). Cerci (Figs 52, 53) longer than *T10*, more tapered towards apex, and less dorsoventrally flattened, having dorsopreapical sinuate seta as long as apical seta.

Etymology. The species is named *pulliceus* (a compound adjective formed from Latin *pullus* = dark + *-ceps* = headed) because of its distinctly darkened head, face in particular.

Comments. *Pteremis pulliceus* sp. nov. externally most resembles *P. fenestralis* but is generally darker (particularly on frons and face), mid tibia has *va* seta shorter and one posterior subapical seta enlarged (Fig. 56). However, its most diagnostic characters, distinguishing it from all

other relatives, are in the male and female terminalia: epandrium broad; male cercus bulging dorsolaterally and with characteristically formed apex (Figs 47, 49); anterior lobe of gonostylus with 4 (not 3) robust curved setae anteroventrally and its ventral projection slender, with finely trifurcate apex (Fig. 48); posterior lobe of gonostylus with terminal spine unusually long and slender; female *T8* relatively long, its dorsomedial part long, pale-pigmented and separated from dark lateral parts (Fig. 53); female *S8* elongate, having posterior submembranous part relatively long and bearing 2 long (lateral) setae and 4 small medial setulae arranged in a transverse row (Fig. 59); spectacles-shaped sclerite represented by a pair of unusually small ovoid rings (Fig. 58).

Judging from the very similar mid leg chaetotaxy and



Figs 55–61. *Pteremis pulliceps* sp. nov., male, female, paratype. 55 – male left t_2 and mt_2 dorsally; 56 – ditto, posteriorly; 57 – ditto, anteriorly; 58 – spectacles-shaped sclerite, ventrally; 59 – S_8 , ventrally; 60 – S_{10} , ventrally; 61 – spermathecae. Scales = 0.2 mm (Figs 55–57), 0.05 mm (others).

structure of male S_5 *P. pulliceps* seems to be the closest relative of *P. fenestralis*. However, the shape and structure of its spermathecae (pyriform, with ringed surface) are arguably synapomorphic with those of *P. canaria* and *P. ferreus* sp. nov. (both from Canary Is.) and possibly also with *P. apterina* sp. nov.

Biology. Type specimens of *P. pulliceps* sp. nov. were largely collected in humid forested habitats in several localities of Madeira, mostly along levadas or near to springs, some specimens also at creeks or rivers, at 600–1,100 m, all in September. Fifteen specimens were sifted from leaf litter in native laurel forest (Figs 44, 45) considered to be the original habitat of this terricolous species; others were swept from low vegetation or from just above the rotten leaves and other vegetation on ground in wet places in secondary woods or under trees in semi-open habitats. The original microhabitat (leaf detritus in laurel forest) of *P. pulliceps* is shared with endemic *Pullimosina* Roháček, 1983 and *Spelobia* Spuler, 1924 species, e.g. in Rabaçal, the type locality of *P. pulliceps*, *Pullimosina kelsoni* Roháček, 2019 and *Spelobia polymorpha* Roháček, 2019 (see ROHÁČEK 2019b).

Distribution: Madeira. The species is considered endemic to this island.

Pteremis tenebricus sp. nov.

(Figs 62–74)

Type material. HOLOTYPE: ♂ (DEBU), labeled: 'SPAIN: Sierra Nevada, Hwy, 2270m; 11.viii.86, J.R.Vockeroth; under grass of dry stream' and 'Holotypus ♂ *Pteremis tenebricus* sp. n., J. Roháček des. 2023' (red label) (Fig. 63). The specimen (see Fig. 62) is dry mounted on triangular pinned card, with abdomen (dissected) and left wing removed and all detached parts preserved in glycerine in coalesced plastic tube pinned below specimen.

Description. Male (Figs 62, 64). Total body length 2.22 mm; general colour blackish brown (darkest of all fully winged *Pteremis* species) with dark greyish brown microtomentum but subshining dorsally on thorax and abdomen.

Head (Figs 62, 64) about 1.55× higher than long, largely dark brown to (posteriorly) almost black. Frons with microtomentose pattern similar to that of *P. fenestralis* but darker, all dark brown to blackish, only anteriorly narrowly brown to reddish brown. Orbits, interfrontalia and frontal (including ocellar) triangle with (rather dark) silvery grey and slightly glittering microtomentum; stripes surrounding (very) narrow interfrontalia almost black, with dull dark grey (with some bluish tinge) microtomentum, forming incomplete (medially interrupted) M-shaped mark; frontal triangle recognized by somewhat glittering microtomentum and reaching to anterior fifth of frons; anterior margin of



Figs 62–66. *Pteremis tenebricus* sp. nov., male holotype. 62 – whole specimen after dissection (most of abdomen and left wing removed), left laterally; 63 – labels of the holotype; 64 – head and thorax, left laterofrontally; 65 – left wing; 66 – left mid tibia, anteriorly. Scales = 0.5 mm. Photo by J. Roháček.

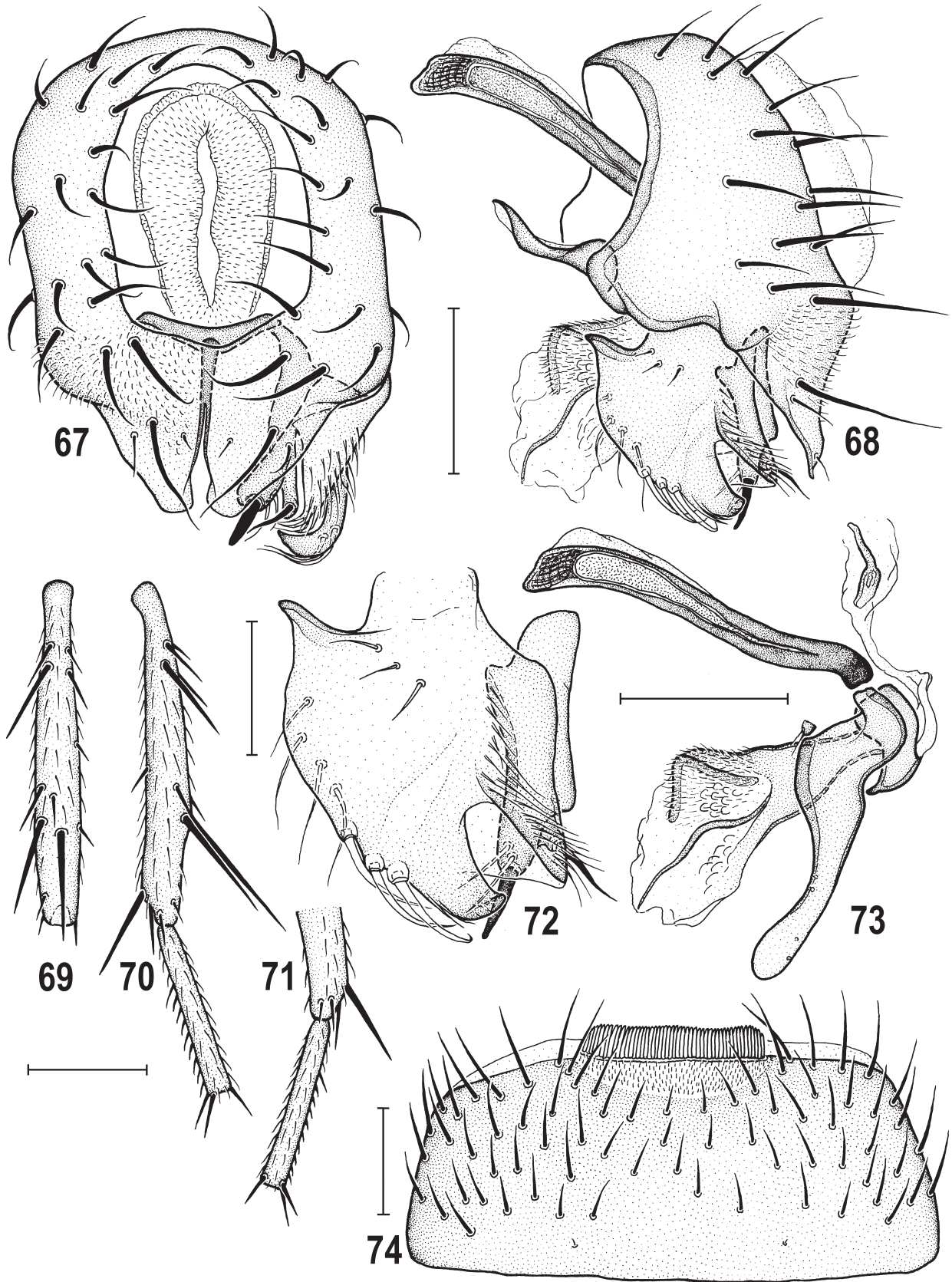
frons only medially and laterally narrowly brown to reddish brown. Frontal lunule pale brown and pale grey microtomentose (lightest of head structures) and contrasting with darker brown face, the latter sparsely grey microtomentose and subshining; medial carina poorly developed. Gena concolorous with face, brown to dark brown and dark dull microtomentose; postgena with shining black perpendicular stripe. Cephalic chaetotaxy (Fig. 64) closely resembling that of *P. fenestralis* but *pvt* weak, with apices meeting medially; *occe* and *occi* subequal but *occi* only very slightly inclinate; *vti* longest of frontal bristles, somewhat longer than *vte*; *oc* only as long as *occe*; posterior *ors* slightly longer than *oc* and about 1.5 times as long as anterior *ors*; 3 strong (all medially meeting or crossed) + 1 small (foremost) *ifr* (the latter on right side only); 3 or 4 distinct *ads*; *g* relatively robust and also 2 setae behind longer than peristomals; both *vi* lost in holotype but obviously very long and robust; 6 short peristomal setulae and also both postgenal setae weak, slightly longer than peristomals. Eye subcircular (23:21), with longest diameter 3.9 times as long as smallest (anterior) genal height. Antenna dark brown, with pedicel darkest; 1st flagellomere with whitish ciliation on apex only slightly longer than cilia on arista. Arista about 3.7 times as long as antenna, with very short dense ciliation.

Thorax as in *P. fenestralis* but generally darker brown, also notopleural area, sutures between pleural sclerites and ventral part of sternopleuron brown (Figs 62, 64). Thoracic chaetotaxy almost identical to that of *P. fenestralis*, only

outer *pa* distinctly longer than *dc* and/or laterobasal *sc* (length of apical *sc* unknown because both setae are broken off) and only 1 long (posterior) *stpl* visible because anterior *stpl* is reduced to a hardly discernible microseta.

Legs distinctly darker and less variegated than those of *P. fenestralis*, having also trochanters, tibiae and tarsi brown or dark brown, only knee of fore leg, mid trochanter and tarsus pale brown or ochreous. Pedal chaetotaxies differing from those of *P. fenestralis* as follows: f_2 anteriorly with a short subapical row of 3 robust but short setae. t_2 dorsally (Figs 69, 70) with all macrosetae more robust, and longest distal dorsal (or slightly posterodorsal) seta inserted more distally than long distal anterodorsal (Fig. 69); *va* seta distinctly shortened, only about half length of *vpa* and much weaker (see Figs 66, 70), and posterior subapical seta more robust although short (Fig. 71). Ratio $t_2 : mt_2 = 1.92$.

Wing probably largest (compared to body) of all *Pteremis* species (Fig. 62), relatively long, distally less rounded and its membrane less brownish clouded (Fig. 65). *C* produced far beyond apex of R_{4+5} . R_{4+5} distinctly sinuate but its distal half somewhat straightened (less curved) than in *P. fenestralis* and anterior outer corner of *dm* cell more obtuse-angled. A_1 well visible (distinctly pigmented) in its distal sinuate part (Fig. 65). Anal lobe and alula also somewhat larger than those of *P. fenestralis*. Wing measurements: length 2.18 mm, width 0.95 mm, *C-index* = 1.28, $r-m \setminus dm-cu$: $dm-cu$ = 2.29. Haltere brown, darker on knob paler on stem and all light grey microtomentose.



Figs 67–74. *Pteremis tenebricus* sp. nov., male, holotype. 67 – external genitalia, caudally (aedeagal complex, left gonostylus and micropubescence of right cercus omitted); 68 – ditto, left laterally; 69 – left t_2 , dorsally; 70 – left t_2 and mt_2 , anteriorly; 71 – apex of left t_2 and mt_2 , posteriorly; 72 – gonostylus, laterally; 73 – aedeagal complex, laterally; 74 – male S_5 , ventrally. Scales = 0.1 mm (Figs 67, 68, 73, 74), 0.2 mm (Figs 69–71), 0.05 mm (Fig. 72).

Abdomen blackish brown, largely constructed as in *P. fenestralis* and with similar setosity. Owing to damage, only posterior half of preabdomen and postabdomen can be described. *T4* more transverse than that of *P. fenestralis* but *T5* similar in both species. Also *S3* and *S4* as those of *P. fenestralis*, thus *S4* longest and widest abdominal sternum. However, *S3* and *S4* with more and stronger short setae than those on disc of adjacent terga but setae in posterior corners of *S3* and *S4* short and weak. *S5* (Figs 74) distinctly shorter and narrower than *S4*, thus less transverse than that of *P. fenestralis* and, in contrast to the latter, relatively densely, shortly and uniformly setose, with only setae at posterior margin somewhat longer and with small (shortened) pale-pigmented and finely micropubescent shortly crescent-shaped area in front of simple but dense posteromedial comb of fine spines. *S6+7* strongly asymmetrical, with usual transverse dark-pigmented ledge but original *S7* with dark posteroventral projection (longer and darker than that of *P. fenestralis*) bent inside postabdomen; *S6+7* with 3 + 2 distinct setae but *S8* with only a pair of setulae, yet smaller than those of *P. fenestralis*.

Genitalia. Epandrium (Figs 67, 68) similarly formed as in *P. fenestralis* but more rectangular in caudal view (Fig. 67), with slightly wider anal fissure. Cerci markedly different from those of both *P. fenestralis* and *P. pulliceus*, prolonged and flattened ventrally, in lateral view (Fig. 68) most resembling those of *P. canaria* but the flattened apex of cercus pale-pigmented and bare, without micropubescence (Fig. 67). Medandrium largely as in *P. fenestralis*. Hypandrium (Fig. 68) with medial apodeme longer and more robust than in *P. fenestralis* but strongly asymmetrical as in all relatives. Gonostylus (Figs 67, 68, 72) larger, compared to epandrium, than in all other *Pteremis* species. Similar to *P. fenestralis* and some other species in having anterior lobe (Fig. 72) with short pointed anterodorsal process but differing from all of them by very robust, distally darkened ventral, posteromedially curved (see Fig. 67) projection having simply pointed apex, and by 3 short external setae dorsally, behind anterodorsal pointed process. Posterior lobe of gonostylus (dotted in Fig. 72) relatively small and with terminal spine slender. Aedeagal complex (Fig. 73) characterized by (dorsoventrally) short phallopore having short but acutely pointed projection on apex. Distiphallus relatively slender (its base in particular) but distally dilated, more than in *P. fenestralis* and with lateral membrane between slender band-like lateral and dorsal sclerites with some pale tubercles among micropubescence (Fig. 73). Postgonite most similar to that of *P. pulliceus* but distally yet more slender (less dilated) and proximally with distinct posterior emargination (Fig. 73). Ejacapodeme larger and with longer and slender distal digitiform, somewhat sinuate process (see Fig. 73).

Female unknown.

Etymology. Named for its unusually dark body colouration. The name is a Latin adjective *tenebricus* (= dark, gloomy).

Comments. *Pteremis tenebricus* sp. nov. is surely the darkest species of the *P. fenestralis* alliance. It differs from relatives also by more elongate wings with less rounded

apex and has *va* seta on mid tibia only about half length of *vpa* seta, thus shorter than that of *P. pulliceus* sp. nov. but longer than that of *P. ferreus* sp. nov. It is best characterized by a shortened pigmented area in front of posteromedial comb of spines (Fig. 74) of male *S5* and by a relatively large (compared to epandrium) gonostylus having particularly enlarged and medially curved ventral, posteromedially directed projection of its anterior lobe (Fig. 72). However, it differs from other species also by detailed formation and structures of male cercus and aedeagal complex (phallopore, distiphallus, postgonite). Unfortunately, the female of *P. tenebricus* remains unknown. It would be particularly important to know the shape and armature of its *S8* and spermathecae to recognize if it is more closely related to *P. fenestralis* or to *P. pulliceus*.

Biology. The only known specimen was collected on 11th August 'under grass of dry stream' in high montane habitat (2,270 m a.s.l.) of the Sierra Nevada Mts. Interestingly, this male holotype was captured by J. R. Vockeroth together with 2 ♂♂ 2 ♀♀ of true *Pteremis fenestralis*.

Distribution. Spain (Sierra Nevada Mts).

Pteremis canaria (Papp, 1977)

(Figs 75–78, 81–97)

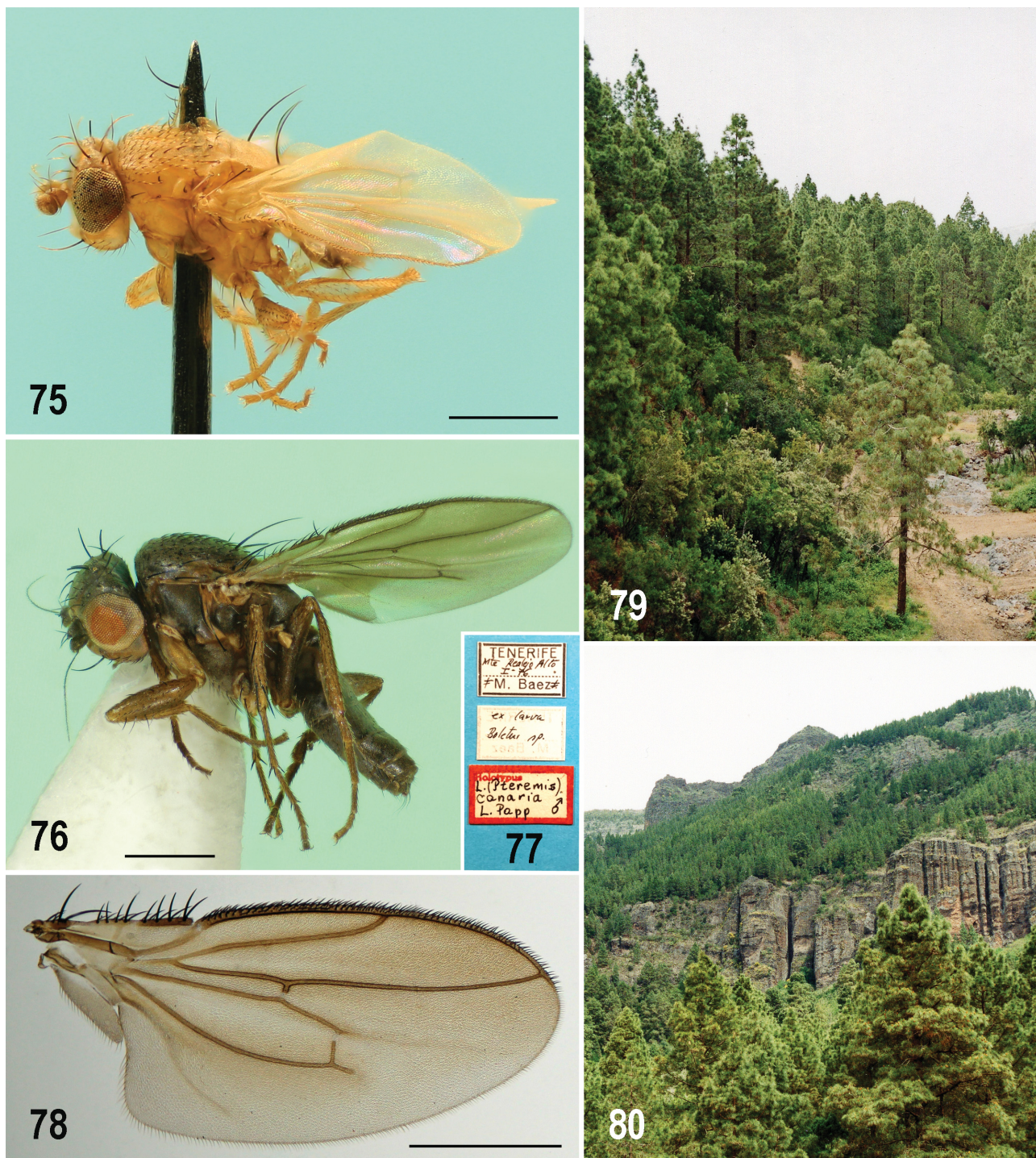
Leptocera (*Pteremis*) *canaria* Papp, 1977: 126 (both sexes, illustr.). Type locality: Canary Islands, Tenerife, Mte Realejo Alto. HT male (ULCI). *Pteremis canaria*: PAPP (1982): 130 (generic combination); PAPP (1984): 87 (Palaearctic catalog); ROHÁČEK et al. (2001): 210 (World catalog); ROHÁČEK et al. (2003): 61 (additional records).

Type material examined. HOLOTYPE: ♂ (ULCI), labelled: 'TENERIFE, Mte Realejo Alto, 1-76, ≠ M. Baez ≠' (obverse) and 'ex larva Boletus sp.' (reverse) and 'Holotypus L. (*Pteremis*) *canaria* L. Papp ♂' (red-framed label with red printed 'Holotypus') (see Fig. 77). The specimen is intact, but immature (Fig. 75), minutia-pinned on oblong card. PARATYPES: SPAIN: CANARY ISLANDS: TENERIFE: 1 ♂, 'TENERIFE, Las Lagunetas, 25-I-74, ≠ M. Baez ≠' (obverse), 'ex - larva on „Boletus“' (reverse) (immature specimen with abdomen mounted on microslide pinned below specimen, ULCI); 1 ♂, 'TENERIFE, Cumbre de Realejo Bajo, 1-11-73, M. Baez' (HNHM, genit. prep.). Both paratypes with type and determination labels as in holotype but with red printed 'Paratypus'. Paratype ♀ (not examined), with same data as the above paratype male from Las Lagunetas (HNHM, see PAPP 1977: 126).

Additional material examined. SPAIN: CANARY ISLANDS: TENERIFE: Las Lagunetas, 29.i.1974, 1 ♀ ex larva on *Boletus*, 19.xii.1973; Tenerife, Realejo Alto, 19.ix.1978, 1 ♀, both M. Baez leg. (ULCI); Tenerife, Aguanansa nr. Orotava 1 km S, sweeping vegetation along brook in ravine, 12.v.1999, 2 ♀♀ (1 ♀ genit. prep.), J. Roháček leg. (SMOC).

Redescription. Male. Because the holotype and one male paratype are immature, pale-pigmented specimens, the only other available male (paratype from HNHM) can be used for description of colour characters. Total body length 1.59–1.79 mm; general colouration and microtomentum of body as in *P. fenestralis*, or somewhat lighter, brown to dark brown.

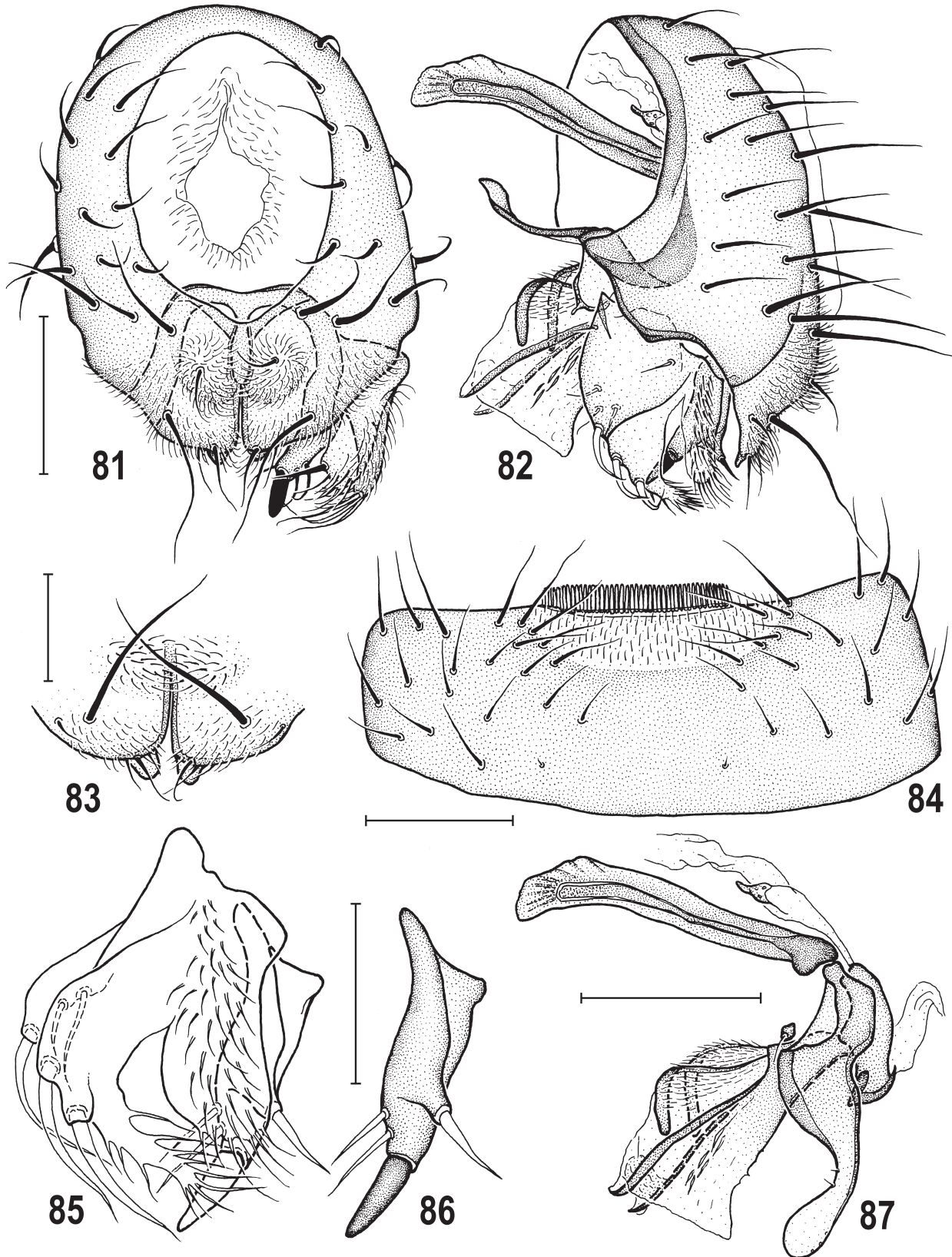
Head (cf. Figs 75, 76) almost 1.6× higher than long (thus shorter than in *P. fenestralis*), darker posterodorsally, paler anteroventrally. Frontal pattern is characterized by pale brown (to ochreous) orbits, interfrontalia and frontal triangle, and darker (blackish brown) stripes surrounding them and almost forming M-shaped mark; also occiput dark brown and all frons grey microtomentose, only interfrontalia with microtomentum lighter, pale to silvery grey; frontal



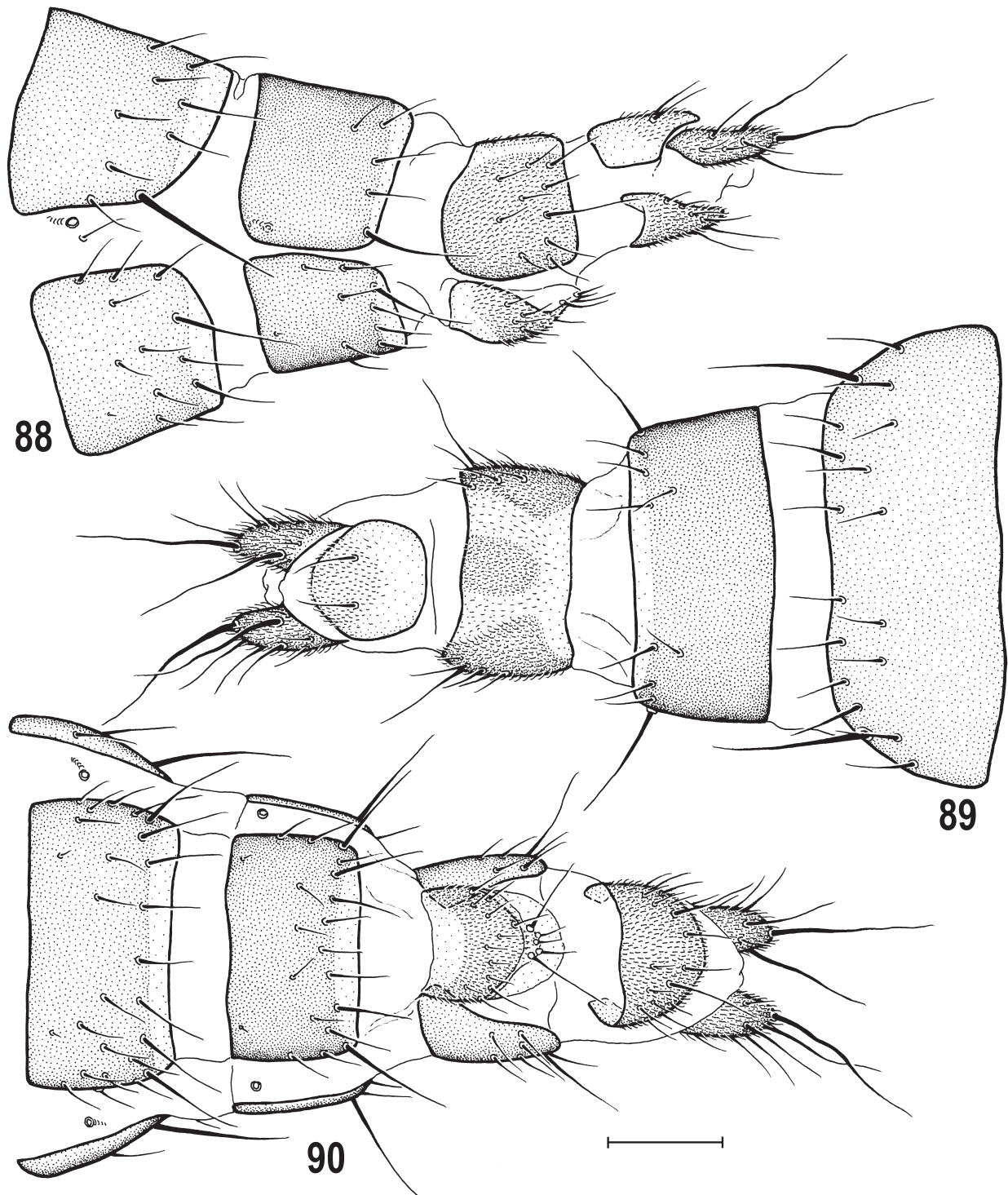
Figs 75–80. *Pteremis canaria* (Papp, 1977) and its habitats. 75 – male, holotype, left laterally; 76 – female (Canary Is, Tenerife, Aguamansa nr. Orotava), left laterally; 77 – labels of the holotype (locality label with obverse and reverse); 78 – right wing, female (from Aguamansa); 79 – valley of a dry brook in a pine forest, habitat of *P. canaria* near Aguamansa; 80 – pine forests (*Pinus canariensis*) in the vicinity of Aguamansa. Scales = 0.5 mm. Photo by M. Deml (76) and J. Roháček (others).

triangle pale as orbits, thus well delimited and reaching to anterior fourth or fifth of frons; anterior margin of frons brown, in contrast to pale ochreous or dirty yellow frontal lunule. Face usually dirty yellow (but it can be unnaturally darkened in some specimens), whitish grey microtomentose; medial carina poorly developed as in *P. fenestralis*. Gena yellowish ochreous and all microtomentose and separated from occiput by dark glossy perpendicular stripe on postgena (as in *P. fenestralis*). Cephalic chaetotaxy

closely resembling that of *P. fenestralis* but differing as follows: *pvt* minute (smaller than in *P. fenestralis*) but with apices meeting medially; *occi* longer than *occe* but markedly shorter than *vti*; 3 *ifr*, two anterior pairs longer and more robust, and sometimes with 1 microseta in front of anterior *ifr*; *g* usually longer than anterior peristomal setula and 1 or 2 setae behind as long as peristomals; *vi* very long and robust, often slightly longer than *vti*; about 5 sparse peristomal setulae being almost as long as 2 post-



Figs 81–87. *Pteremis canaria* (Papp, 1977), male, paratype. 81 – external genitalia, caudally (aedeagal complex and left gonostylus omitted); 82 – ditto, left laterally; 83 – apical parts of cerci, ventrocaudally; 84 – male S5, ventrally; 85 – gonostylus, left sublaterally; 86 – posterior lobe of gonostylus, left laterally; 87 – aedeagal complex, laterally. Scales = 0.1 mm (Figs 81, 82, 84, 87), 0.05 mm (others).



Figs 88–90. *Pteremis canaria* (Papp, 1977), female (Tenerife, Aguamansa nr. Orotava). 88 – postabdomen, laterally; 89 – ditto, dorsally; 90 – ditto, ventrally. Scale = 0.1 mm.

genal setae. Eye subcircular (18:17), with longest diameter about 4 times as long as smallest genal height. Antenna with scape and 1st flagellomere only slightly lighter than pedicel; 1st flagellomere and arista similarly ciliate as those of *P. fenestralis*, the latter about 3.8 times as long as antenna.

Thorax dark brown to ochreous and grey microtomentose; mesonotum dark brown but humeral callus and notopleural area pale brown to ochreous; pleuron brown to (sternopleuron) pale brown, sutures between pleural

sclerites and also ventral corner of sternopleuron can be pale ochreous. Scutellum large, flat and formed as in *P. fenestralis*. Thoracic chaetotaxy as in *P. fenestralis* but 1 *hu* longer than anterior *npl*; 1 *prs* as long as anterior *npl* and 1 shorter *sa*; the outer *pa* as long as *dc*, the latter relatively longer than that of *P. fenestralis*; 4 or 5 *dc* microsetae in front of *dc* distinctly longer than *ac* microsetae; 6 or 8 rows of *ac* microsetae on suture; 2 very long and robust *sc*, laterobasal longer than that of *P. fenestralis* because

apical *sc* only 1.2–1.4 times as long as laterobasal; only 1 distinct and very long *stpl* because anterior *stpl* is reduced to a hardly visible microsetula or is absent.

Legs (in contrast to those of *P. fenestralis*) uniformly coloured, ochreous to brown, with trochanters, tibiae and tarsi very little or not paler than femora and coxae (cf. Fig. 76); tibiae not variegated, i.e. without lighter basal and apical ends. Chaetotaxy of femora and tibiae as in *P. fenestralis* but t_2 ventrally (see Figs 95, 97) with only 2 setae, 1 long and strong *vpa* and 1 short and weak *av* near middle, i.e. *va* seta absent; dorsally (Fig. 96) with the same setae as in *P. fenestralis* but distal anterodorsal seta longer; apex of tibia provided with only 2 short (1 longer) subapical setae anteriorly (Fig. 97) and 2 posteriorly (Fig. 95). Mid basitarsus (mt_2) often with 1 enlarged ventral setula (see Fig. 97). Ratio $t_2 : mt_2 = 1.85–1.94$.

Wing always normally developed (cf. Fig. 78). Membrane distinctly brownish fumose, more darkened along some veins. Wing relatively broad, with venation closely resembling that of the macropterous form of *P. fenestralis* but *C* less produced beyond apex of R_{4+5} , the sinuate A_1 darker pigmented and alula with apex more rounded. Wing measurements: length 1.54–1.69 mm, width 0.66–0.73 mm, *C-index* = 0.81–0.92, $r-m \setminus dm-cu : dm-cu = 1.85–2.08$. Haltere with pale ochreous stem and brown knob having often lightened apex.

Abdomen constructed, coloured and setose similarly as that of *P. fenestralis* but slightly differing as follows: $T1+2$ (largest tergum) posteriorly as wide as or slightly wider than $T3$. Seta in posterior corner of $T5$ very long and robust, longer than this sclerite. $S1+2$ (or $S2$) larger, posteriorly as wide as $S3$ anteriorly, ochreous in contrast to all subsequent abdominal sterna. $S5$ (Fig. 84) distinctly shorter than $S4$ and also somewhat shorter and more transverse than that of *P. fenestralis*, characterized by short and sparsely micropubescent pale area in front of posteromedial comb of more numerous and denser spines; setae laterally surrounding posteromedial pale area and also those on lateral parts of $S5$ relatively sparse. Postabdominal sterna ($S6–S8$) very similar to those of *P. fenestralis* including setae.

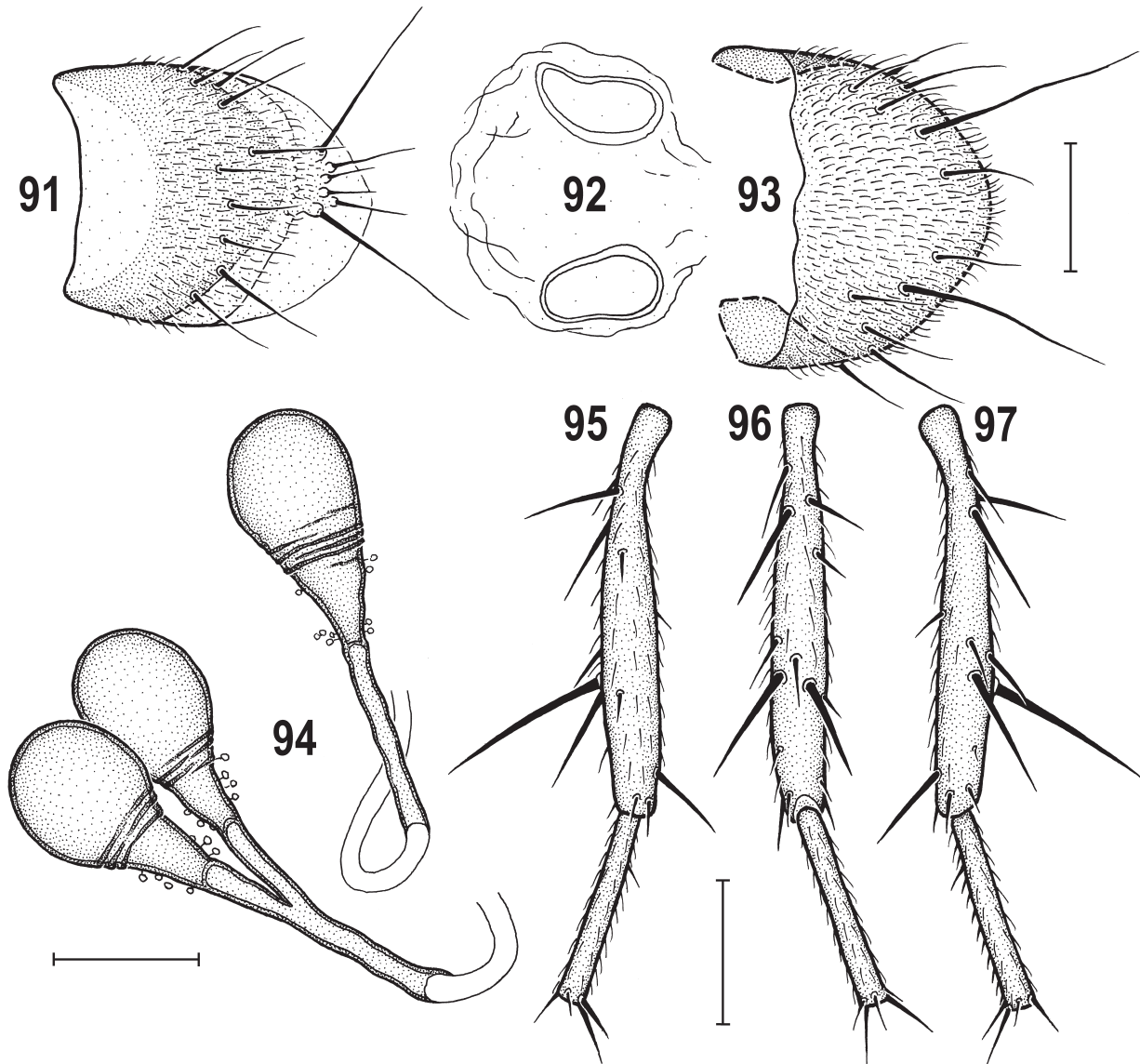
Genitalia. Epandrium (Figs 81, 82) somewhat shorter and narrower in caudal view (Fig. 81) and anal fissure distinctly wider and more rounded than in *P. fenestralis*. Cerci distinguished by characteristic micropubescent (in two separate groups: on convex posteromedial part and on distal part), medially separated with relatively short but very narrow incision. Each cercus terminated by a small rounded and bare lappet (see Fig. 83) and with 1 long sinuate subventral seta, 1 shorter seta more dorsally and 2 short setae near apex, close to above lappet. Medandrium low (short) and broad as in *P. fenestralis* but with posteromedial part not darker than other parts of sclerite (Fig. 81). Hypandrium with distinctly longer and somewhat curved but also strongly asymmetrical flattened anterior apodeme (Fig. 82). Gonostylus (Figs 82, 85) having anterior lobe without projecting anterodorsal process, with only a corner (cf. Fig. 82), 3 curved anteroventral setae more robust, and posteriorly directed ventral projection spiky jagged and pale-pigmented (Fig. 85); posterior lobe

of gonostylus differing from that of *P. fenestralis* by shorter and more robust seta on posterior subconical process (see Fig. 86). Aedeagal complex (Fig. 87) with phallopore more acute ventrally, distiphallus (dorsoventrally) distally dilated and postgonite distally elongately spatulate, with apex rounded; its minute anterodorsal sclerite (= remnant of pregonite) very small. Ejacapodeme also very small, as in *P. fenestralis*.

Female. Head, thorax, legs and wings as in male unless mentioned otherwise below. Total body length 1.82–2.26 mm. Body colouration (thorax in particular) somewhat darker (Fig. 76). Anterior fourth or third of frons sometimes (seen in one specimen) orange ochreous and concolorous with frontal triangle, interfrontalia and orbits. Frons with 3 or 4 *ifr* setae and *ads* more distinct. Prescutellar *ac* microsetae (2 pairs) often somewhat enlarged (as in *P. fenestralis*) and anterior *stpl* sometimes represented by well-developed microseta. Mid basitarsus relatively longer: ratio $t_2 : mt_2 = 1.71–1.80$. Wing measurements: length 1.91–2.04 mm, width 0.83–0.91 mm, *C-index* = 0.87–1.08, $r-m \setminus dm-cu : dm-cu = 1.88–2.31$. Abdomen generally as in *P. fenestralis* but $S1+2$ longer and wider (as in male), with reduced setosity; $S3$ and $S4$ subequal in length and $S5$ distinctly shorter than $S4$ (only slightly longer than $S1+2$).

Postabdomen (Figs 88–90) generally similar to that of *P. fenestralis* but with $T6$ and $T7$ more transverse (Fig. 89), the latter with pale posterior margin; $T8$, on the contrary, longer and less transverse (and more distinctly micropubescent) and $T10$ more rounded (Fig. 89). $T7$ and $S7$ almost meeting laterally (Fig. 88). $S6$ more suboblong, markedly narrower than $T6$ and with pale-pigmented posterior margin; $S7$ only a little narrower than $S6$ (Fig. 90) dark-pigmented but with marginal pale-pigmented posterior band. $S8$ (Figs 90, 91) distinctive, longer than broad, pale-pigmented both anteriorly and posteriorly, with more but fine setae in the middle, and with a posteromedial group of 6 (2 more lateral long, 4 medial short) setae on elevated sockets (Fig. 91). $S10$ (in largest extension) wider than $S8$, more elongate and tapered posteriorly than that of *P. fenestralis*, and with projecting anterolateral corners (Figs 88, 93), setose along posterior margin including 2 long setae. Spectacles-shaped sclerite represented by distinct but unpigmented ovoid rings (Fig. 92). Spermathecae 2+1 (Fig. 94) blackish, pyriform, each having basal conical part separated from spherical body by 3 or more transverse (usually incomplete) rings; terminal parts of ducts long, but thicker than those of *P. fenestralis* and those of paired spermathecae connected close to body of spermatheca. Cerci (Figs 88, 89) relatively robust and rather conical, only slightly dorsoventrally flattened (see Fig. 88) in contrast to those of *P. fenestralis*.

Comments. *Pteremis canaria* was originally described from a series collected by M. Báez in Tenerife (PAPP 1977). However, it was later also recorded from two other islands of the Canarian archipelago, viz. Gran Canaria (PAPP 1982) and El Hierro (PAPP 1982, ROHÁČEK et al. 2003). During this study specimens from El Hierro proved to belong to a different species, *P. ferreus* sp. nov., described below. Unfortunately, the only specimen (male) recorded by PAPP (1982) from Gran Canaria (Barranco de Firgas) has not



Figs 91–97. *Pteremis canaria* (Papp, 1977), female (Tenerife, Aguamansa nr. Orotava). 91 – *S8*, ventrally; 92 – spectacles-shaped sclerite, ventrally; 93 – *S10*, ventrally; 94 – spermathecae; 95 – left t_2 and mt_2 , posteriorly; 96 – ditto, dorsally; 97 – ditto, anteriorly. Scales = 0.05 mm (Figs 91–94), 0.2 mm (others).

been traced so that its true identity remains unknown; it could possibly represent another unnamed species.

Pteremis canaria is best characterized by pale brown (to ochreous) orbits, interfrontalia and frontal triangle, entire absence of *va* seta on t_2 (Fig. 97), *S5* (Fig. 84) with short, broad and sparsely micropubescent pale area in front of posteromedial comb spines, male cercus with micropubescent in two separate groups (Fig. 81) and ventroapically with small rounded and bare lappet (Fig. 83), anterior part of gonostylus with ventral projection unusually spiky jagged and pale-pigmented (Fig. 85), female *S8* (Figs 90, 91) longer than broad and with more fine setae in the middle than in relatives and spermathecae pyriform, with 3 or more transverse surface rings.

The shape and structure of female *S8* and of spermathecae indicate affinity of *P. canaria* to *P. pulliceps* sp. nov.; also apex of ventral process of anterior lobe of gonostylus

can be considered similar in both species, in having apex more or less spiky (cf. Figs 48 and 85).

Biology. All eight specimens of *P. canaria* hitherto found in Tenerife were collected in native pine (*Pinus canariensis*) forests (Figs 79, 80), including those (2 ♂♂ 2 ♀♀) reared from larvae found in sporocarps of *Boletus* sp. (M. Báez, personal communication, 2023). Hitherto, no specimens of this species have been found in laurel forests in Tenerife despite much collecting effort in this habitat (cf. ROHÁČEK et al. 2003). Consequently, *P. canaria* seems to really be closely associated with *Pinus canariensis* forests and probably develops in fungi.

Distribution. Canary Is.: Tenerife. *P. canaria* is to be considered endemic to Tenerife I. The *Pteremis* specimens from El Hierro proved to belong to a different species (see below) while specimen from Gran Canaria requires revision (see above).

***Pteremis ferreus* sp. nov.**

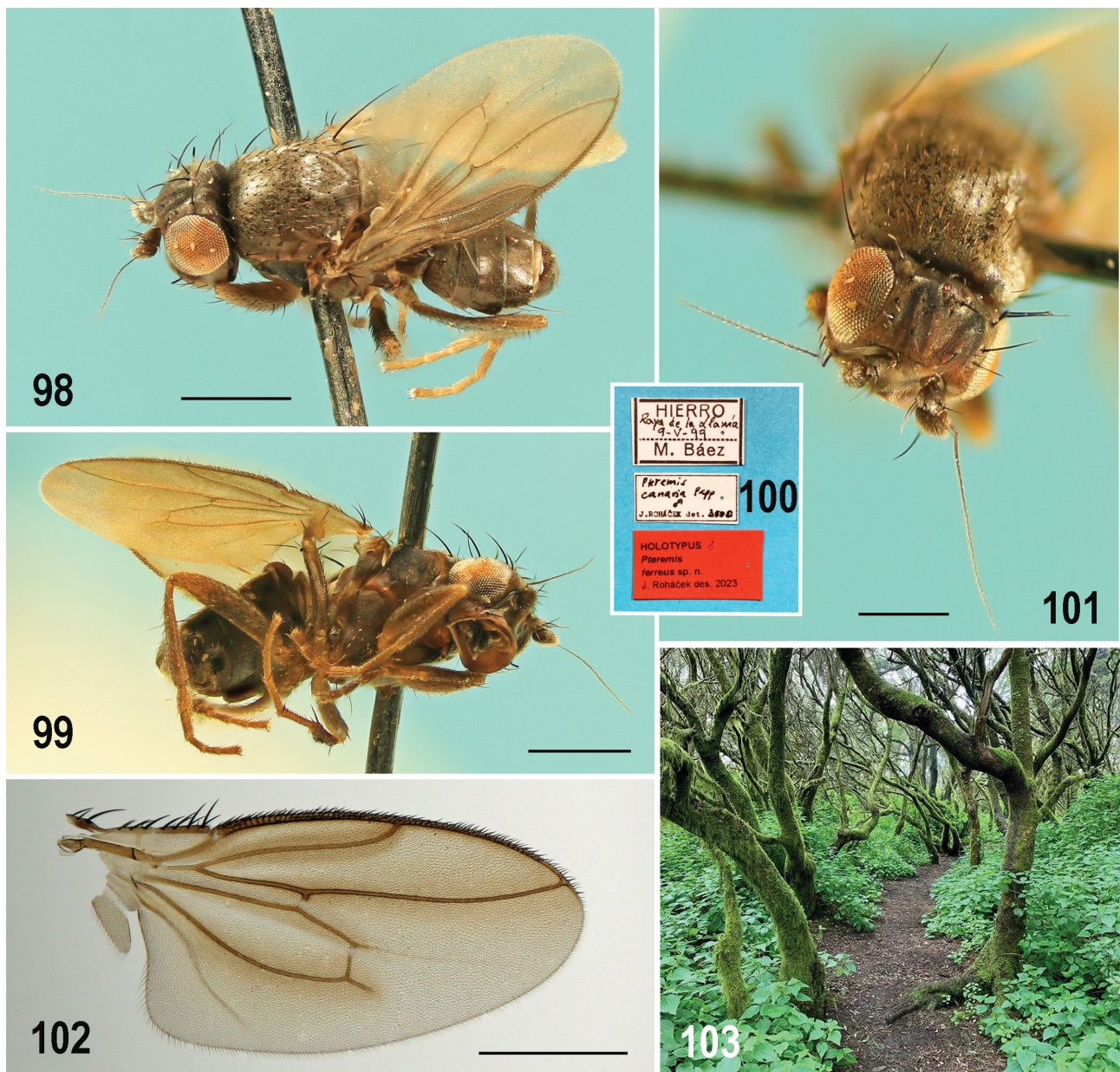
(Figs 98–102, 104–118)

Pteremis canaria (in part.): PAPP (1982): 130 (record from El Hierro, misidentification); ROHÁČEK et al. (2003): 62 (record from El Hierro, misidentification).

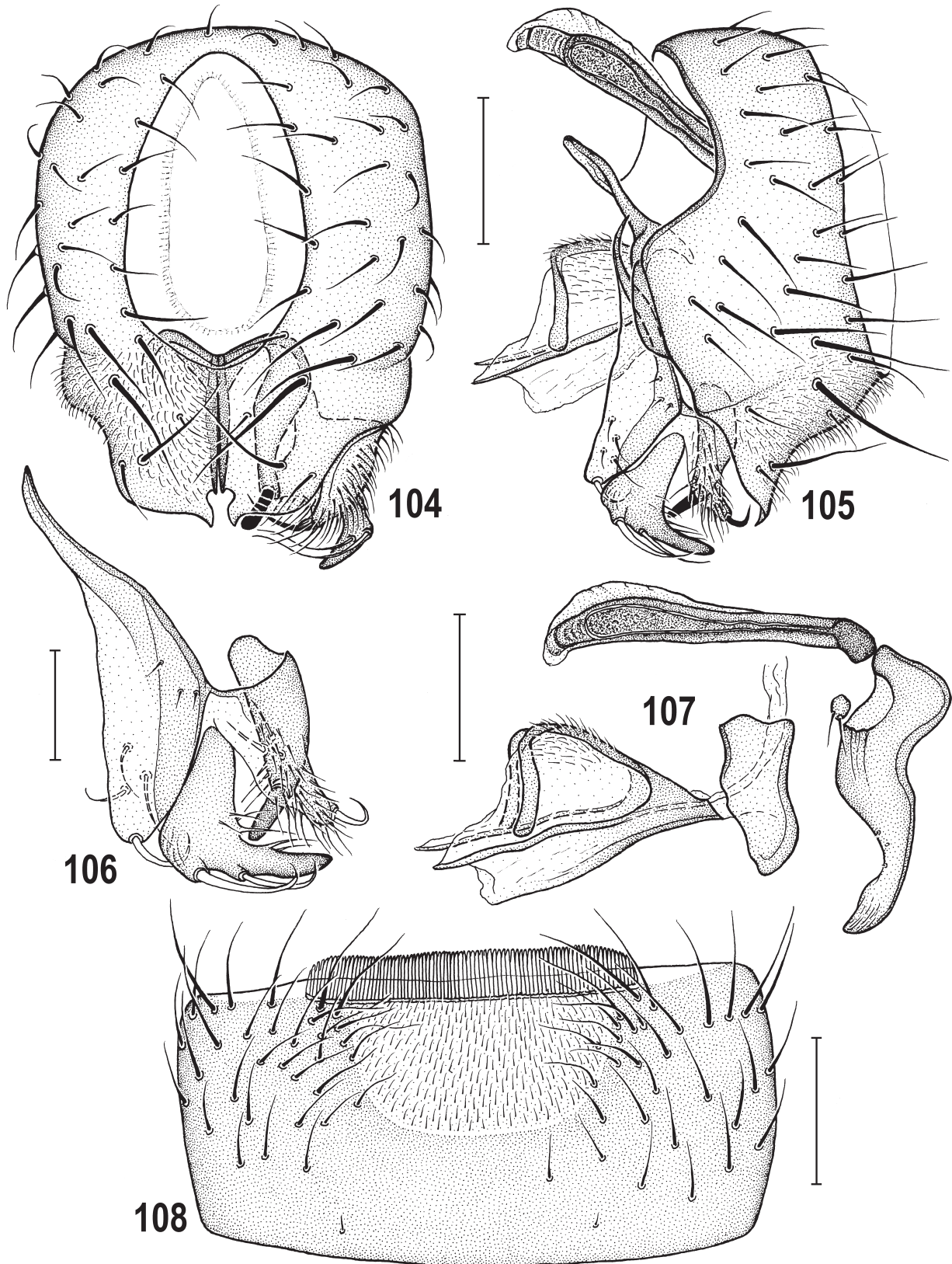
Type material. HOLOTYPE: ♂ (ULCI), labelled: 'HIERRO, Raya de Llanía, 9-V-99, M. Báez' (partly handwritten), '*Pteremis canaria* Papp ♂, J. Roháček det. 2000', 'HOLOTYPE ♂, *Pteremis ferreus* sp. n., J. Roháček des. 2023' (red label) (Fig. 100). The specimen (see Figs 98, 99) is intact, dry mounted on minutia pinned to rectangular card. PARATYPES: SPAIN: CANARY ISLANDS: EL HIERRO: 1 ♂♂ 4 ♀♀ (1 ♂ 2 ♀♀ genit. prep.), with same data as for holotype (1 ♂ 2 ♀♀ SMOC, 2 ♀♀ ULCI); 1 ♂ (immature, mid leg mounted on microslide, pinned below specimen), labelled: 'Can. Hierro, El Pinar, 27. 3. 50, Lindberg' (MZHF). All paratypes with yellow label 'PARATYPUS ♂ or ♀, *Pteremis ferreus* sp. n., J. Roháček des. 2023'.

Description. **Male** (Figs 98, 99) closely resembling *P. fenestralis* and *P. canaria*, in particular. Total body length 1.97–2.10 mm; general colour as in both these species but head (lower parts in particular) darker.

Head (Figs 98, 99, 101) about 1.45× higher than long. Frons dark brown to blackish except for orange-brown or reddish brown anterior margin. Microtomentose pattern well developed, including silvery grey glittering orbits, interfrontalia and frontal triangle and dull blackish brown M-shaped mark surrounding them (see Fig. 101); frontal triangle narrow and almost reaching anterior margin of frons. Extent of reddish or orange-brown colouration of frontal margin rather variable, narrow (as in Fig. 101) to extend over anterior third of frons and also including



Figs 98–103. *Pteremis ferreus* sp. nov. and its habitat. 98 – male, holotype, left laterodorsally; 99 – ditto, right lateroventrally; 100 – labels of the holotype; 101 – head and thorax of the holotype, subdorsally; 102 – right wing, male paratype; 103 – laurel forest (Laurisilva) in type locality (El Hierro, La Llanía), habitat of the species. Scales = 0.5 mm (Figs 98, 99, 102), 0.3 mm (Fig. 101). Photo by E. García (103) and J. Roháček (others).



Figs 104–108. *Pteremis ferreus* sp. nov., male, paratype. 104 – external genitalia, caudally (aedeagal complex and left gonostylus omitted); 105 – ditto, left laterally; 106 – gonostylus, left laterally; 107 – aedeagal complex (with aedeagus separated), laterally; 108 – male S5, ventrally. Scales = 0.1 mm (Figs 104, 105, 107, 108), 0.05 mm (Fig. 106).

anterior corner of frontal triangle. Frontal lunule more or less concolorous with anterior frontal margin and face, but seemingly paler due to light grey microtomentum. Face orange-brown to brown, usually lighter at ventral margin, grey microtomentose; medial carina better developed than in *P. fenestralis*, distinct also more ventrally. Gena reddish brown to brown, usually darker than face, particularly posteriorly, grey microtomentose; shining dark postgenal stripe as in other species. Cephalic chaetotaxy (cf. Fig. 101) very similar to that of *P. fenestralis* but *pvt* yet smaller, with apices not meeting medially; *occi* longer than *occe* and nearly parallel (hardly inclinate) and about two-thirds of *vti*; *vti* normally longer (sometimes distinctly) than *vte*; posterior *ors* as long as or longer than *oc* (sometimes as long as *vte*) and about 1.4 times as long as anterior *ors*; 4 *ifr*, two middle pairs distinctly longer, more robust and usually crossed medially; *g* short but usually longer and more robust than anterior peristomal setula. Eye subcircular (10:9), with longest diameter about 5 times as long as smallest genal height hence gena lower than that of *P. fenestralis*. Antenna with scape brown to pale brown, pedicel and 1st flagellomere blackish brown. Arista about 3.8 times as long as antenna, very shortly and densely ciliate.

Thorax generally coloured and microtomentose in *P. fenestralis*, including brown (not ochreous) notopleural area (in contrast to that of *P. canaria*) but not only sutures between pleural sclerites ochreous but also sternopleuron distinctly paler than other pleural sclerites. Thoracic chaetotaxy: mesonotal macrosetae somewhat longer than in *P. fenestralis*; 1 *hu*, anterior *npl* and, particularly, *prs* distinctly longer (the latter only slightly shorter than *hu* markedly longer than *sa*); outer *pa* as long as *dc* but inner *pa* distinctly longer than those of *P. fenestralis* and *P. canaria*; *dc* microsetae (in front of *dc*) more enlarged, 2.5–3 times as long as *ac* microsetae and also the latter longer than in *P. fenestralis*; both *sc* very long and robust, latero-basal *sc* as long as or almost as long as apical *sc* (longest thoracic seta); only 1 long (posterior) *stpl* because anterior *stpl* reduced to a hardly visible hair.

Legs coloured similarly as those of *P. fenestralis* but usually only fore leg with knee yellowish ochreous, *t*₂ and *t*₃ unicolorous brown. Pedal chaetotaxies differing from those of *P. fenestralis* as follows: *f*₂ anteriorly with a short row of 3 distinct subapical setae, the most distal longest. *t*₂ chaetotaxy (Figs 116–118) most similar to that of *P. canaria* (cf. Figs 95–97) but distinguished by strongly reduced but present *va* seta (Fig. 118), 3 short setae dorsally above distal pair of long setae (Fig. 117), proximal posterior short seta situated more distally (almost at level of short *av* seta, cf. Figs 116, 117) and apex of *t*₂ posteriorly with 3 small setae (Fig. 118). Mid basitarsus (*mt*₂) usually without enlarged ventral (or anteroventral) setula (Fig. 118). Ratio *t*₂ : *mt*₂ = 1.75–1.80.

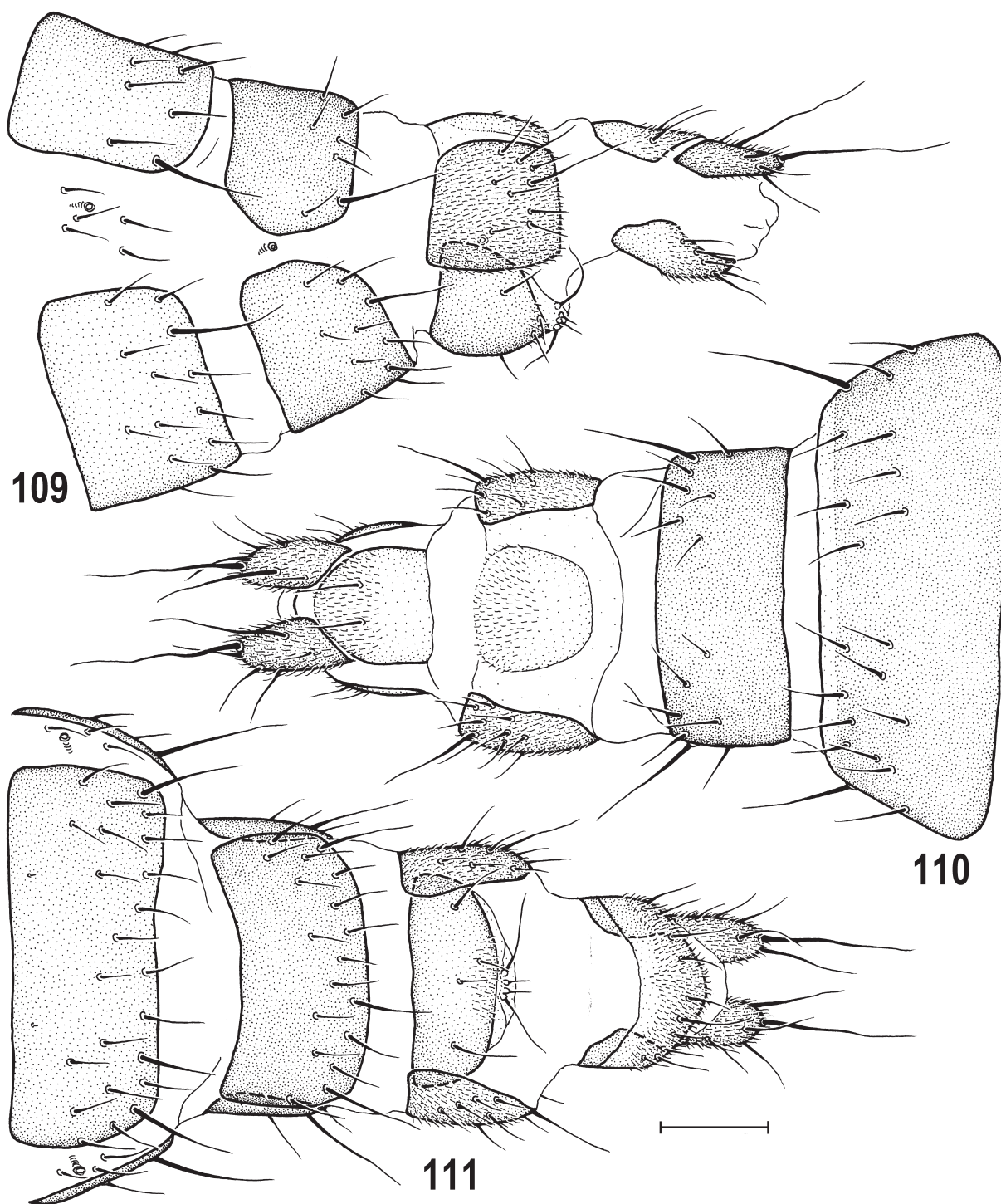
Wing normally developed (Fig. 102), most resembling that of *P. canaria* (with *C* less produced beyond apex of *R*₄₊₅ and *A*₁ darker pigmented) but relatively (length compared to width) shorter, also *dm* cell somewhat shorter and membrane yet more darkened along veins (cf. Figs 78 and 102). Wing measurements: length 1.87–1.93 mm, width

0.83–0.85 mm, *C-index* = 1.03–1.05, *r-m\dm-cu* : *dm-cu* = 1.94–2.14. Haltere bicolorous, with pale ochreous to yellow stem and brown knob, the latter more slender than that of *P. fenestralis*.

Abdomen generally formed and coloured as *P. fenestralis* but *T1+2* longer, about 1.6 times as long as *T4*; *T3* not wider than *T1+2*; *T4* narrower but slightly longer than *T3*; *S1+2* longer and wider (similar to that of *P. canaria*); both *S3* and *S4* large, trapezoidal (wider posteriorly); *S3* narrower but slightly longer than *S4*. *S5* (Fig. 108) as broad as but shorter and more transverse than *S4*, with large pale-pigmented and finely micropubescent semicircular area (much larger than in *P. canaria*) in front posteromedial comb of spines, being widest of all those in *Pteremis* species and composed of dense fine spines; lateral setae of *S5* fine but more numerous than in *P. canaria*. *S6+7* as in *P. fenestralis*, but with 2 + 2 setae finer and *S8* dorsally with a pair minute microsetae.

Genitalia. Epandrium (Figs 104, 105) resembling that of *P. canaria* but with setae denser and finer, more asymmetrical in caudal view (Fig. 104), and anal fissure more narrow, elongately ovoid, thus tapered dorsally. Cerci large, each dorsally laterally somewhat bulging (Fig. 104) and ventrally flattened, projecting into distinctive ventromedial flat but acutely pointed and bare apex (Figs 104, 105). Medandrium medially long, narrowly darkened and reaching almost to apex of cerci (Fig. 104). Hypandrium with apodeme distinctly longer than in *P. fenestralis*, thus more similar to that of *P. canaria* but less flattened. Gonostylus (Figs 104–106) very characteristic, unlike all other W Palaearctic species its anterior lobe with anterodorsal process extremely long, far projecting (almost) dorsally (Fig. 106); also division of anterior lobe of gonostylus into anterodorsal pale part and posteroventral dark-pigmented and strongly sclerotized part very characteristic; the latter part ventrally with 2 strong curved setae and 1 robust, darkened, posteriorly directed projection with simply pointed apex (Fig. 106); posterodorsal part of anterior lobe pale-pigmented and also more or less separate, carrying usual oblique longitudinal spinulose ledge. Posterior lobe (see Fig. 106) relatively small, hidden behind anterior lobe because situated medially (cf. Fig. 104) and terminated by robust blunt spine and 2 or 3 fine subapical setae; its posterior subconical process robust and projecting more ventrally than main part, with 1 usual, medially curved seta on apex. Aedeagal complex (Fig. 107) constructed similarly as in other *Pteremis* species, characterized by combination of relatively robust phallosophore with blunt (ventral) apex, proximally strongly tapered and distally strongly dilated distiphallus having a small finely haired area in middle part of its dorsal side. Postgonite sinuate in lateral view as that of *P. fenestralis* but its dilated apex different, rather shortly lancet-shaped than knob-like, and minute anterodorsal sclerite (= remnant of pregonite) with 2 fine setulae. Ejacapodeme not observed.

Female. Similar to male unless mentioned otherwise. Total body length 2.02–2.26 mm. Mid basitarsus (*mt*₂) sometimes with 1 slightly enlarged ventral setula in proximal fourth; *mt*₂ longer on the average: ratio *t*₂ : *mt*₂



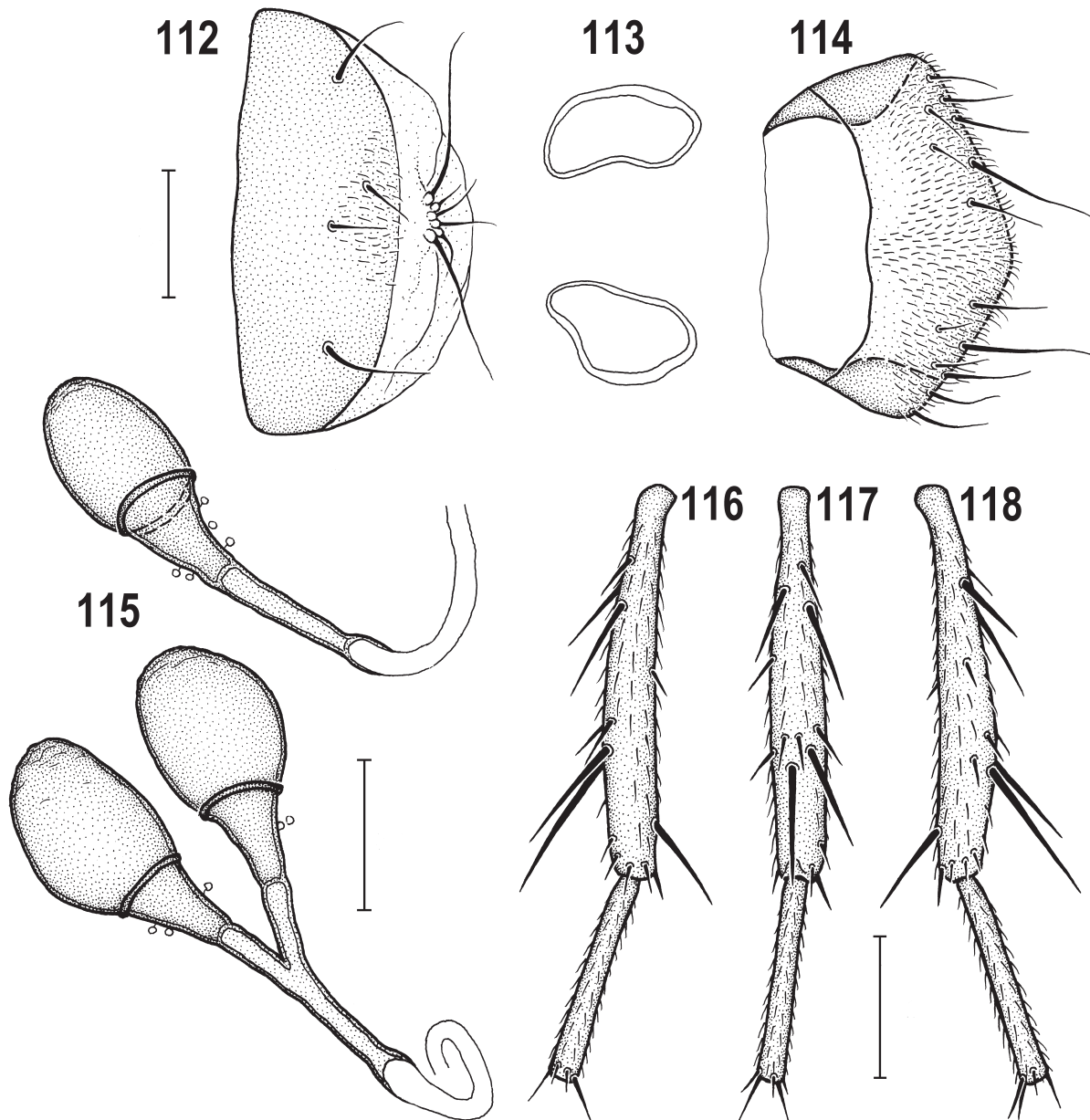
Figs 109–111. *Pteremis ferreus* sp. nov., female, paratype. 109 – postabdomen, laterally; 110 – ditto, dorsally; 111 – ditto, ventrally. Scale = 0.1 mm.

= 1.78–1.80. Wing measurements: length 1.73–1.95 mm, width 0.77–0.85 mm, *C-index* = 0.91–1.06, $r-m/dm-cu$: $dm-cu$ = 1.53–1.87.

Abdomen resembling that of *P. fenestralis* but *T1+2* longer (about 1.7 times as long as *T3*); *T3* somewhat narrower than *T1+2*; *T5* distinctly longer than *T4*; *S1+2* longer and wider, *S3* and *S4* subequal in length and *S5* distinctly shorter than *S4* (as those of *P. canaria*); *S3* narrower than *S4* and more trapezoidal; *S5* only slightly narrower than *S4* and posteriorly somewhat tapered, thus not transversely

oblong but trapezoidal, with rounded corners.

Postabdomen (Figs 109–111) also similar to those of *P. fenestralis* and *P. canaria*. *T6* transversely subtrapezoidal and yet wider than that of *P. canaria* but with posterior margin pale-pigmented; *T6* and *T7* (Fig. 110) with more setae than those of both these relatives and lacking pale posterior marginal stripe. *T8* with dorsomedial part relatively broad, pale-pigmented and micropubescent in only posterior half (membranous areas between the latter and dark lateral parts without micropubescent - Fig. 110).



Figs 112–118. *Pteremis ferreus* sp. nov., male and female, paratypes. 112 – *S8*, ventrally; 113 – spectacles-shaped sclerite, ventrally; 114 – *S10*, ventrally; 115 – spermathecae; 116 – male left t_2 and mt_2 , posteriorly; 117 – ditto, dorsally; 118 – ditto, anteriorly. Scales = 0.05 mm (Figs 112–115), 0.2 mm (others).

T10 slightly longer than broad, roughly pentagonal and its posterior half micropubescent (Fig. 110). *S6* more transverse and uniformly pigmented as in *P. fenestralis* but with richer setae (Fig. 111). *S7* entirely dark-pigmented (Figs 109, 111), larger, wider and more setose than that of both *P. fenestralis* and *P. canaria*. *S8* species-specific (Figs 111, 112), transversely semioval, with only 2 pairs of setae (lateral longer) and micropubescent sparse and restricted to small posteromedial area of anterior pigmented part; posterior membranous part provided with a medial group of 2 long sinuate and 4 short setae between them, all on elevated sockets (Fig. 112). *S10* (in largest extension) only slightly narrower than *S8*, transversely subpentagonal, but anteriorly broadly emarginate (deeper than in *P. fenestralis*), largely micropubescent and relatively long but finely setose in front of posterior margin (Fig. 114).

Spectacles-shaped sclerite (Fig. 113) developed as a pair of unpigmented, irregularly ovoid rings, most similar to those of *P. canaria*. Spermathecae 2+1 most resembling those of *P. canaria*, pyriform, but having basal conical part separated from ovoid body by only 1 complete ring-shaped ledge; terminal parts of ducts formed as in *P. canaria* but those of paired spermathecae more divergent (see Fig. 115). Cerci (Figs 109, 110) robust and subconical, thus resembling those of *P. canaria* including setosity.

Etymology. The name is a Latin adjective *ferreus* (= iron, ferrous, but also meaning hard) and is derived from El Hierro (= iron in Spanish), the island from which the new species originates and also refers to the hard, heavily sclerotized ventral process of the anterior lobe of its gonostylus. **Comments.** *Pteremis ferreus* sp. nov. externally resembles *P. canaria* in having strongly reduced *va* seta on the mid

tibia (Fig. 118) but it differs from this and other *Pteremis* species as follows: male *S5* armed by a very wide posteromedial comb of dense spines (Fig. 108), apex of male cercus flat but acutely projecting (Fig. 104), anterior lobe of gonostylus somewhat tripartite and with anterodorsal process extremely long and projecting dorsally, and its ventral projection robust, dark, simply pointed (Fig. 106), distiphallus dorsoventrally strongly dilated but with micropubescence restricted to small dorsal area (Fig. 107). Female *P. ferreus* is best characterized by the transversely semioval shape of *S8* (Fig. 112) and spermathecae with the basal conical part separated from the ovoid body by only 1 complete ring-shaped ledge (Fig. 115). Spermathecal structures suggest a relationship to *P. pulliceps*, *P. canaria* and (possibly) *P. apterina*, as discussed above under *P. pulliceps*. The long anterodorsal process of the anterior lobe of the gonostylus is similar to that of the Nearctic *P. wirthi* (see below) but the latter species is considered more closely allied to *P. fenestralis* (see comments above under this species).

Biology. Six type specimens were collected by sweeping undergrowth of native laurel forest (Fig. 103) in the protected area Raya de La Llanía in the central montane part of El Hierro I. in May 1999 (M. Báez, personal communication, 2023). The remaining (immature) paratype was captured in March.

Distribution. Canary Is.: El Hierro. Apparently, *P. ferreus* is endemic to this island.

Pteremis apterina sp. nov.

(Figs 119–145)

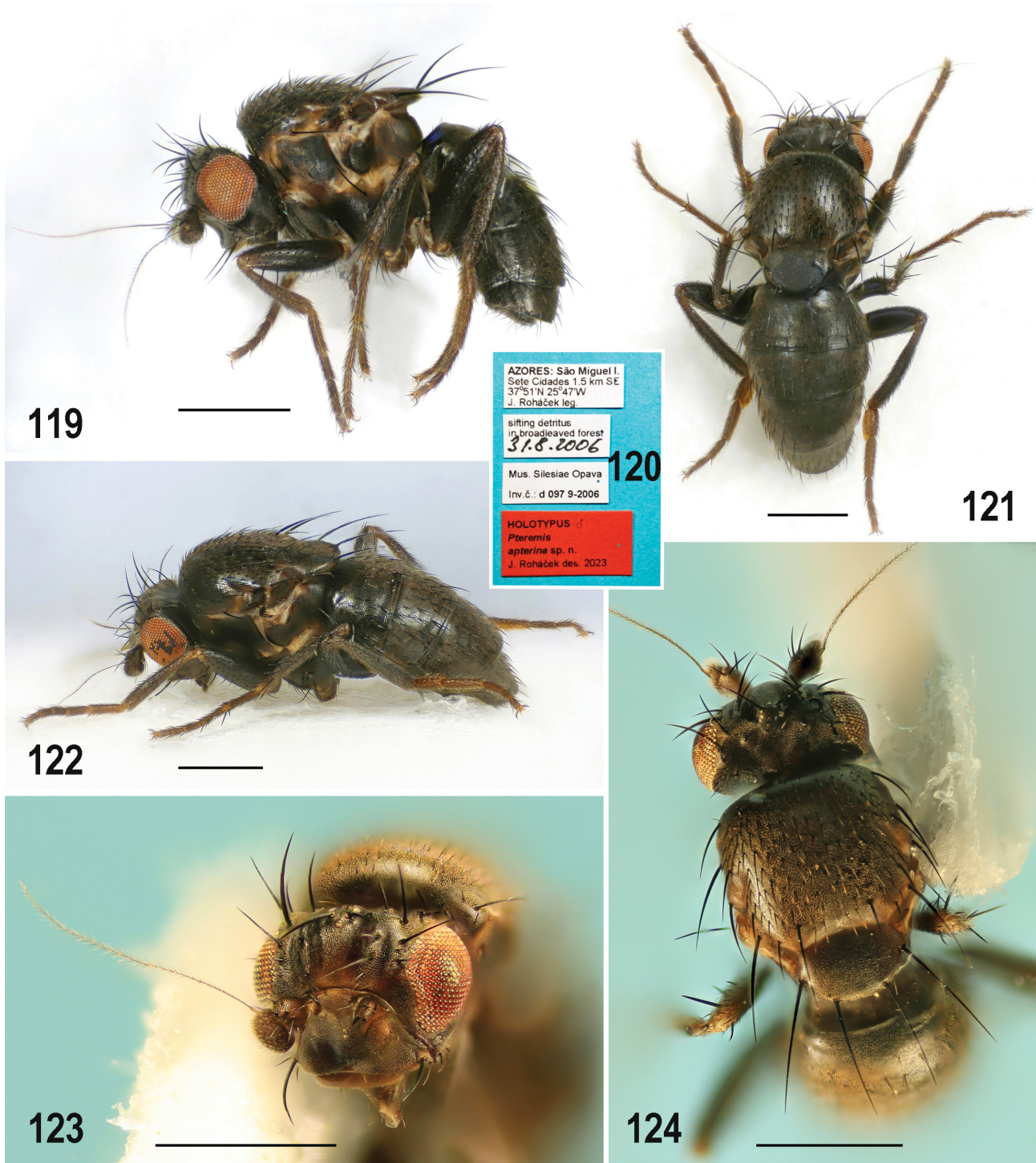
Type material. HOLOTYPE: ♂ (SMOC), labelled: 'AZORES: São Miguel I., Sete Citades 1.5 km SE, 35°51'N 25°47'W, J. Roháček leg.', 'sifting detritus in broadleaved forest, 31.8.2006', 'Mus. Silesiae Opava, Inv.č. d 097 9-2006', 'HOLOTYPE ♂, *Pteremis apterina* sp. n., J. Roháček des. 2023' (red label) (Fig. 120). The specimen (see Fig. 119) is intact, dry mounted on triangular pinned card. PARATYPES: PORTUGAL: AZORES: SÃO MIGUEL I.: 8 ♂♂ 4 ♀♀ (1 ♂ headless, 2 ♂♂ 1 ♀ genit. prep.), with same data as for holotype; 2 ♂♂ 3 ♀♀ (1 ♀ genit. prep.), with same data but collected 8.ix.2006; 3 ♂♂ 2 ♀♀, with same data but collected 11.ix.2006; 2 ♂♂, São Miguel I., Caldeiras nr. Ribeira Grande, 37°48'N 25°29'W, sifting detritus in broadleaved forest, 5.ix.2006; 2 ♀♀, São Miguel I., Caldeira Velha (nr. Ribeira Grande), 37°47'N 25°30'W, sifting detritus in broadleaved forest, 7.ix.2006, all J. Roháček leg. (SMOC). TERCEIRA I.: Caldeira de Serra de Santa Bárbara (TER-NFSB-T164), 38°44'06"N, 27°18'26"W, 940 m, laurel forest, pitfall trap T92-E4, 1 ♂ 1 ♀, T92-E8, 1 ♂, T92-E12, 1 ♂ 1 ♀, T92-E14, vii. 2008, 1 ♂ 1 ♀, T92-E22, vii. 2008, 3 ♂♂ 2 ♀♀, T92-E24, 1 ♀, T92-E26, 1 ♀, T92-E28, 2 ♀♀, T92-E30, 1 ♂ 2 ♀♀, T92-T11, 2 ♀♀, T92-T15, 1 ♂ (all dried from ethanol, 1 ♂ 1 ♀ genit. prep.), all P. A. V. Borges et al. leg. (7 ♂♂ 11 ♀♀ DTP, 2 ♂♂ 2 ♀♀ SMOC). SANTA MARIA I.: Pico Alto, 36°58'25"N, 25°05'23.07"W, 437 m, pitfall traps in exotic plantation of *Cryptomeria japonica*, 26.v.–12.vi.2009, 3 ♂♂ 3 ♀♀ (all dried from ethanol, 1 ♂ genit. prep.), P. A. V. Borges et al. leg. (2 ♂♂ 2 ♀♀ DTP, 1 ♂ 1 ♀ SMOC); Santa Maria I., Anjos, 36°59'29"N, 25°08'23"W, 181 m, pitfall traps in exotic plantation of *Acacia* sp., 12.–18.vi.1990, 79 ♂♂ 42 ♀♀ (all dried from ethanol, 1 ♂ 1 ♀ genit. prep.), P. A. V. Borges et al. leg. (64 ♂♂ 32 ♀♀ DTP, 5 ♂♂ 5 ♀♀ SMOC, 10 ♂♂ 5 ♀♀ NMPC). All paratypes with 'PARATYPE ♂ or ♀, *Pteremis apterina* sp. n., J. Roháček des. 2023' (yellow label).

Additional material examined (excluded from type series, poorly preserved or damaged specimens, all in ethanol). PORTUGAL: AZORES: TERCEIRA I.: Caldeira de Serra de Santa Bárbara (TER-NFSB-T164), 38°44'06"N, 27°18'26"W, 940 m, laurel forest, pitfall trap T92-E10, vii. 2008, 1 ♂ 1 ♀, T92-E14, vii. 2008, 1 ♂ 2 ♀♀, P. A. V. Borges et al. leg.

SANTA MARIA I.: Anjos, 36°59'29"N, 25°08'23"W, 181 m, pitfall traps in exotic plantation of *Acacia* sp., 12.–18.vi.1990, 120 ♂♂ 29 ♀♀ (7 ♂♂ 1 ♀ immatures), P. A. V. Borges et al. leg.; Santa Maria I., Pico Alto, 36°58'25"N, 25°05'23.07"W, 437 m, pitfall traps in exotic plantation of *Cryptomeria japonica*, 26.v.–12.vi.2009, 1 ♂ (headless), Paulo A. V. Borges et al. leg (all in DTP).

Description. Male (Figs 119, 124). Fully apterous, also halteres entirely absent. Total body length 1.67–2.58 mm; general colour blackish brown (only teneral specimens pale brown) with greyish brown microtomentum, dorsal side of thorax and abdomen subshining (cf. Fig. 121), head, thoracic pleuron and abdominal sterna duller (Fig. 119).

Head (Figs 119, 123, 124) 1.3–1.4× higher than long, blackish brown to (posteriorly) black, with only frons anteriorly lighter. Frons generally darker but with microtomentose pattern (see Fig. 123) resembling that of *P. fenestralis*; dark brown to blackish except for orange-brown or reddish brown anterior margin but extent of this anterior colouration variable, ranging from narrow marginal stripe to covering (medially, between interfrontalia and frontal triangle) anterior half of frons; occiput almost black but with dense greyish brown microtomentum (as is that on mesonotum). Orbits, interfrontalia and frontal (and ocellar) triangle with silvery grey (more or less glittering) microtomentum; also incomplete (medially interrupted) dull blackish M-shaped mark between them developed; frontal triangle delimited by silvery grey microtomentum and almost reaching anterior margin of frons but its apex often unclear due to sparse microtomentum. Frontal lunule orange-brown to brown, always with light grey microtomentum, thus looking somewhat lighter than face or anterior margin of frons. Face brown to dark brown (darkest in facial cavities below antennae), sparsely grey microtomentose and subshining; medial carina developed, mainly distinct dorsally. Gena brown to dark brown, greyish brown microtomentose; postgena with usual blackish and shining perpendicular stripe. Cephalic chaetotaxy (Figs 119, 123): cephalic setae somewhat stronger than in other *Pteremis* species; true *pvt* absent but a pair of minute divergent medial postocellar setulae behind ocellar triangle present; and *occi* distinctly inclinate, slightly to distinctly longer than *occe* and about two-thirds of *vti*; *vti* and *vte* subequal or *vti* somewhat longer (longest of frontal bristles); *oc* usually shorter than posterior *ors*; 2 *ors* but only posterior robust and long; anterior *ors* short and weak, less than half length of posterior *ors*; 4 (rarely only 3 on one side) *ifr*, two middle pairs usually long and robust (one of them usually longer and crossed), others short and weak, 1 microseta in front of anterior *ifr* also developed; 2 or 3 very minute *ads* as in *P. fenestralis*; *g* and 1 or 2 shorter setae behind it weak, *g* only slightly longer and thicker than anterior peristomal setula; *vi* very long and robust, often as long as *vti*; peristomal setulae sparse (4 or 5) and those posterior about as long as 2 small postgenal setae; postocular setulae shorter than peristomals but numerous, in single long row. Eye subcircular (8:7), but somewhat tapered ventrally, with longest diameter 3–3.3 times as long as smallest genal height. Gena (Fig. 119) higher than in relatives except for *P. vlasovi*. Antenna with scape and 1st flagellomere more or less paler than (usually) blackish



Figs 119–124. *Pteremis apterina* sp. nov. 119 – male, holotype, left laterally; 120 – labels of the holotype; 121 – female, paratype, dorsally; 122 – ditto, left laterally; 123 – head of the male paratype, frontally; 124 – head and thorax of the same specimen, dorsally. Scales = 0.5 mm. Photo by M. Deml (119, 121, 122) and J. Roháček (others).

pedicel; 1st flagellomere brown to dark brown, relatively short, subovoid, with whitish ciliation on apex (Fig. 124) longer than in *P. fenestralis* and relatives. Arista relatively long, about 4.4 times as long as antenna, with ciliation (Fig. 123) dense and longer than in all other congeners under study.

Thorax largely dark brown (Fig. 119) and brown to golden brown microtomentose (Fig. 124); mesonotum subshining, pleuron duller. Sutures between humeral callus,

notopleural area, mesonotum and pleural sclerites pale brown to ochreous-yellow or the whole notopleuron pale (Fig. 119). Scutellum shorter than in relatives, nearly twice wider than long, flat on disc, rather subcircular (Fig. 124). Thoracic chaetotaxy (cf. Figs 119, 121, 124): mesonotal macrosetae long and some robust; 1 *hu* (only as long as posterior *npl*) and 2 microsetae on humeral callus (that more medial twice longer); 2 relatively long *npl* (anterior unusually long, twice longer than posterior, see Fig. 124);

1 distinct *prs* (as long as *hu*) and 1 much shorter *sa*; 2 *pa*, the outer very long, as long as or longer than *dc*, the inner short, as long as *sa*; only 1 long and robust *dc* in prescutellar position but 4 *dc* microsetae (in front of *dc*) distinctly enlarged, twice longer and thicker *ac* microsetae; 8 rows of *ac* microsetae on suture but only 4 (less often 6) in front of scutellum; prescutellar *ac* microsetae (or only medial pair) usually somewhat longer but not thicker than other *ac* microsetae; 2 very long and robust *sc*, laterobasal (longest thoracic seta) slightly to distinctly longer than apical (Fig. 124); only 1 long and robust posterior *stpl* (as long as *dc*, Fig. 119), anterior *stpl* reduced to fine microseta or absent.

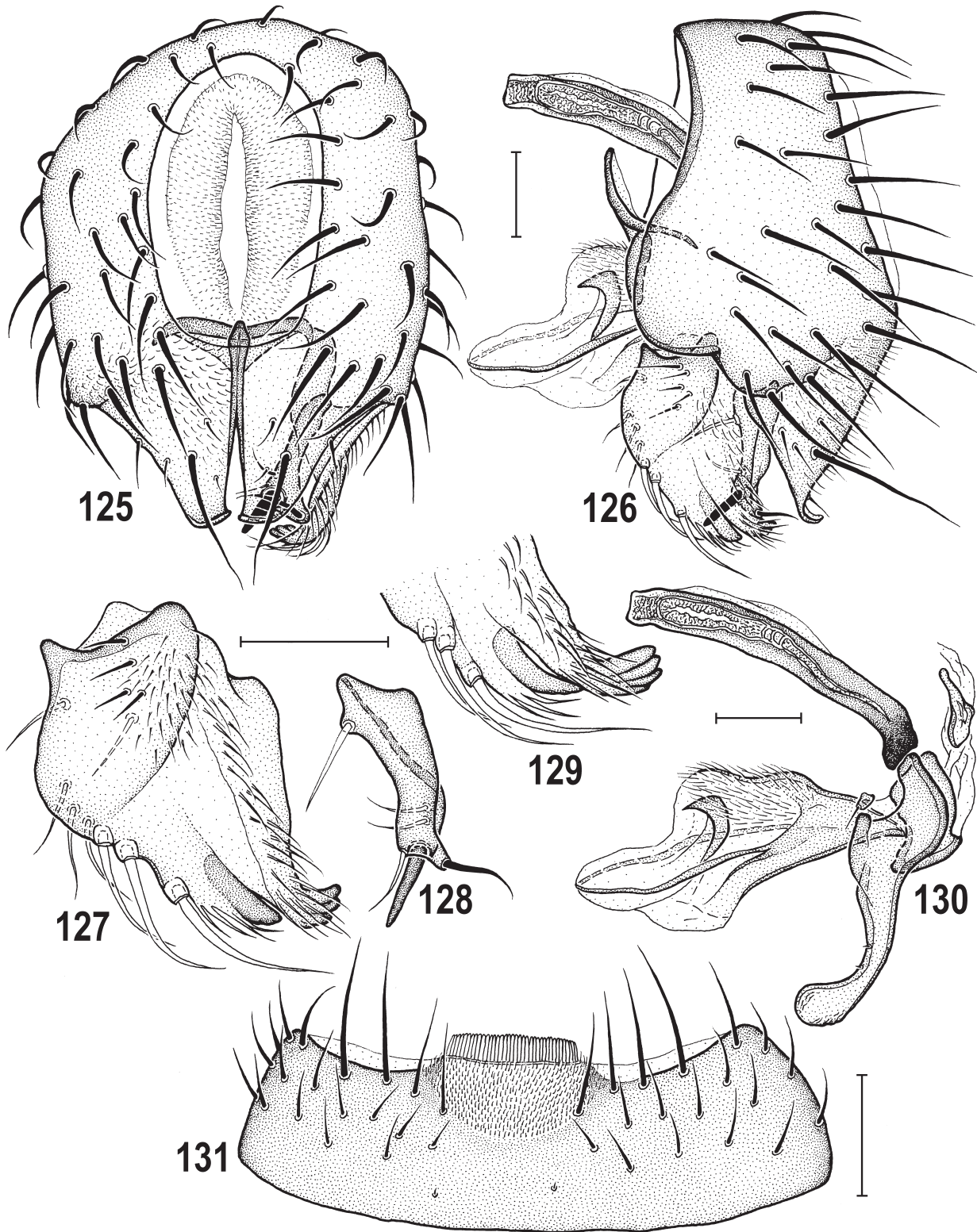
Legs largely dark brown (coxae, femora, tibiae), with brown to pale brown trochanters, knees, apices of tibiae and tarsi (Fig. 119, 121). Pedal chaetotaxies: f_1 with 3 erect setae in posterodorsal row, and with 3 or 4 longer setae in distal three-fifths in longer posteroventral row. f_2 anteriorly with 1 robust and long subapical seta and 1 short seta in front of it, and posteriorly with 1 short curved posteroapical seta. t_2 ventrally (see Figs 138, 140) with only 1 long robust subapical (diverging from axis of tibia) seta considered to be a distally shifted *vpa* and 1 small *av* seta near middle; dorsally (Fig. 139) with setosity very similar to that of *P. fenestralis* and relatives but above 1 long proximal posterodorsal seta there is 1 small additional seta (thus as in *P. tenebricus*) and there is only 1 small posterior seta in about proximal two-fifths (Figs 138, 139); apex of t_2 provided with 2 short (1 longer, 1 small) subapical setae anteriorly (Fig. 140) but with a group of small setae posteriorly (Fig. 138) unlike all other relatives. f_3 with 1 short and weak anterior subapical seta; t_3 with ventroapical setula stronger and more distinct than in other *Pteremis* species. Other parts of femora and tibiae uniformly finely setulose. Mid basitarsus (mt_2) almost always with 1 enlarged ventral setula (Figs 138, 140). Ratio $t_2 : mt_2 = 1.90\text{--}2.12$.

Wing absent, only small scale-like tegula with 3 marginal setulae retained (cf. Fig. 124). Haltere entirely missing, with no remnant preserved.

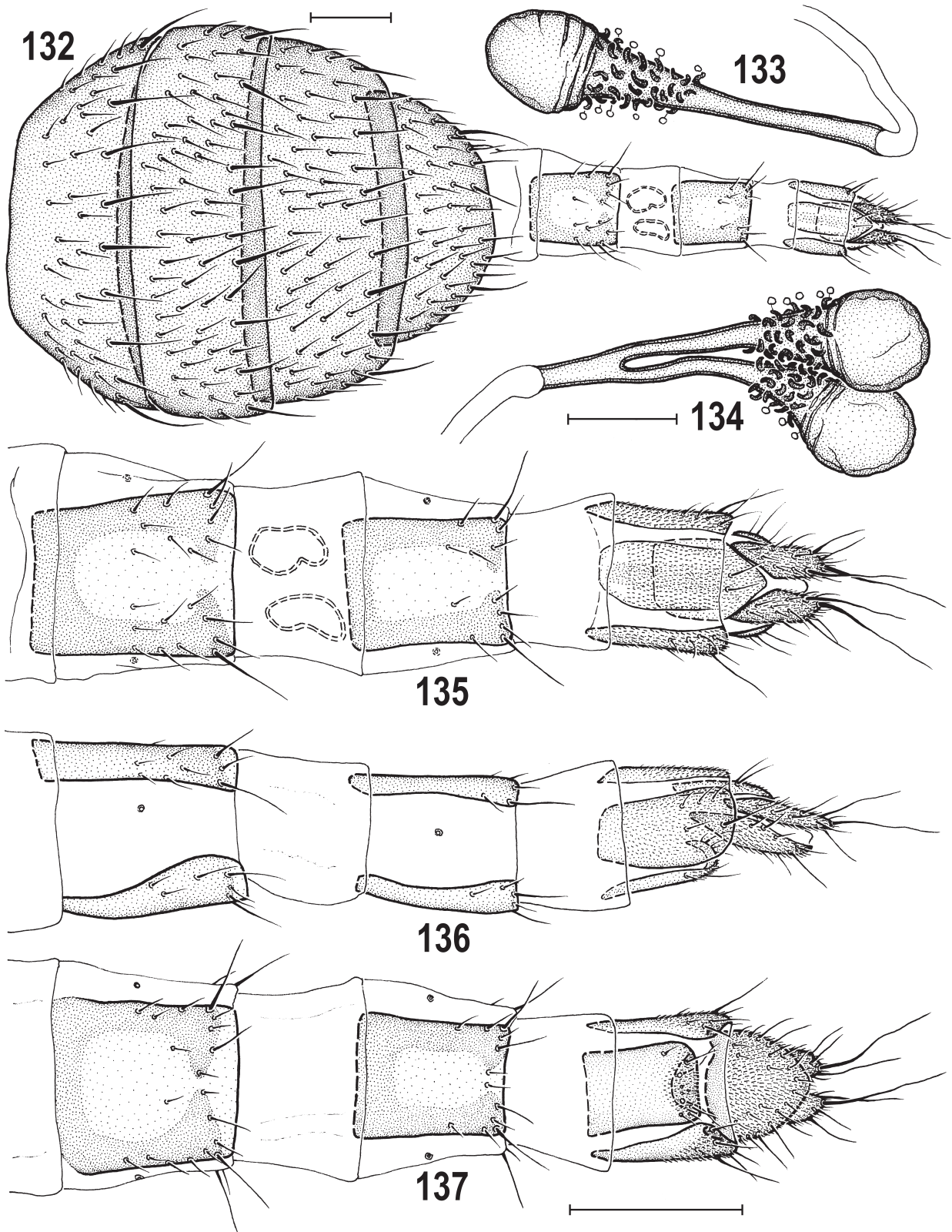
Abdomen blackish brown to black, but dorsally with golden brown microtomentum (cf. Fig. 124) and rather subshining ventrally. Dorsal side of abdomen strongly convex (Fig. 119) of ovoid to elongately ovoid outline (cf. Fig. 121), widest at 3rd segment and being similar both in male and female. *T2–T5* more densely but shortly setose than in relatives, with only setae at posterior margins longer and more robust but those in posterior corners not markedly longer (cf. Fig. 132). In contrast to other *Pteremis* species, *T1+2* is not the largest abdominal tergum, being as long as (or slightly shorter than) *T4* but strongly narrower anteriorly, widest at posterior margin; *T3* widest and most transverse sternum but shorter than *T4* or *T1+2*; *T4* slightly narrowed posteriorly (distinctly less than *T1+2* is anteriorly); *T5* markedly shorter and narrower than *T4* and posteriorly strongly tapered, transversely rounded trapezoidal. Preabdominal sterna also strongly convex: *S1+2* smallest, transversely trapezoidal, strongly narrowed anteriorly, pale brown (lightest anteriorly) but with posterior marginal area darkened, blackish brown. *S3* and *S4* distinctly shorter and much narrower than adjacent

terga but similarly blackish brown to black, with sparser and finer short setae; *S3* slightly tapered anteriorly and smaller (shorter and narrower) than *S4*, the latter distinctly largest (widest and longest) sternum. *S5* (Fig. 131) short, only about half length of *S4* and also shorter than *S3*, more transverse than in other congeners, with twice emarginated posterior margin on both sides of posteromedial comb of spines; this comb short (narrow) and composed of fine apically blunt spines. Posteromedial membranous area in front of this comb relatively small but somewhat protruding posteriorly, very finely micropubescent. Lateral parts of sternum simply setose, with longest and unusually robust setae in row at posterior margin; no group of curved setae at lateral margin of posteromedial membranous area, there is a single seta on each side instead. *S6+7* and *S8* formed as in other *Pteremis* species but original *S7* with posteroventral projection dark-pigmented; *S6+7* with setae in both pairs finer and more distant; *S8* bare, without a pair of small dorsal setae.

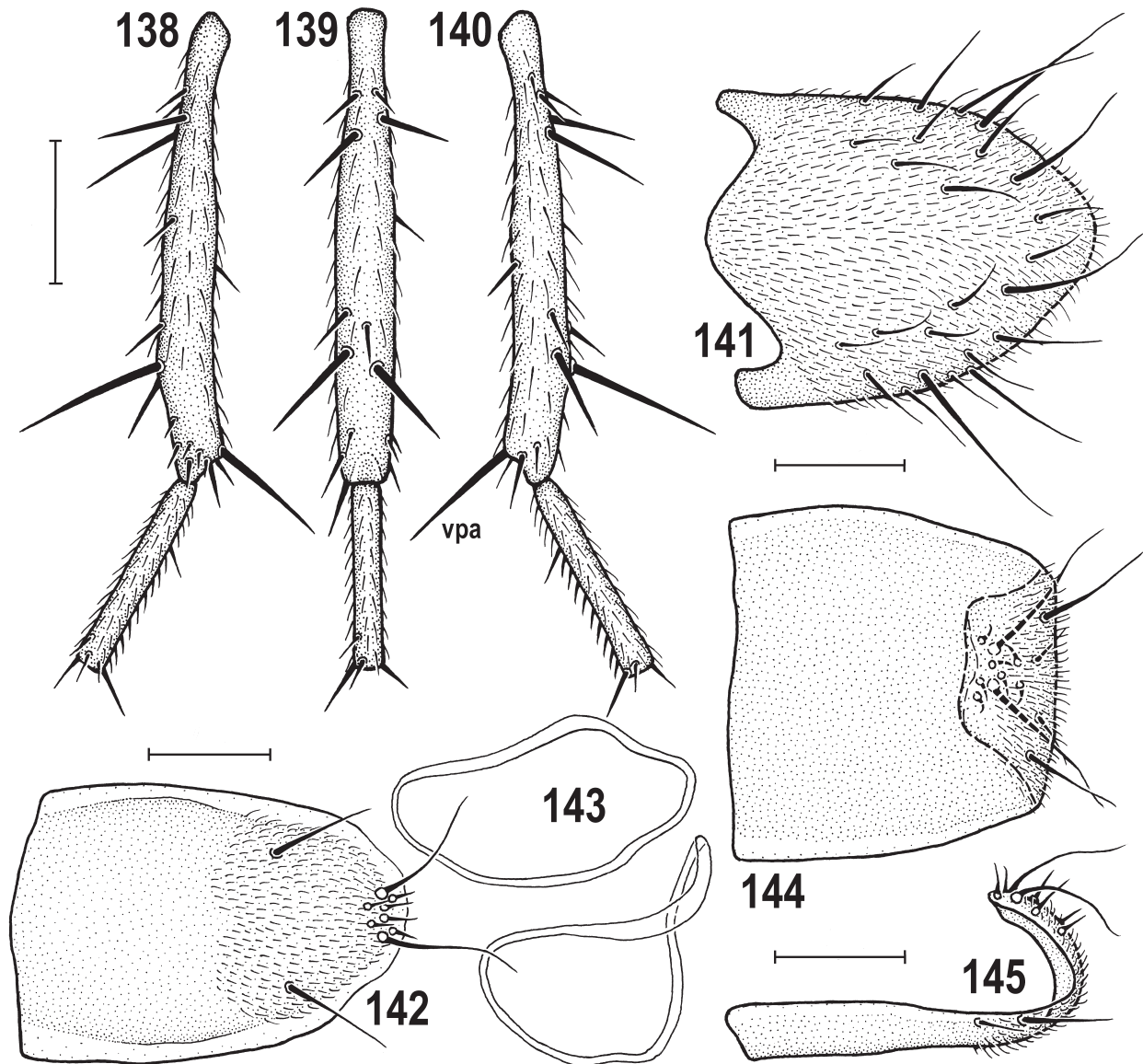
Genitalia. Epandrium (Figs 125, 126) of medium length and width, somewhat asymmetrical dorsally in caudal view (Fig. 125), with rather uniform and robust setae, those posteroventral somewhat longer than others. Anal fissure elongately suboval, yet narrower than that of *P. fenestralis*. Cerci large and long (Fig. 125), each distally narrowed, flattened and bare as that of *P. tenebricus* but its flat apex bent posteriorly (see Fig. 126). Medandrium as in most relatives. Hypandrium with anteromedial apodeme short, strongly asymmetrical as usual, but directed more dorsally (Fig. 126). Gonostylus (Figs 125–129) with anterior lobe much larger than posterior. Anterior lobe (Fig. 127) rather compact, anterodorsally with short dark subtriangular process and distinctive setosity (4 short setae plus micropubescent) on outer side (Fig. 127); ventrally with 3 usual robust and long bent setae, and shortened, robust, dark-pigmented posteriorly directed projection and 3 or 4 spinulae between the latter and posterior robust seta; posterolateral oblique longitudinal spinulose ledge narrow but posteroventrally terminated by unique group (comb) of 4 (3 robust, 1 smaller) dark, heavily sclerotized blunt spines (Figs 127, 129) directed medially (see Fig. 125). Posterior lobe (separated in Fig. 128) narrow, largely hidden behind anterior lobe (in lateral view, Fig. 126) terminated by relatively slender spine, 1 fine subapical seta, posteriorly with relatively small subconical process having sinuate, medially directed seta on apex and anterodorsally with 1 unusually robust seta (see Fig. 128). Aedeagal complex (Fig. 130) of typically simple *Pteremis* construction, distinguished from other species by simple phallopodeme without dorsal keel; phallopore yet lower (dorsoventrally shorter) and stouter than that of *P. ferreus* having relatively blunt apex; distiphallus most dilated in the middle as in some other *Pteremis* species, but a pair of slender band-like lateral sclerites apically connected (Fig. 130) and dorsolateral sclerite apparently separated from slender and elongate dorsal sclerite. Postgonite distinctly sinuate in lateral view but relatively slender also proximally, and its apex club-shaped although flatter than that of *P. fenestralis*. Ejacapodeme medium sized, having slightly



Figs 125–131. *Pteremis apterina* sp. nov., male, paratype (São Miguel I., Sete Citades). 125 – external genitalia, caudally (aedeagal complex and left gonostylus omitted); 126 – ditto, left laterally; 127 – anterior lobe of gonostylus, left laterally; 128 – posterior lobe of gonostylus, left laterally; 129 – posteroventral part of anterior lobe of gonostylus, left laterocaudally; 130 – aedeagal complex, laterally; 131 – male S5, ventrally. Scales = 0.05 mm (Figs 125–130), 0.1 mm (Fig. 131).



Figs 132–137. *Pteremis apterina* sp. nov., female, paratype (São Miguel I., Sete Citades). 132 – whole abdomen, dorsally; 133 – single spermatheca; 134 – paired spermathecae; 135 – postabdomen, dorsally; 136 – ditto, laterally; 137 – ditto, ventrally. Scales = 0.2 mm (Figs 132, 135–137), 0.05 mm (others).



Figs 138–145. *Pteremis apterina* sp. nov., male and female, paratypes. 138 – male left t_2 and mt_2 posteriorly; 139 – ditto, dorsally; 140 – ditto, anteriorly; 141 – female S_{10} , ventrally; 142 – female S_8 (unfolded), ventrally; 143 – spectacles-shaped sclerite, ventrally; 144 – female S_8 (with posterior part incurved), ventrally; 145 – ditto, laterally. Fig. 142 based on paratype from Santa Maria I., others on paratypes from São Miguel I. Scales = 0.2 mm (Figs 138–140), 0.05 mm (others).

sinuate distal digitiform process gradually projecting from wider proximal part (see Fig. 130).

Female (Figs 121, 122). Head, thorax, legs and preabdomen very similar to those of male unless given otherwise. Total body length (measured with postabdomen retracted) 1.87–2.78 mm. Ratio $t_2 : mt_2 = 1.90$ –2.11.

Abdomen with ovoid, strongly convex preabdomen (Figs 121, 132) and very long and narrow, telescopic postabdomen (at rest retracted in preabdomen). Preabdominal terga (Fig. 132) very similarly sized and formed as in male, only T_5 distinctly longer (as long as or somewhat longer than T_3) and strongly posteriorly tapered and rounded; all preabdominal terga somewhat more densely setose (Fig. 132). Preabdominal sterna: S_{1+2} , S_3 and S_4 formed, coloured and setose as in male but S_5 unmodified, as long as or even slightly longer than S_4 but much narrower,

transversely trapezoidal (strongly tapered posteriorly), with rounded corners.

Postabdomen (Figs 135–137) very slender, elongate, with sclerites pale-pigmented to partly desclerotized, so differing from that of all other known *Pteremis* species. T_6 distinctly longer than broad, slightly narrower anteriorly, pale-brown pigmented only laterally and anteriorly, with short and fine setae in posterior half including 1 longer in posterior corners. T_7 also longer than broad, elongately oblong, narrower and shorter than T_6 , similarly pigmented and setose but setae fewer; T_8 about as long as broad, but its lateral parts reaching far ventrally (cf. Fig. 136), dorsally with tripartite pigmentation composed of a paler tongue-shaped medial part and larger and darker lateral parts (Fig. 135), both micropubescent except for anterior parts but only lateral parts with 1 longer and a few short fine



Figs 146–148. *Pteremis apterina* sp. nov., type locality and habitats. 146 – type locality at Lagoa verde near Sete Citades (Azores: São Miguel I.), with collecting sites (arrows); 147 – lush forest, habitat in the type locality; 148 – leaf litter in laurel forest near Caldeira Velha, microhabitat of the species. Photo by J. Roháček.

setae (Fig. 136). *T10* narrow, longer than broad, elongately pentagonal, very finely micropubescent and with a medial pair of small setae in posterior third (Fig. 135). *S6* similar to *T6* in setosity and pigmented pattern, also elongate but somewhat shorter and narrower posteriorly (Fig. 137). *S7* closely resembling *T7* but somewhat narrower, or slight-

ly tapered posteriorly (Fig. 137), distinctly smaller and narrower than *S6*. *S8* (Figs 136, 142, 144, 145) elongate, narrower than *S7*, with rounded posterior margin (Fig. 142), thus tongue-shaped but normally with posterior third or two-fifths upcurved dorsointernally (Figs 144, 145); posterior part of *S8* micropubescent, with 1 or 2 lateral setae,

and posteromedially with a group of 6–8 (4 or 6 very short, 2 long sinuate) setae, all on elevated sockets. *S10* (in largest extension) somewhat shorter but wider than *S8*, also longer than broad (Fig. 141), posteriorly narrowed and rounded, almost completely micropubescent and with rather rich setosity, including several long but fine marginal setae; anterior margin of *S10* sinuately emarginate (Fig. 141). Spectacles-shaped sclerite submembranous, represented by a pair of rather large ovoid but often distorted rings (Fig. 143). Spermathecae 2+1 (Figs 133, 134) unique by combining characters known in several other species: elongately pyriform, having main body (ball-shaped to broadly ovoid) separated from conical bases by 2 or 3 incomplete rings but conical bases densely overgrown by short, blunt, dark and curved spines; terminal parts of ducts long, well-sclerotized and dark-pigmented, and those of paired spermathecae connected far from body of spermathecae (Fig. 134) though not so far as in *P. fenestralis*. Cerci (Figs 135, 136) relatively small, moderately broad but somewhat dorsoventrally flattened (see Fig. 136), micropubescent, setose as in most other *Pteremis* species, including 2 long sinuate setae (dorsopreapical shorter than apical).

Etymology. The species name is derived from *Apterina* Macquart, 1835, a genus of Copromyzinae (currently a synonym of *Crumomyia* Macquart, 1825), to refer to aptery of the new species. It is a Latin noun in the nominative singular standing in apposition.

Comments. *Pteremis apterina* sp. nov. is (together with *P. vlasovi*, see below) externally most dissimilar to other species of the genus *Pteremis*. Apart from the entire aptery, it is also characterized by *pvt* absent, scutellum shortened and with very long laterobasal *sc* seta (Fig. 124), long and robust, distally shifted *vpa* (Fig. 140) on t_2 and strongly convex preabdomen and very narrowed female postabdomen (Fig. 142). However, apart from the modified female postabdomen, the structures of male and female terminalia generally resemble those of other congeners. As discussed above, it can be more related to *P. pulliceus*, *P. canaria* and *P. ferreus* than to *P. fenestralis*, mainly because of the spermatheca with surface rings separating the basal conical part from the distal ovoid main body (Fig. 133).

Pteremis apterina also differs from all congeners in a number of features in the male terminalia, including male *S5* with projecting posteromedial comb of spines (Fig. 131), male cercus with flattened apex bent posteriorly (Fig. 126), anterior lobe of gonostylus with longitudinal spinulose ledge terminated by a group (comb) of 4 heavily sclerotized blunt spines (Figs 127, 129) and distiphallus with slender band-like lateral sclerites apically connected (Fig. 130). Also, its unusually long and slender female postabdomen is characterized by a number of features, including all sclerites elongated and often partly depigmented (Figs 135, 137), tongue-shaped *S8* (Fig. 142) normally dorsointernally upcurved (Figs 144, 145), *S10* with anterior margin sinuately emarginate (Fig. 141) and spermathecae with conical bases densely overgrown by blunt, dark and curved spines (Figs 133, 134).

Biology. This wholly apterous species is associated with the leaf litter stratum, probably originally in laurel forests

(Laurisilva) of Azores, as found by means of pitfall trapping in Caldeira de Serra de Santa Bárbara in Terceira I. and by sifting leaf detritus under laurel trees in São Miguel I. (Fig. 148). However, material obtained by pitfall traps operated in Santa Maria I. shows that it now can also be abundant in exotic forest plantations. The habitat in the type locality at Lagoa verde near Sete Citades (Fig. 146) is also mostly secondary forest with only remnants of laurel trees preserved (Fig. 147).

Distribution. Azores: Terceira I. (Ilha Terceira), São Miguel I. (Ilha de São Miguel, type locality), Santa Maria I. (Ilha de Santa Maria). Because it is wholly wingless, *P. apterina* is surely endemic to the Azores. However, its presence on three different islands (distance between São Miguel I. and Santa Maria I. is ca 80 km, distance between São Miguel I. and Terceira I. is ca 135 km) seems to be peculiar and in need of explanation. Because there is no distinct morphological difference between specimens from these three island populations it is improbable they arose simultaneously and independently from a common winged ancestor three times. It is more likely that the species originated on only one of these islands and has been relatively recently introduced (as apterous adults or larvae) to other islands, e.g. via transport of forest detritus when planting trees during reforestation.

Pteremis vlasovi (Duda, 1938) comb. nov.

(Figs 149–167)

Limosina (*Paraspelobia*) *Vlasovi* Duda, 1938: 96 (both sexes, illustr.).

Type locality: Turkmenistan, Ashkhabad env. Lectotype: ♂ (designated by ROHÁČEK 1983: 230) (ZISP).

Paraspelobia vlasovi: ROHÁČEK (1983): 230–232 (generic combination, redescription, illustr.); PAPP (1984): 87 (Palaearctic catalog); ROHÁČEK et al. (2001): 189 (world catalog).

Type material examined. LECTOTYPE (designated by ROHÁČEK 1983): ♂ (ZISP), labelled (in Russian handwritten alphabet, cf. Fig. 150): ‘okr. Ashkhabada 28.II.32 Vlasov’, ‘Bugristye peski, glubokaya raskopka nory Sp. lept.’, ‘Paraspelobia Vlasovi Duda ♂ d. Duda’ (handwritten by O. Duda) and ‘Lectotypus ♂, Paraspelobia vlasovi Duda, J. Roháček des. 1980’ (red-framed label) (intact). PARALLECTOTYPES (examined by ROHÁČEK 1983): 7 ♂♂ 6 ♀♀, with same data as for lectotype; 2 ♂♂ 1 ♀, labelled: ‘okr. Ashkhabada 18.III.933 Vlasov’, ‘Bugrist. peski, v nachale Sp. lept.’; 1 ♀, labelled: ‘19 23/IV nora Rhombomys opimus Licht., Vlasov’. All deposited together with about 40 additional type specimens (to be considered paralectotypes) in ZISP. There are 11 more type specimens (also to be considered paralectotypes, 5 of them pinned on the same brick of elder pith, examined by author in 2022) in the collection of O. Duda (ZMHB), labelled similarly as those in ZISP but with red labels ‘Typus’ or ‘Paratypus’ (see Fig. 150).

Redescription (adapted from ROHÁČEK 1983). **Male** (cf. Figs 149, 151). Total body length ca 1.3–1.6 mm; general colour brown to pale brown (probably dark brown when alive), with greyish brown microtomentum, subshining on thorax and abdomen, otherwise relatively dull.

Head (Figs 149, 151, 155) about 1.5× higher than long, brown, paler anteriorly. Frons relatively wide in consequence of strongly reduced eyes (Fig. 151), brown, darker posteriorly, ochreous to yellowish at anterior margin, microtomentose, largely dull; occiput dark brown. Orbits, very narrow interfrontalia and ocellar triangle with pale grey (slightly glittering) microtomentum; frontal triangle similarly but very sparsely microtomentose. Dull brown



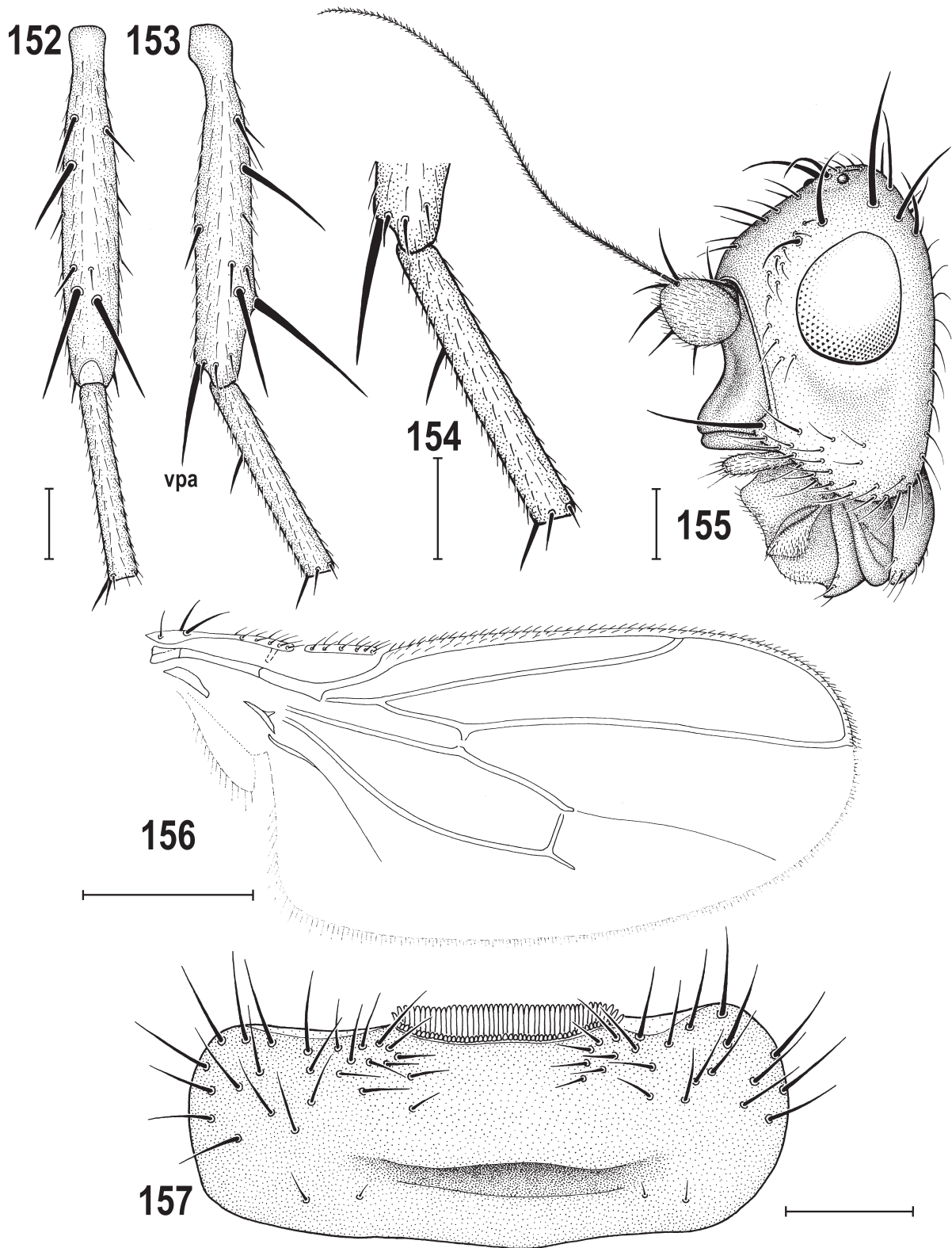
Figs 149–151. *Pteremis vlasovi* (Duda, 1938), female paralectotype. 149 – female, right laterally; 150 – labels of this specimen; 151 – head and thorax of the same specimen, dorsofrontally. Scales = 0.5 mm. Photo by E. Wolff.

stripes between orbits and interfrontalia twice wider than those between interfrontalia and frontal triangle, together almost forming dull M-shaped mark (Fig. 151) although less distinct than in other *Pteremis* species; frontal triangle very narrow and almost reaching anterior margin of frons; the latter narrowly ochreous to dirty yellow. Frontal lunule relatively long and narrow (almost as long as broad), ochreous-yellow, yellowish white microtomentose, hence lighter than anterior margin of frons or face. Face brown (Fig. 151), sparsely whitish grey microtomentose; facial cavities below antennae deeply concave (see Figs 149, 155) and medial carina well developed, both more shining than rest of head. Gena high because of reduced eye (Fig. 155), brown, greyish microtomentose and distinctly separated from occiput by a very narrow shining perpendicular stripe on postgena (Fig. 149). Cephalic chaetotaxy (Figs 151, 155): macrosetae less robust and shorter than in congeners; *pvt* small but well developed, strongly convergent to crossed; *occe* and *occi* subequal, about half length *vti*; *vti* longest of frontal setae; *vte* shorter than *vti*, and about as long as posterior *ors*; *oc* as long as *vte*; 2 *ors*, posterior about as long as *oc* and about 1.5 times as long as anterior *ors*; 4 or 5 *ifr*, all relatively short and weak, two middle pairs usually longer but also slender; 5–9 *ads* inside and below *ors* well developed and also setulae on ocellar triangle unusually long; *g* short weak and almost hidden among a number of (only slightly shorter) setae behind and below it (Fig. 155); *vi* long (slightly shorter than *vti*) but not robust, peristomal setulae almost as long as but finer than *g* and rather numerous (8–10); postocular setulae somewhat shorter than peristomals, in single long row. Eye reduced and flattened (Figs 149, 155), subcircular to suboval, narrowed posterodorsally (Fig. 155), with longest diameter 1.2 to 1.3 times as long as smallest genal height. Antenna brownish yellow (obviously darker when alive), with 1st

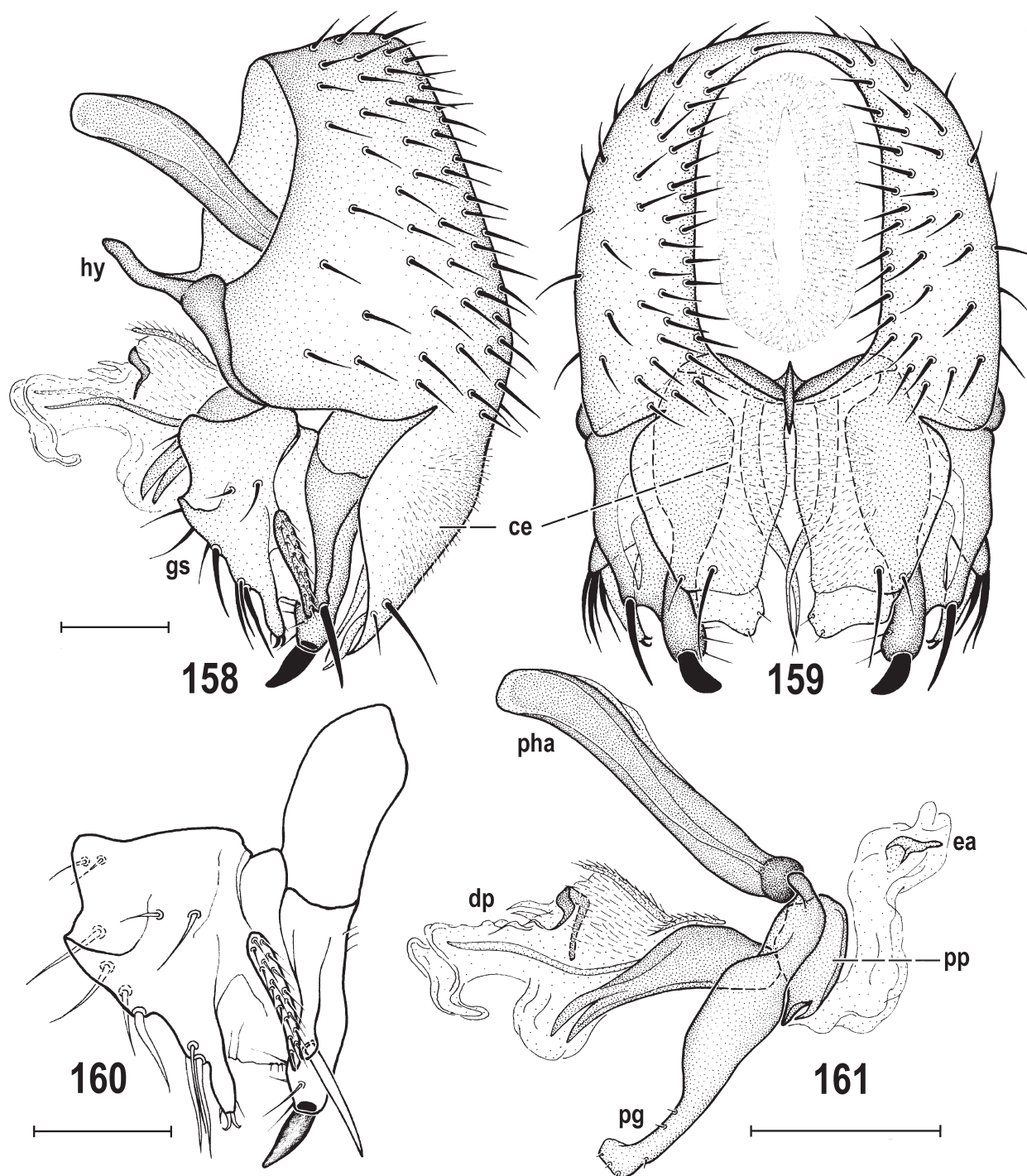
flagellomere usually darker and only a little longer than pedicel, having whitish ciliation on apex slightly longer than cilia on arista. Arista long, about 5.3 times as long as antenna, with short but dense ciliation.

Thorax dark brown to brown, greyish brown microtomentose; mesonotum subshining, pleuron dull. Sutures between pleural sclerites narrowly pale brown to ochreous only in posterior half of pleuron (Fig. 149). Mesopleuron with small and narrow shining spot above fore coxa. Scutellum large and relatively long, rounded subtriangular, slightly convex dorsally. Thoracic chaetotaxy: mesonotal macrosetae relatively weak (Figs 149, 151); 1 *hu* (almost as long as anterior *npl*) and 1 enlarged microseta on humeral callus; 2 *npl* (posterior short, as long as *sa*); 1 small *prs* and 1 small *sa*; 2 *pa*, the outer long (as long as *dc*), the inner small and situated rather far from outer *pa*; only 1 long posterior *dc* (shorter than laterobasal *sc*) in prescutellar position, 2 or 3 *dc* microsetae in front of *dc* macroseta only slightly enlarged, somewhat longer than *ac* microsetae; 6–8 rows of *ac* microsetae on suture but only 4 in front of scutellum; medial prescutellar *ac* pair not longer than other *ac* microsetae; 2 very long and robust *sc*, laterobasal longer than *dc* or outer *pa*, apical (by far longest thoracic seta) almost twice longer than laterobasal; 2 *spl*, posterior not very long (as long as anterior *npl*) but also anterior distinct though short (one-third to half length of posterior).

Legs relatively long and slender (particularly tarsi), yellowish brown, trochanters, knees and tarsi often yellow, femora usually darker. Pedal chaetotaxies: *f*₁ with a row of 4 or 5 posterodorsal setae and with a longer and denser row of 8 or 9 posteroventral setae (those in middle of tibia longest). *f*₂ anteriorly with a short subapical row of 1 (most distal) longer seta and 2 or 3 short setae. *t*₂ ventrally (see Fig. 153) with only 2 setae, 1 long robust subapical (slightly diverging from axis of tibia) seta considered to be a distally



Figs 152–157. *Pteremis vlasovi* (Duda, 1938), male paralectotype. 152 – left t_2 and mt_2 dorsally; 153 – ditto, anteriorly; 154 – apex of left t_2 and mt_2 anteriorly (enlarged); 155 – head, left laterally; 156 – right wing; 157 – male $S5$ ventrally. Scales = 0.1 mm (Figs 152–155, 157), 0.5 mm (Fig. 156). Adapted from ROHÁČEK (1983: Figs 1–4, 9).

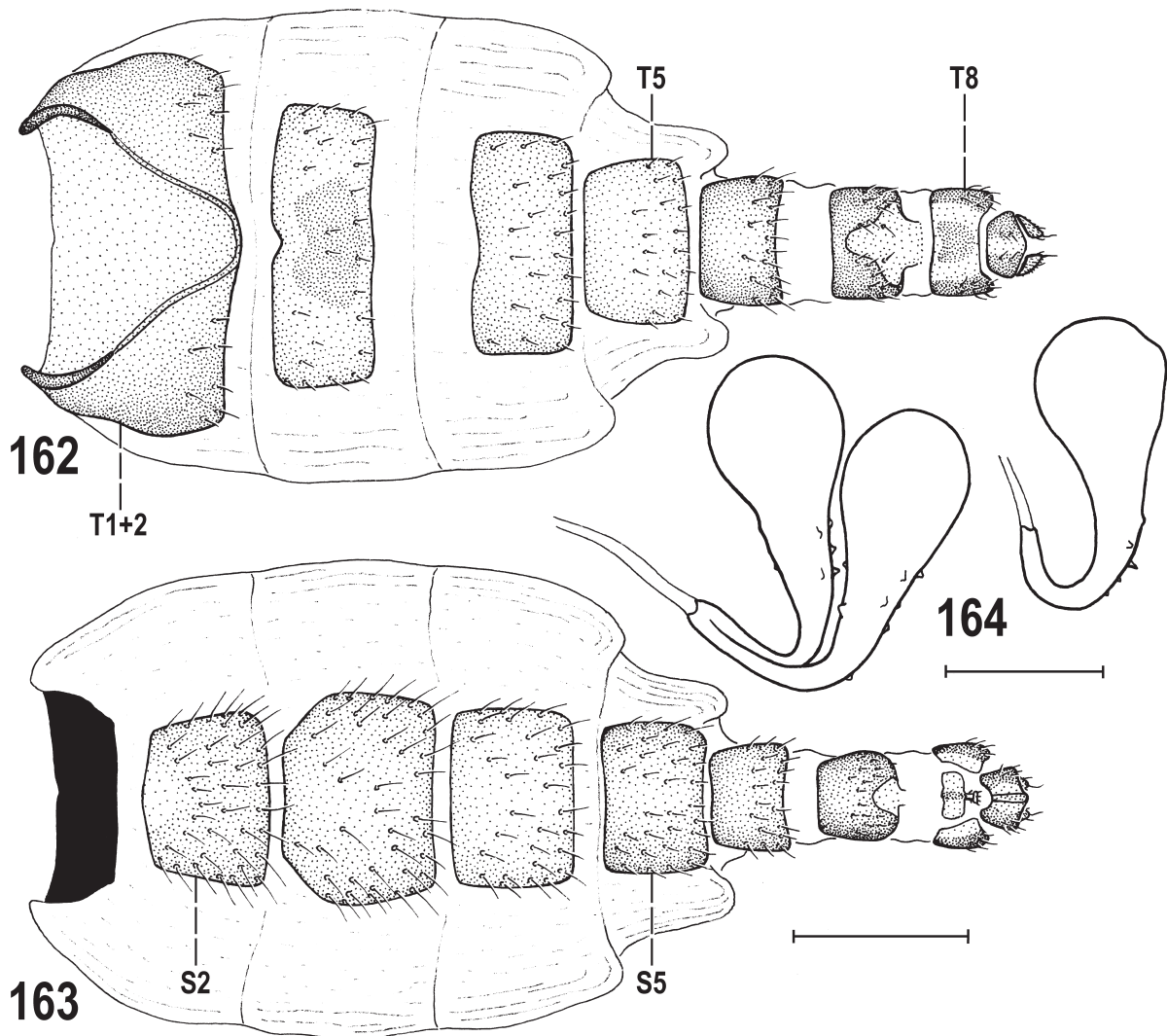


Figs 158–161. *Pteremis vlasovi* (Duda, 1938), male paralectotype. 158 – external genitalia, left laterally; 159 – ditto, caudally (aedeagal complex omitted); 160 – gonostylus, left laterally; 161 – aedeagal complex, laterally. Adapted from ROHÁČEK (1983: Figs 5–8). Scales = 0.05 mm (Figs 158–160), 0.1 mm (Fig. 161). For abbreviations see Material and methods.

shifted *vpa* and 1 short anteroventral below middle; thus *va* seta absent; dorsally (Fig. 152) with chaetotaxy similar to that of other *Pteremis* species but both posterior setae very small and weak (often hair-like), and also both short setae above distal pair of long setae weak; apex of tibia provided with 3 small subapical setae anteriorly (Fig. 154) and 2 longer posteriorly. t_3 with 1 small but distinct *va* setula. Other parts of femora and tibiae uniformly finely

setulose. Mid basitarsus (mt_2) long and always with 1 short but distinct ventral seta (Figs 153, 154). Hind basitarsus (see Fig. 149) relatively slender and more elongate than in all other congeners as are also all other segments of tarsi. Ratio $t_2 : mt_2 = 1.53–1.73$.

Wing (Fig. 156) peculiar with its whitish membrane (Fig. 149) and yellowish white veins, only *C* pale yellowish brown. *C* not extended beyond apex of R_{4+5} . Cs_1 with



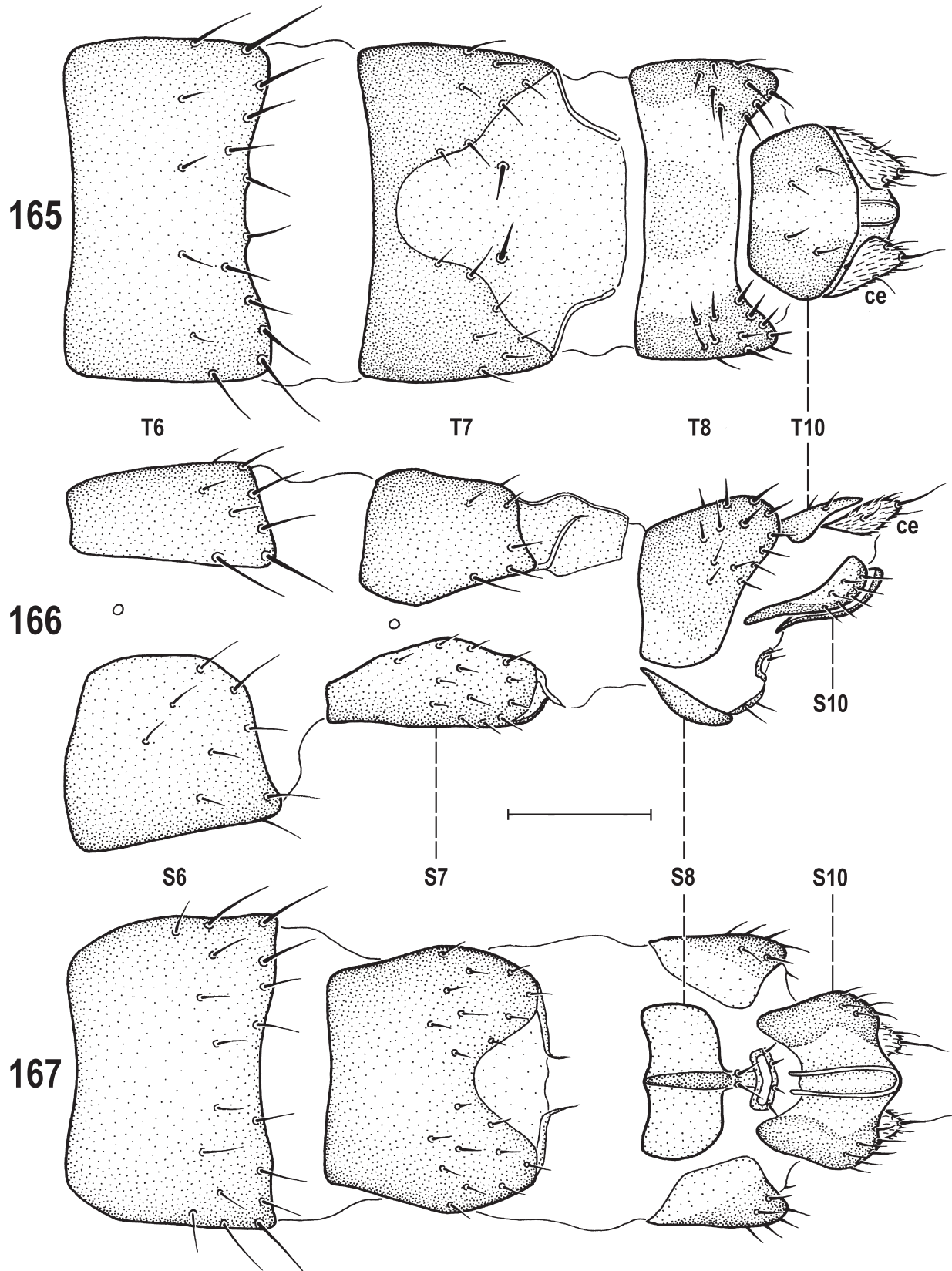
Figs 162–164. *Pteremis vlasovi* (Duda, 1938), female paralectotype. 162 – whole abdomen, dorsally; 163 – ditto, ventrally; 164 – spermathecae. Adapted from ROHÁČEK (1983: Figs 10–12). Scales = 0.3 mm (Figs 162, 163), 0.05 mm (Fig. 164). For abbreviations see Material and methods.

relatively short setulae, though longer than those on rest of *C*. Cs_2 distinctly longer than Cs_3 . R_{2+3} relatively long, basally almost straight, apically slightly upcurved to *C*; R_{4+5} sinuate, but distally only slightly upcurved to *C* and ending closer to apex of wing, than to venal fold of *M*. Discal cell (*dm*) relatively long but not narrow and distally slightly tapered, with small process of *M* and longer one of CuA_1 beyond *dm-cu*; that of *M* continued by venal fold almost to wing margin; both outer corners of *dm* cell slightly obtuse-angled. A_1 moderately long, with only basal part fully developed, more distally represented by colourless fold ending far from wing margin. Anal lobe well developed; alula small and narrow. Wing measurements: length 1.33–1.78 mm, width 0.51–0.70 mm, *C-index* = 1.48–1.72, $r-m\backslash dm-cu : dm-cu = 2.33-3.27$. Haltere yellowish, knob slightly darker.

Abdomen brown, sparsely greyish microtomentose, rather weakly sclerotized. Preabdominal terga $T2-T5$ sparsely (less than sterna) and relatively shortly setose, also setae in posterior corners short and weak. $T1+2$ largest

tergum, with rather characteristic structure and pigmentation (cf. Fig. 162, same in both sexes). In contrast to female, preabdominal terga ($T3-T5$) and sterna ($S2-S5$) not reduced, broad. $S5$ (Fig. 157) comparatively large, transversely oblong, with rounded corners. It carries a posteromedial, relatively long, comb consisting of a row of blunt spines (those lateral shortened) and a row of small tuberculiform spines in front of it. In contrast to other *Pteremis* species, there is no pale-pigmented and micropubescent semicircular area in front of posteromedial comb but a group of shorter inclinate setae on each side is present (Fig. 157); setae in posterior two-thirds of lateral parts of $S5$ well developed, longer and thicker. Disc of $S5$ (medially, behind anterior margin) with transverse, strongly sclerotized and dark-pigmented stripe.

Genitalia. Epandrium (Figs 158, 159) small compared to other parts of postabdomen, symmetrical, uniformly shortly and densely setulose, particularly around anal fissure (Fig. 159), the latter narrow, elongately suboval, with lateral margins almost parallel. Cerci large, each



Figs 165–167. *Pteremis vlasovi* (Duda, 1938), female paralectotype. 165 – postabdomen, dorsally; 166 – ditto, left laterally; 167 – ditto, ventrally. Adapted from ROHÁČEK (1983: Figs 13–15). Scale = 0.1 mm. For abbreviations see Material and methods.

partly (anterolaterally) separated by an incision from epandrium, far projecting ventrally but distally flattened (Fig. 158) and weakly sclerotized, finely micropubescent, lateroventrally with 1 long and 1 short seta, and ventrally terminated in flat, submembranous appendage, with 2 microsetae on apex (Fig. 159). Cerci medially separated by a deep and very narrow incision, only dorsally, below anal fissure, narrowly fused (Fig. 159). Medandrium low (short) and broad, with usual lateral arms, each connected with posterior part of gonostylus, posteromedially with narrow but short, dark-pigmented keel (Fig. 159). Hypandrium with short and asymmetrical anterior apodeme (Fig. 158) as in other *Pteremis* species, but its internal arms (connected posteriorly with postgonites) carrying a pair of very slender, long and apically acutely pointed appendages projecting ventrally (visible medially between cerci, see Fig. 159). Gonostylus (Figs 158–160) of the same general construction as in other *Pteremis* species (Figs 28–30), of complex structure, composed of larger (longer) anterior lobe and of smaller (shorter and more medial) posterior lobe. Anterior lobe (Fig. 160) pale-pigmented, flat, with rounded rectangular anterodorsal corner, 3 thicker, slightly curved to sinuate setae anteroventrally plus 1 slender seta close to posterior pair and terminated by 1 ventral, posteriorly directed projection having a pair of small curved spines on apex; posterior part of anterior lobe of gonostylus with oblique longitudinal spinulose ledge (as in other congeners). Posterior lobe of gonostylus more heavily sclerotized and dark-pigmented (cf. Fig. 158), projecting ventrally and terminated by robust (somewhat bent medially) spine (see Figs 158, 159) apart from 2 fine subapical setae; posterolaterally there is a short process carrying a robust, slightly bent and ventrally (or posteroventrally) directed seta (see Fig. 160). Aedeagal complex (Fig. 161) of typically simple construction, surprisingly most similar to that of *P. apterina*. Phallopodeme simply rod-like, as long as aedeagus, with reduced dorsal keel. Aedeagus with compact, relatively long (as in *P. apterina*) phallopore (Fig. 32) having shortly bicuspidate (ventral) apex. Distiphallus largely membranous, weakly sclerotized and pale-pigmented mainly proximoventrally, basally narrow, distally dilated (most in the middle), laterally with an usual pair of slender, pale, band-like sclerites. Middle part of distiphallus with small and slender transverse horseshoe-shaped dorsolateral sclerite (similar to that of *P. apterina*); dorsoproximal part of distiphallus finely haired and its dorsal sclerite very slender and pale-pigmented (Fig. 161). Postgonite as long as distiphallus or phallopore, slightly sinuate in lateral view, with proximal third more slender than in all relatives, widest in the middle; distal third slender and relatively straight but ending in terminal knob having a few microsetulae on apex. Ejacapodeme small, with short digitiform process distally (see Fig. 161).

Female (Fig. 149). Head, thorax, legs and wings as in male unless mentioned otherwise. Total body length 1.3–2.3 mm. Legs more slender than in male; t_2 with setae longer on the average, and often with an additional small seta above most proximal anterodorsal seta; mid tarsus slightly longer including mt_2 . Ratio $t_2 : mt_2 = 1.50–1.67$.

Wing measurements: length 1.15–1.75 mm, width 0.53–0.81 mm, $C\text{-index} = 1.40–1.89$, $r\text{-}m\backslash dm\text{-}cu : dm\text{-}cu = 2.35–3.18$.

Abdomen (Figs 162, 163) with preabdominal terga and (less so) sterna reduced and pleural membranous part enlarged, very dilatable during gravidity. $T1+2$ as large as that of male but $T3–T5$ markedly shortened and narrowed: $T3$ as long as but distinctly wider and more transverse than $T4$ and is the largest and widest tergum; $T5$ longer but narrower than $T4$ (Fig. 162), all very shortly and sparsely setose. Preabdominal sterna narrower but $S3$ and $S4$ longer than adjacent terga. $S2$ (or $S1+2$) unusually larger than $S5$ but slightly transverse (narrower anteriorly); $S3$ larger than other sterna (Fig. 163), roughly transversely hexagonal; $S4$ transversely suboblong, slightly larger than (darker) $S5$; $S2–S5$ with long, dense fine setae.

Postabdomen (Figs 165–167) narrow and telescopically retractile into preabdomen (cf. Fig. 162). $T6$ narrower but darker than $T5$, simply suboblong (Fig. 165), with short setae in posterior half; $T7$ as wide as but yet longer than $T6$, distinctive by its posterior, almost membranous part being anteromedially deeply extended into anterior darker and shortly setulose part; medially, in submembranous part, there is a pair of robust short setae (Fig. 165). $T8$ dorsally with tripartite pigmentation composed of pale brown medial spot and dark-pigmented lateral parts (Fig. 165) being shortly setose posterodorsally, and bare, with broadly pale ventral margin (see Figs 166, 167). $T10$ relatively broad, transversely rounded pentagonal, medially pale-pigmented and carrying 2 pairs of short setae (Fig. 165). $S6$ slightly narrower and longer than $T6$, with rounded anterior corners and shortly setulose in posterior half. $S7$ narrower than $S6$, somewhat tapered anteriorly, with subcordate darker pigmentation, thus posteromedially with pale-pigmented rounded triangular area; dark part of $T7$ with very short setulae. $S8$ (Fig. 167) small, of peculiar form, besides main anterior pale-pigmented but bare plate with dark medial stripe, there is a very small, posterior, transverse, frame-shaped structure carrying 4 setulae posteriorly; an additional pair of small setulae arise on connective membrane between these structures. $S10$ also distinctive: its lateral parts convex, dark, heavily sclerotized and shortly setulose; its pale medial part bears an unusual, ventrally projecting, fillet-like structure resembling a very narrow U in ventral view (Fig. 167). Spectacles-shaped sclerite not observed. Spermathecae (Fig. 164) blackish, pear-shaped, with elongate, strongly curved and sclerotized distal parts of ducts; proximal part of spermathecal bodies with several small tubercles and thornlets. Cerci (Figs 165, 166) small, subconical, micropubescent, each with several short, hair-like, slightly sinuate or curved setae, apical longest.

Comments. DUDA (1938) placed this unusual species in its own subgenus *Paraspelobia* and discussed its affinity (on the basis of some external characters) to *Spelobia* Spuler, 1924 and *Chaetopodella* Duda, 1920, both clearly unrelated groups of Limosiniinae. HACKMAN (1969) placed it near *Chaetopodella*. ROHÁČEK (1983), based on examination of the male and female terminalia, recognized its affinity to *Pteremis* species but retained it in the redescribed genus *Paraspelobia* because of several distinct differences.

For the reasons given in the introduction, but mainly because of clearly identical construction of the male genitalia, the species is now considered a member (albeit most aberrant) of the genus *Pteremis* and a sister group to the rest of the genus. *Pteremis* species other than *P. vlasovi* share the following putative synapomorphies: mid basitarsus with ventral seta reduced or absent; male *S5* with membranous area in front of posteromedial comb of spines; ventral projection of anterior lobe of gonostylus projecting posteriorly, posterior lobe of gonostylus with setae adjacent to terminal spine long and strong; female *S8* with posteromedial group of setae on elevated sockets; paired spermathecae with sclerotized parts of ducts fused behind its common proximal end.

Externally, *P. vlasovi* can easily be recognized by the reduced eyes and high gena (Fig. 155), t_2 with *vpa* seta shifted distally and so resembling *va* seta (Fig. 153), mt_2 with distinct basitarsal seta (Fig. 154), wing with milky white membrane and *C* not extended beyond apex of R_{4+5} (Fig. 156). Further, its epandrium is very shortly setose (Fig. 159), female *T7* (Fig. 165) and *S7* (Fig. 167) are modified, female *S8* and *S10* (Fig. 167) carry peculiar structures, female *T10* has 2 pairs of small setae, cerci are small (Fig. 165) and spermathecae (Fig. 164) have distal sclerotized parts of ducts strongly curved.

Biology. Judging from label data of type specimens and also the adult morphology (reduced eyes, prolonged legs, partly desclerotized abdomen) the species is microcavernicolous, inhabiting burrows and nests of small rodents, viz. the long-clawed ground squirrel *Spermophilopsis leptodactylus* (Lichtenstein, 1823) (for its current classification see KRYŠTUFEK et al. 2016) and (less frequently) also the great gerbil *Rhombomys opimus* (Lichtenstein, 1823) in sandy desert habitats, see also ROHÁČEK (1983). Adults were recorded in II–V and VIII (DUDA 1938, ROHÁČEK 1983, type material examined) but surely occur in burrows also in other months of year as is usual for strictly subterranean species of Limosininae.

Distribution. Turkmenistan; the species is hitherto only known from (the long) type series from the vicinity of Ashkhabad, the capital of the country.

Key to West Palearctic species of *Pteremis*, including *P. vlasovi* from Central Asia

- 1 Apterous, with halteres also absent (Figs 119, 121) or winged but with eyes strongly reduced (Fig. 155) and wings milky whitish (Fig. 149); t_2 terminally with only 1 subapical *vpa* seta (Figs 140, 153). 2
- Fully winged (Figs 1, 40) or wings shortened (Figs 2, 3, 17–21), wing membrane pale brown fumose (Figs 16–21, 78) and eyes never reduced (Figs 1, 2, 42); t_2 terminally always with *vpa* (Figs 23, 97, 118) more distant from apex of tibia and often also *va* seta (directed in axis of tibia), which can be shortened (Figs 23, 57, 70). 3
- 2(1) Wingless and without halteres, eye relatively large (Figs 119, 121); laterobasal *sc* slightly to distinctly longer than apical *sc* (Fig. 124); preabdomen convex,

- strongly sclerotized and blackish (Fig. 121); epandrium long-setose (Fig. 126); anterior lobe of gonostylus with posterior oblique longitudinal spinulose ledge terminated by 4 robust blunt spines (Figs 127, 129); female postabdomen strongly narrowed, with *S8* relatively large, long and usually upcurved (Figs 144, 145), setose as in Fig. 142; female *S10* with long setae and medially simple (Fig. 141). *P. apterina* sp. nov.
- Fully winged (Fig. 156) but veins pale and wing membrane milky white (Fig. 149), eye reduced (Fig. 155); laterobasal *sc* markedly shorter than apical *sc* (Fig. 151); preabdomen weakly sclerotized, pale brown and in female with sclerites reduced (Figs 162, 163); epandrium very shortly setose (Fig. 158); anterior lobe of gonostylus with posterior oblique longitudinal spinulose ledge terminally without robust spines (Fig. 160); female postabdomen less narrowed, with *S8* small, transverse, bare, medially narrowly dark-pigmented and posteriorly bearing small, transverse, frame-shaped structure with 4 setulae (Fig. 167); female *S10* very shortly setulose only posterolaterally, medially with narrow, ventrally projecting U-shaped fillet-like structure (Fig. 167). *P. vlasovi* (Duda, 1938)
 - 3(1) t_2 with distinct *va* seta, as long as (Fig. 24) or slightly shorter than *vpa* (Fig. 56) or at least half length of *vpa* (Fig. 71). 4
 - t_2 with *va* seta reduced (Fig. 116) or absent (Fig. 95). ... 6
 - 4(3) t_2 with *va* seta only half length of *vpa* seta (Fig. 71); wing relatively elongate, less rounded apically (Fig. 65), with R_{4+5} distally almost straight, with apex a little upcurved. Generally darker both on head (frons dark brown to blackish and face dark brown) and thorax (almost entirely dark brown, also with pleural sutures and ventral part of sternopleuron brown). Male *S5* rather uniformly a densely setose and with posteromedial microtomentose area reduced, short (Fig. 74); gonostylus large compared to epandrium (Fig. 68), and its anterior lobe with ventral, posteriorly directed projection very robust, heavily sclerotized and strongly bent medially (Fig. 67); postgonite distally only slightly dilated (Fig. 73). Female unknown. *P. tenebricus* sp. nov.
 - t_2 with *va* seta long (Figs 24, 56); wing relatively wider, with apex broadly rounded (Figs 16, 43) and R_{4+5} distally more strongly upcurved to *C* or wing shortened (Figs 17–21), usually with *dm-cu* absent. Head and thorax relatively pale: frons anteriorly reddish brown to orange yellow, face pale brown or yellow, thorax with sutures between pleural sclerites ochreous and/or ventral part of sternopleuron pale brown. Male *S5* setose mainly laterally and at sides of much larger posteromedial microtomentose area (Figs 26, 51); gonostylus small compared to epandrium (Figs 29, 46), with ventral, posteriorly directed projection slender (Figs 30, 48); postgonite distinctly dilated distally (Fig. 50) to knob-like (Fig. 32). 5
 - 5(3) Wing normal (Fig. 16) or shortened (Figs 17–21). t_2 with *va* seta as long as *vpa* seta (Figs 23, 24) and both posterior subapical setae short (Fig. 24). Head with frontal lunule, face and gena yellow to ochreous.

- Male *S5* with setae thicker and posteromedial comb formed by more robust, less dense and less numerous spines (Fig. 26); male cercus not bulging dorsolaterally, also ventrally micropubescent, and with only a small tubercle on apex (Fig. 28); anterior lobe of gonostylus with ventral, posteriorly directed projection shorter and apically simple (Fig. 30); posterior lobe of gonostylus with terminal spine robust (Figs 28, 30). Phallopore more robust, distiphallus not dilated dorsoventrally and postgonite strongly sinuate, with apex knob-like (Fig. 32). Female *T8* short, with medial pigmented part small (Fig. 35); *S8* also shorter, tapered posteriorly and posteromedially (on margin or in membrane behind it) with a pair of small setulae on elevated sockets (Fig. 38); spermathecae ovoid, with a group of spine-like tubercles on tapered base (Fig. 33); sclerotized terminal parts of ducts long and slender, in paired spermathecae fused far from their bodies (Fig. 37). *P. fenestralis* (Fallén, 1820)
- Wing always fully developed (Fig. 43). t_2 with *va* seta somewhat shorter than *vpa* seta (Figs 56, 57) and one of posterior subapical setae distinctly enlarged (Fig. 24). Head with frontal lunule, face and gena reddish brown to brown. Male *S5* with setae finer and posteromedial comb formed by thinner, dense and more numerous spines (Fig. 51); male cercus distinctly bulging dorsolaterally, ventrally bare (Fig. 47), and terminally modified, provided with subapical protruding curved ledge (with 2 setulae) and flattened apex (see also Fig. 49); anterior lobe of gonostylus with ventral, posteriorly directed projection longer, slender and with finely trifurcate apex (Fig. 48); posterior lobe of gonostylus with terminal spine slender and elongate (Figs 47, 48). Phallopore slender with tapered acute apex; distiphallus distinctly dilated dorsoventrally and postgonite slightly sinuate, with less clubbed apex (Fig. 50). Female *T8* distinctly longer, with medial part pale-pigmented but large (Fig. 53); *S8* longer, with posterior half membranous and provided with a transverse row of 2 long (lateral) setae and 4 medial setulae on elevated sockets (Fig. 59); spermathecae pyriform, with distinct conical part, separated from distal subcircular part by 3 or 4 (some incomplete) rings (Fig. 61); sclerotized terminal parts of ducts relatively shorter and thicker, in paired spermathecae fused near conical parts of spermathecae (Fig. 61). *P. pulliceps* sp. nov.
- 6(3) t_2 with *va* seta reduced but present and apex of t_2 posteriorly with 3 small setae (Fig. 118). Humeral callus and notopleural area of thorax brown. Male *S5* with large pale-pigmented and micropubescent semicircular area and posteromedial comb of spines wide and composed of dense fine spines (Fig. 108); male cercus micropubescent except for ventral part being flattened and projecting into distinctive ventromedial flat but acutely pointed apex (Figs 104); anterior lobe of gonostylus with anterodorsal process extremely long, far projecting dorsally (Figs 104, 106) and its (more or less separate) dark posteroventral part with robust ventral, posteriorly directed ventral projection heavily

sclerotized with simply pointed apex (Fig. 106); phallopore relatively robust and with blunt (ventral) apex (Fig. 107); postgonite with apex dilated but rather shortly lancet-shaped (Fig. 107). Female *S8* transversely semioval, with only 2 pairs of setae and reduced micropubescent and its posterior membranous part with a medial group of 2 long sinuate and 4 short setae between them, all on elevated sockets (Fig. 112); *S10* transversely subpentagonal, anteriorly broadly emarginate and finely setose (Fig. 114); spermathecae pyriform, with basal conical part separated from ovoid body by only 1 complete ring-shaped ledge (Fig. 115). *P. ferreus* sp. nov.

– t_2 with *va* seta absent and apex of t_2 posteriorly with only 2 small setae (Fig. 95). Humeral callus and notopleural area of thorax pale brown to pale ochreous. Male *S5* with small (short) pale-pigmented and micropubescent semicircular area and posteromedial comb of spines narrower, composed of shorter, less dense and thicker spines (Fig. 84); male cercus with micropubescent in two separate groups (on convex posteromedial part and on ventral part, Fig. 81) and its apex terminated by a small rounded lappet (Fig. 83); anterior lobe of gonostylus with short anterodorsal corner (Figs 82, 85) and its posteriorly directed ventral projection spiky jagged and pale-pigmented (Fig. 85); phallopore with (ventral) apex more acute (Fig. 87); postgonite distally elongately spatulate, with apex rounded (Fig. 87). Female *S8* longer than broad, pale-pigmented both anteriorly and posteriorly, with more setae in the middle, and with a posteromedial group of 6 longer setae on elevated sockets (Fig. 91); *S10* more elongate, semi-oval, with projecting anterolateral corners and longer setae at posterior margin (Figs 88, 93); spermathecae pyriform, but each with basal conical part separated from spherical body by 3, or more, usually incomplete, rings (Fig. 94). *P. canaria* (Papp, 1977)

East Palaearctic and Nearctic species in *Pteremis*

Pteremis kaszabi (Papp, 1973)

Leptocera (*Pteremis*) *kaszabi* Papp, 1973a: 415 (male). Type locality: Mongolia, Central aimak, Bogdo ul, Bugijn až achuj [1,650 m]. Holotype: ♂ (HNHM).

Pteremis kaszabi: PAPP (1984): 88 (generic combination, Palaearctic catalog); ROHÁČEK et al. (2001): 211 (world catalog).

Comments. This species is known from only the male holotype. According to PAPP (1973a) it has the wing fully developed and differs from *P. fenestralis* mainly by its small body (ca. 1.2 mm), very large head (wider than thorax and longer than high), 3 equally long *ifr* and R_{4+5} distally more strongly upcurved to *C*. The colouration of face (considered by PAPP 1973a also to be different) falls in fact within the variability of *P. fenestralis*. Judging from these characters *P. kaszabi* possibly is a valid species but its relationships are unknown because PAPP (1973a) did not describe structures of its male terminalia.

Distribution. Palaearctic: Mongolia.

***Pteremis mongolicus* (Papp, 1973)**

Leptocera (*Pteremis*) *fenestralis* spp. *mongolica* Papp, 1973a: 414 (female). Type locality: Mongolia, Bulgan aimak, between Somon Chischig-Öndör and Somon Orchon, 23 km NNE from Chischig-Öndör [1,390 m]. Holotype: ♀ (HNHM).

Pteremis mongolica: PAPP (1984): 88 (generic combination, species status, Palaearctic catalog); ROHÁČEK et al. (2001): 211 (world catalog).

Comments. *Pteremis mongolicus* was originally described as a subspecies of *P. fenestralis* based on 4 brachypterous females, and only subsequently elevated to species status by PAPP (1984). According to PAPP (1973a: 415) the only distinct differences from the brachypterous form of *P. fenestralis* (treated by PAPP 1973a, as *L. (P.) fenestralis nivalis*) are the more abbreviated wings with incomplete R_{2+3} . However, this type of wing reduction with similarly modified R_{2+3} vein (see Fig. 21) is also known in the brachypterous form of *P. fenestralis* described from Finland by FREY (1947) as *P. subapterus*, see above. Consequently, *P. mongolicus* may only be a strongly brachypterous form of *P. fenestralis* identical to f. *subapterus*. Nevertheless, without study of the female postabdominal structures (*S8* and spermathecae in particular) this suspicion cannot be demonstrated.

Distribution. Palaearctic: Mongolia.

***Pteremis unicus* (Spuler, 1924)**

Leptocera (*Pteremis*) *unica* Spuler, 1924: 134 (female). Type locality: USA, Wyoming, Yellowstone National Park. Holotype: ♀ (USNM).

Leptocera (*Pteremis*) *unica*: RICHARDS (1965): 722 (Nearctic catalog); MARSHALL (1984): 397 (taxonomic notes).

Pteremis unica: ROHÁČEK et al. (2001): 211 (world catalog, generic combination).

Comments. MARSHALL (1984) revised the female holotype, the only known specimen, but it is extremely damaged and could not be redescribed. It has been retained in *Pteremis* as a doubtful species although its generic placement is uncertain (ROHÁČEK et al. 2011).

Distribution. Nearctic: USA (Wyoming).

***Pteremis wirthi* (Marshall, 1984)**

Leptocera (*Pteremis*) *wirthi* Marshall, 1984: 397 (both sexes, illustr.). Type locality: Canada, Quebec, Mt. Albert, Gaspé Provincial Park. Holotype: ♂ (CNCI).

Pteremis wirthi: ROHÁČEK et al. (2001): 212 (world catalog, generic combination).

Material examined. CANADA: ONTARIO: Algonquin Provincial Park, Swan Lake Station, Scott Lake Survey, Sphagnum, 6.v.1995, 3 ♂♂ 1 ♀ (1 ♂ 1 ♀ f. brach), S. A. Marshall leg. et det. (DEBU, 1 ♂ 1 ♀ genit. prep.).

Comments. This Nearctic species was described by MARSHALL (1984) as a very close relative of *P. fenestralis* differing from the latter species by its longer *stpl* seta and brown gena and some detail of the structure of gonostylus. However, this wing polymorphic species also differs from *P. fenestralis* in having wings of a macropterous form shorter than the abdomen. In order to evaluate its relationships to other species of *Pteremis* I have examined male and female terminalia of *P. wirthi* in more detail. Its closest affinity to *P. fenestralis* has been confirmed (see above under *P. fenestralis*) and the most distinct differences against the latter species can be summarized as follows:

Male *S5* is most similar to that of *P. fenestralis* both as

regards the posteromedial comb of spines and the shape of the pale-pigmented area in front of it but setae on the sides of this area are sparse, longer and more robust. Male genitalia with cercus relatively short and hence most similar to that of *P. fenestralis* including apical tubercle but the latter is more broad. Anterior lobe of gonostylus with ventral process darkened and formed as in *P. fenestralis* but anterodorsal process of this lobe is distinctly different, markedly prolonged, more resembling that of *P. ferreus* (cf. Fig. 106) although shorter and more slender, and the posterolateral oblique longitudinal ledge finely long-spinulose; posterior lobe of gonostylus, besides the robust terminal spine with also 2 adjacent setae strongly thickened, spine-like (unlike all congeners). Distiphallus in the middle dorsoventrally dilated (as in most species, except for *P. fenestralis*); postgonite not knob-like apically, distally most similar to that of *P. pulliceus*, cf. Fig. 50).

Female *S8* different from that of *P. fenestralis*, distinctly more transverse, its pigmented part with 2 pairs of setae (lateral and medial), those medial very close each to other and its membranous posterior part with a transverse row of 6 setae (2 lateral long), on elevated sockets, resembling that of *P. pulliceus* (see Fig. 59). Spermathecae most similar to those of *P. fenestralis*, including spine-like tubercles on tapered base but of more elongate to pyriform shape and with distal sclerotized parts of ducts fused relatively close to bodies of paired spermathecae. Female cerci broad and distinctly flattened as are those of *P. fenestralis* (cf. Figs 34, 35).

Pteremis wirthi can also be recognized by means of the sequence of the barcoding region of COI (see BIN BOLD:ACB9048 in BOLD database), with pairwise distance from *P. fenestralis* being about 5%, see https://v4.boldsystems.org/index.php/Public_BarcodeCluster?clusteruri=BOLD:ACB9048.

Distribution. Nearctic: Canada (Alberta, Northwest Territories, Ontario, Quebec, Saskatchewan) (ROHÁČEK et al. 2011).

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