

SUPPLEMENTARY INFORMATION

Title

New fossil insect order Permopsocida elucidates major radiation and evolution of suction feeding in hemimetabolous insects (Hexapoda: Acercaria)

Short Title

New fossil order elucidates evolution of Acercaria

Authors

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S1 Text

(A) Extended Material and Methods. (B) Systematic Paleontology. (C) SI References.

(A) Extended Material and Methods

Specimen depositories

MCZ - Museum of Comparative Zoology at Harvard University, Cambridge, USA

NHM - The Natural History Museum London, UK

NIGP - Nanjing Institute of Geology and Paleontology, Academia Sinica, China

PIN - Paleontological Institute of Russian Academy of Sciences, Moscow, Russia

PU - Perm State University, Perm, Russia (specimen stored at PIN)

SMNS - Staatliches Museum für Naturkunde Stuttgart (SMNS), Germany

Preparations of specimens

The holotype of *Psocorrhyncha burmitica* gen. et sp. nov. (NIGP161473) is embedded in a large piece of amber containing several syninclusions (more than 20 arthropods). The amber piece was cut to separate each inclusion. The piece containing the holotype was subsequently ground to remove excess amber and then polished. Following this procedure, we found the included insect specimen was not clearly visible resulting from a series of fractures in the amber, causing mirror effects. In addition, there was a large bubble enveloping the abdomen (including genitalia), and a large portion of the thorax and wings.

To remedy these optical disturbances we infused the amber piece with Canada balsam. First, the specimen was manually polished using Emery papers with varying and successively finer grains until the apices of the fractures were reached (Fig. S1a). The polished piece was then immersed into Canada balsam and slowly heated until boiling (Fig. S1b), a procedure repeated several times until all fractures were infilled with the Canada balsam, rendering a clear view of the specimen. To clear the obscured view created by the bubble, the specimen was polished again to minimize the distance between bubble and amber surface (Fig. S1c). The amber was punctured manually with a thin (size ‘00’) entomological pin, which had been previously modified so that its apex was flattened and sharpened like a chisel (acting as a miniaturized drill bit) (Fig. S1d). Afterwards, the specimen was immersed again into Canada balsam and heated gently until the resin filled the bubble. Once completed, the preparation was left for two days to permit the Canada balsam to enter the inclusion, clear it, and set. The final result perfectly revealed all internal structures of the insect as well as the pollen grains that fill much of the abdomen.

Specimens SMNS Bu-135 and SMNS Bu-157 of *P. burmitica* were prepared using Struers Dap-6 and LaboPol-4 grinding and polishing machines. These specimens were not coated nor embedded in artificial resin to avoid disturbances during μ CT scanning.

Extraction of pollen grains from abdomen of holotype NIGP161473

After the Canada balsam settled uniformly inside the insect's body, the result was an appearance similar to that of an extant insect treated with potassium hydroxide (KOH), allowing a detailed observation of internal structures and gut contents (pollen grains of *Nyssapollenites*). To extract some of these pollen grains, the cuticle was pierced with a minuten pin, with a hook-like tip, mounted to a handle. The pin was used to pierce the abdomen of the insect and then turned smoothly to scrape the internal surface and dislodge some of the pollen grains (Fig. S1e). The narrowed tip of a drawn-out Pasteur pipette was then introduced into the abdomen adjacent to detached pollen grains. Repeated pumping allowed extraction of some palynomorphs (Fig. S1f). Subsequently, the pollen grains were washed with toluene to eliminate all residues of Canada balsam and then isolated with a pin and mounted for SEM study with a Tescan Vega LSU scanning electron microscope at the MNHN.

Examination of fossils with 3D X-ray micro-computer tomography

Searching for preserved internal morphological characters inside the amber inclusions, we applied 3D X-ray micro-computer tomography with synchrotron radiation (micro-CT)¹⁻³. Scans were performed at the TOPO-TOMO beamline⁴ of the ANKA Synchrotron Radiation Facility at Karlsruhe Institute of Technology (KIT). The parallel-beam tomographic scans covered an angular range of 180°, measured using a filtered polychromatic beam with a spectral peak at about 15 keV. Under such experimental conditions conventional absorption

contrast and phase contrast (in the so-called edge-enhancement regime) are the physical image formation mechanisms. An indirect detector system composed of a 12 μ m LSO:Tb scintillator, diffraction limited optical microscope (Optique Peter) and 12 bit pco.dimax high speed camera (2016 x 2016 pixels resolution) was employed to capture 3000 projections per tomographic scan with an exposure time of 10 ms each. A 5x optical magnification led to an effective pixel size of 2.44 μ m.

Prior to volume reconstruction, all projection images were processed with the phase retrieval ImageJ plugin ANKAphase⁵. Volume reconstruction was done by the PyHST software developed by the European Synchrotron Radiation Facility, Grenoble, France, and KIT⁶.

Specimen SMNS Bu-157, even though appearing perfectly preserved under light microscopy, did not give any image contrast with μ CT under any parameters (e.g. phase contrast).

Specimen SMNS Bu-135 gave contrast, but even here the remaining internal structure had a relative poor quality only allowing an incomplete reconstruction of the mandibles and maxillae. The results indicate that internal morphological characters were not (SMNS Bu-157) or only partly (SMNS Bu-135) preserved, with the interesting exception of pollen inside the gut of the latter specimen (Fig. S1g-h). One possible explanation for the poor results may be that specimen Bu-157 was fully enfused with resin prior to fossilization, as observed in various other insect inclusions before. In this case, intensity modulations would occur only on the surface of the specimen. However, since all modalities of X-ray CT are volumetric, contrast in the tomographic reconstruction can only be observed if the change in the complex refractive index occurs in a volume comparably as large as a voxel. For visible light observations, interference based reflections are visible even from surface structures, as evidenced by the interference from a few nm thin oil film on water. We suspect that an

analogous mechanism is responsible for the lack of contrast for the X-ray tomography in the present case.

Observation of fossils with microscopy

SMNS Bu-135 and SMNS Bu-157 were studied at SMNS with a Leica M80 stereo-microscope and 1.6* Plan Achromat lens. Photographs were taken with a Leica DFC490 digital macro camera on a Leica Z16-Apo Macroscope.

All specimens from NIGP (Nanjing, China) and SMNS (Stuttgart, Germany) were loaned and examined at the MNHN (Paris, France) using Olympus SZX-9 and Nikon SMS-1500 stereomicroscopes. Photographs were taken with a Canon D550 digital camera with reverse lens MP-E 65mm, and line drawings prepared using a camera lucida. Original photographs were processed using Adobe PhotoshopTM CS4.

Observations and photographs of the specimens at NIGP were taken using a Zeiss Discovery V20 stereomicroscope and a Zeiss Axio Imager 2 light microscope with an attached digital camera. Some photomicrographs were taken using green fluorescence as a light source attached to a Zeiss Axio Imager-2 light microscope and confocal laser scanning microscopy (CLSM) Zeiss LSM 710 with $\times 10$ objectives and 488 nm laser.

The compression fossils from MCZ and NHM were examined with Nikon SMZ 645 and Wild M5 stereomicroscopes in a dry state and under a thin layer of ethanol. Photographs were taken using a Canon D550 digital camera with MP-E 65mm lens and processed with Adobe PhotoshopTM CS4.

Most microphotographs were generated from focus stacks using the Helicon Focus Pro software, apart from the SMNS specimens for which Leica Application Suite 3.8.0 was used for focus stacking.

(B) Systematic Paleontology

Revision of Permopsocida Tillyard, 1926

Standard wing venation terminology was employed throughout the descriptions as it has been applied to representatives of Acercaria⁷. We elevate the previous psocodean suborder Permopsocida to ordinal rank, revise the permopsocidan families, and redescribe the crucial psocidiid species *Dichentomum tinctum* Tillyard, 1926.

Clade Acercaria Börner, 1904

Definition. Acercaria Börner, 1904 comprises Psocodea (including ‘Psocoptera’ and Phthiraptera), Thripida (including Thysanoptera), and Hemiptera. The order Zoraptera has been considered as sister group of Acercaria and both taxa have been classified together as Paraneoptera^{8,9}. However, polyneopteran affinities of Zoraptera recently gained further support¹⁰⁻¹², so that Paraneoptera either has to be rejected as polyphyletic¹¹ or considered as synonymous with Acercaria¹³. We herein add the extinct order Permopsocida and the family Hypoperlidae to Acercaria.

Order Permopsocida Tillyard, 1926 stat. nov. (= Permopsocina Tillyard, 1926)¹⁴

Stratigraphic range. Permopsocida are relatively frequent in Permian outcrops¹⁵, but the clade is also known from Liassic, Middle Jurassic, and Lower Cretaceous outcrops.

Psocorrhyncha gen. nov. from the earliest Upper Cretaceous is the latest occurrence of and only known amber representative of Permopsocida.

Included families. Permian to Liassic (with some doubt) Psocidiidae Tillyard, 1926, Permian Permopsocidae Tillyard, 1926, and Jurassic to earliest Upper Cretaceous (with a problematic Permian taxon) Archipsyllidae Handlirsch, 1906, incl. the new archipsyllid genus

151 *Psocorrhyncha*. Cyphoneuridae Carpenter, 1932 (with *Cyphoneura* Carpenter, 1932;
152 *Australocypha* Tillyard, 1935; *Lophiocypha* Tillyard, 1935) were later included in
153 Permopsocida¹⁶, but more recently demonstrated to belong to Thripida¹⁷. Likewise, the family
154 Edgariekiidae Jell and Duncan, 1986 (*Edgariokia una* Jell and Duncan, 1986), originally
155 placed in Permopsocida¹⁸, is a junior synonym of the thripidan family Lophioneuridae
156 Tillyard, 1921¹⁷.

157

158 Family Archipsyllidae Handlirsch, 1906

159 **Stratigraphic and geographic range.** Permian?, Jurassic to earliest Upper Cretaceous.

160 **Emended diagnosis.** The venation of the previously described Archipsyllidae agrees with
161 that of *Psocorrhyncha*, with the following two exceptions: subcosta posterior ScP basally
162 reaching the costal margin and distally re-emerging to end into radius anterior RA basal of
163 pterostigma, not only in the forewings, but also in the hind wings; longer areola postica
164 reaching the level of the pterostigma. This special shape of the ScP in forewings is a putative
165 synapomorphy of the Archipsyllidae, even if this character is convergently present in a few
166 modern Psocodea of the family Lepidopsocidae. The Archipsyllidae with bodies (partly)
167 preserved (*A. sinica*, *E. sojanense*) share with *Psocorrhyncha* elongate mouthparts, with long
168 and narrow labra, long laciniae with one apical tooth, male genitalia with a large hypandrium,
169 four-segmented tarsi, simple and symmetrical pretarsal claws, large arolia, and flagellomeres
170 annulate and long.

171 **Included genera.** *Archipsylla* Handlirsch, 1906, *Archipsyllodes* Vishniakova, 1976,
172 *Archipsyllopsis* Vishniakova, 1976, *Eopsylla* Vishniakova, 1976, and *Psocorrhyncha* gen.
173 nov.

174

175 Family Psocidiidae Tillyard, 1926 sensu nov.

176 **Stratigraphic and geographic range.** Permian; Australia, Russia and USA.

177 **Composition.** This family previously comprised five genera, only two of which can be
 178 accurately considered as Permopsocida, viz. *Dichentomum* Tillyard, 1926 and *Stenopsocidium*
 179 Tillyard, 1935.

180 **Emended diagnosis.** Fore- and hind wing with similar venation; ScP long, ending on RA
 181 distal of base of radius posterior RP in all wings; RP two-branched; media vein M four-
 182 branched; areola postica longer than high; no crossvein between M and first branch of cubitus
 183 anterior CuA1. At least *Dichentomum* has small crossveins between costa C and ScP.

184

185 *Dichentomum tinctum* Tillyard, 1926

186 **Redescription.** The genus *Dichentomum* and its type species *D. tinctum* rank among the
 187 better preserved and complete of the Permian Permopsocida, but have not been re-examined
 188 since the original description by Tillyard¹⁴ and the two revisions by Carpenter¹⁹⁻²⁰. A
 189 comparison with the amber material of *Psocorrhyncha* offered a unique opportunity to detect
 190 and verify crucial characters for *Dichentomum*. This complementary study is based on
 191 specimens 3324a, 3331a-b, 3348, 3323a-b, and 3347a-b (all at MCZ). The following
 192 important characters supplement the previous descriptions: head in lateral view more flat than
 193 in *Psocorrhyncha* and without a strong angle between posterior and anterior parts of dorsal
 194 side; frons narrow, as long as a narrow sclerotized postclypeus, which is separated from
 195 anteclypeus by a furrow; compound eyes well developed and well separated; two well-
 196 separated lateral ocelli, each closer to compound eye than to other ocellus; anterior ocellus
 197 hardly visible but situated far from lateral ocelli; antennae inserted well below compound
 198 eyes, well separated from each other, with a subquadrate scape, pedicel as long as scape but
 199 narrower; exact number of flagellomeres undeterminate, but all of them long and finely
 200 annulated; *Dichentomum* has certainly not 50 short antennomeres, contra Carpenter²⁰

201 (flagellomeres are finely annulated and Carpenter obviously misinterpreted the annulations as
202 flagellomeres); anteclypeus short, distinctly shorter than labrum, with two lateral parts
203 (paraclypeus), rounded elongate (Fig. S8a); labrum elongate, ca. two times as long as wide,
204 apically rounded and flat; mandibles elongate, ca. three times as long as wide at base, with a
205 broad base and distal two-thirds narrow; molar plate possibly visible, but incisor teeth not
206 visible; anterior condyle of mandible visible, connected with latero-basal angle of
207 paraclypeus; gena large and broadly quadrangular with a transverse furrow dividing it
208 obliquely into anterior (mandibular plate) and posterior (maxillary plate) parts (Fig. S8c),
209 subgena between anterior part of gena and mandible; three labial palpomeres, with basal
210 palpomere shortest, second palpomere longest, third palpomere slightly shorter than second
211 palpomere; maxillary palps long, four palpomeres (Fig. S8a), apical palpomere long,
212 subapical palpomere shorter than apical palpomere, basal palpomere relatively short, second
213 palpomere as long as apical palpomere; lacinia and galea long, overlapping apices of
214 mandibles, apically narrowed and without visible subapical tooth (Fig. S8d); reconstruction of
215 wing venation proposed by Carpenter²⁰ accurate, in particular in presence of a series of short
216 crossveins between C and ScP, at least in forewing (Nel et al.⁷ re-analysed the pattern of wing
217 venation of *Dichentomum* and considered it to be of acercarian type); legs long and thin;
218 tibiae with two apical spurs (Fig. S8c,d); all tarsi four-segmented; tarsomeres without
219 plantulae; strong pretarsal claws without subapical tooth (Fig. S8b); arolium between pretarsal
220 claws not visible; a strong constriction between thorax and abdomen due to small first
221 abdominal segment (Fig. S8c); cerci absent (confirmation of Carpenter²⁰); ovipositor well
222 developed with ventral valvulae (gonapophyses VIII) with ventral margin bearing at least
223 small denticles.
224
225 Family Permopsocidae Tillyard, 1926

Stratigraphic and geographic range. Permian, USA.

Emended diagnosis. Fore- and hind wing with similar venation; ScP long, ending on RA distal of base of RP in all wings; RP two-branched; M four-branched; areola postica higher than long; a crossvein between M and CuA1.

Remark. The family Permopsocidae currently comprises four genera (see Table S1), i.e. *Permopsocus* Tillyard, 1926, *Lithopsocidium* Carpenter, 1932, *Orthopsocus* Carpenter, 1932, and *Progonopsocus* Tillyard, 1926.

Redefinition of Hypoperlidae Martynov, 1928

As indicated by Shcherbakov²¹, the Permopsocida (*Dichentomum*) have a forewing venation similar to those of some taxa (especially *Boreopsocus* Shcherbakov, 1994) currently attributed to the Permian family Hypoperlidae. Thus it is crucial to discuss the composition and phylogenetic relationships of Hypoperlidae.

Rasnitsyn²² included seven genera in the Permian family Hypoperlidae: *Hypoperla* Martynov, 1928, *Hypoperlopsis* Zalesky, *Martynopsocus* Karny, 1930, *Kaltanelmoa* Rohdendorf, 1961, *Fatjanoptera* Martynova, 1961, *Tshunicola* Rasnitsyn, 1977, and *Tshekardobia* Rasnitsyn, 1977. Shcherbakov²¹ restricted the Palaeozoic Hypoperlidae to embrace the four genera *Hypoperla*, *Idelopsocus* Zalesky, 1929, *Kaltanelmoa*, and *Boreopsocus* Shcherbakov, 1994.

The venation of *Hypoperla elegans* Martynov, 1928 (type species of Hypoperlidae, type family of the order Hypoperlida) is typical for Acercaria by having a common stem R+M+CuA, M+CuA separating from R distally; convex CuA immediately emerging from M+CuA; long crossvein cua-cup between concave cubitus posterior CuP and CuA, concave near CuP and convex near CuA, CuA, with an areola postica (see Figs. S9c-d). The only other group having a common stem R+M+CuA is Archaeorthoptera. But, Archaeorthoptera have

251 CuA with a higher number of distal branches and a concave anterior branch of CuP ending on
252 convex CuA instead of a cua-cup³⁰. Nevertheless, *H. elegans* differs from Permopsocida in
253 several important plesiomorphies: RP with a series of parallel posterior branches instead of a
254 single fork, as in modern Acercaria and Permopsocida (a likely plesiomorphy because
255 numerous posterior branches of RP are known in the ground plans of polyneopterous orders
256 and in Neuropterida and Panorpidia); no distinct angle of radius at base of M+CuA;
257 pterostigma more ‘rudimentary’ and consisting of a darker zone covering apical parts of ScP,
258 RA, and apical part of area between RA and RP, not delimited posteriorly by RA. The same
259 pattern occurs in *Hypoperla grata* Novokshonova, 1998 and *Hypoperla vaulevi*
260 Novokshonov, 2001.

261 The venation of *Idelopsocus tataricus* Zalesky, 1929 is clearly acercarian, showing a
262 convex CuA emerging with concave M from a common stem with R, a long brace cua-cup
263 between concave CuP and CuA, concave near CuP and convex near CuA, and two convex
264 simple anal veins. The CuA of *I. tataricus* is simple, concave ScP ends on RA, and concave
265 RP and M both have three branches with few crossveins. This venation is closer to modern
266 Acercaria than to that of *Hypoperla*. It differs from *Psocorrhyncha* in lacking a strong angle
267 between RA and basal stem R+M+CuA, and not having a sclerotized pterostigma.
268 *Idelopsocus diradiatus* Rasnitsyn, 1996 also has a venation closer to non-hypoperlid
269 Acercaria in that the RP only has two branches, and M with only three branches, but lacking
270 any angle in the course of R at base of M+CuA. *Idelopsocus diradiatus* has a forked CuA,
271 unlike *I. tataricus*. *Idelopsocus tataricus* and *I. incommendatus* Novokshonov et al., 2002
272 share similar venation characters except for presence of an areola postica. The venation is
273 somewhat variable among the *Idelopsocus* species, especially the number of main vein
274 branches. Unlike *Hypoperla*, where only the distal parts of the wings have darkened
275 membranes, species of *Idelopsocus* possess sclerotized pterostigmata in fore- and hind wings

(Figs. S9f and S11a-b)¹⁵, not homologous to that of Permopsocida because the pterostigmata cover a zone crossing the distal area between the anterior wing margin and RA and part of the area between RA and RP. In Permopsocida, the pterostigmata are delimited posteriorly by RA. *Idelopsocus mutovinus* Rasnitsyn and Aristov, 2013 is probably also a Hypoperlidae, although the basal part of the vein CuA is not clearly visible. *Idelopsocus diradiatus* and *Idelopsocus splendens* (Zalessky, 1948) have five-segmented tarsi (specimens PIN 1700/3298 or PU 2/129 attributed to *I. splendens* by Novoskshonov²⁴ and Rasnitsyn¹⁵), while the type specimen of *I. splendens* is an isolated wing originally described as *Hypoperlopsis splendens*. This tarsal character is a plesiomorphic in Acercaria and most insects.

Boreopsocus has a venation most suggestive to that of Permopsocida, with RP having a distal fork, pterostigmata in fore- and hind wings delimited by a posterior curve of RA, with a crossvein below it and RP (but narrower than in Permopsocida, except *Stenopsocidium*). Unlike Permopsocida²¹, it lacks an angular R, and possesses five-segmented tarsi. *Kaltanelmoa sibirica* (based on the basal two-thirds of an isolated wing) also has a venation typical of Acercaria (courses of M and cubital veins, simple fork of CuA). RP and M in this species appear to be simply forked, as in modern acercarians and Permopsocida, but R lacks an angle in its course distal to base of M. The area of the putative pterostigma is hardly preserved.

In summary, the Hypoperlidae *sensu* Shcherbakov²¹ appear to be a ‘group’ of acercarian genera, but lack a clear apomorphy that could support them as a clade. They may represent a paraphyletic ‘evolutionary grade’ (with regard to wing venation and number of tarsomeres) from *Hypoperla* to *Boreopsocus* sharing several apomorphies with Permopsocida (similar pterostigmata and venation). The venation of *Idelopsocus* could represent an ‘intermediate’ stage, having reduced branchings in RP and M, compared to the situation observed in *Hypoperla*, but with a particular pterostigma different from *Boreopsocus*

and Permopsocida. Interestingly, a strikingly similar phenomenon happened during the evolution of the odonatopteran pterostigmata: the basal clades (Meganisoptera) have no pterostigma, whereas Odonata have a pterostigma delimited posteriorly by RA. The pterostigma in the ‘intermediate’ clade Protanisoptera is almost identical in shape and position to that of *Idelopsocus*²⁵.

The wing venation of Hypoperlidae lacks any synapomorphy with the palaeodictyopteran groups (Dictyoneuridea sensu Rasnitsyn¹⁵). In particular the common stem R+M+CuA, present in the Hypoperlidae and the Acercaria, is absent in palaeodictyopteran orders. Also, Hypoperlidae has only two convex simple anal veins, identical to Acercaria, but different from the anal veins of Palaeodictyoptera, where there are numerous anal veins reinforced by a prominent anal ridge (the so-called ‘anal brace’). This neopteran family cannot be considered as a member of a grade that would have given rise to these palaeopterous insects.

Rasnitsyn¹⁵ considered the mouthparts as diagnostic characters for the order Hypoperlida. He described them as ‘chewing though often beak-like elongate, with lacinia rod- or styletlike, clypeus convex indicating strong cibarial muscles, or, if flat, mandibles and laciniae long, jointly forming short beak’. Such structures are barely visible in the few described Hypoperlidae with preserved bodies. In fact, the mouthparts of *Idelopsocus splendens* (specimens PIN 1700/3298 and PU 2/129), *Idelopsocus diradiatus*, and *Idelopsocus galinae* Novokshonov, 2001 are not particularly elongate and resemble the mouthparts of Psocodea, especially in the non-divided gena (see Fig. S11d).

Rasnitsyn¹⁵ considered the piercing rostrum of Palaeodictyoptera and Hemiptera as homologous and derived from a hypoperlidan ancestor. Kukalová-Peck²⁶ presented a detailed reconstruction of palaeodictyopteroid mouthparts, with structures (lacinia, ante- and postclypeus, mandibular condyles, etc.) generally unavailable for observation in fossils, or

undissected modern insects. Other interpretations by Kukalová-Peck²⁷, Laurentiaux²⁸, or even Dohrn²⁹, remain more reasonable, describing very long stylet-like mandibles, and long maxillary palps, but without information on other parts such as laciniae. Even though these structures are reminiscent of those of Hemiptera (except presence of maxillary palps), they are certainly the result of convergence as already proposed by Laurentiaux¹⁶ and Emeljanov³⁰, and are not synapomorphies with those Acercaria with piercing mouthparts. All other structures (especially the wing venation) exhibit no synapomorphies between Palaeodictyoptera and Acercaria.

Redescription of the hypoperlid *Idelopsocus splendens* (Zalessky, 1948)

A re-examination of two specimens PIN 1700/3298 and PU 2/129 attributed to *I. splendens* by Novoskshonov²⁴ and Rasnitsyn¹⁵ revealed the following characters: head without a clear subdivision into sub-horizontal posterior part and subvertical anterior part bearing ocelli; flagellomeres numerous, relatively short, apparently annulated; ocelli present (two visible) on vertex; compound eyes large; clypeus apparently not subdivided into ante- and postclypeus; paraclypeal lobes absent; mouthparts short; labrum not elongate; mandibles strong and psocodean-like; maxillary palps long, five palpomeres; lacinia elongate, not guided by paraglossa nor by galea at its apex, as in Psocodea, but exact structure cannot be recognized; division between cardo and stipes probable, but not clearly visible; labium short with short prementum and paraglossae not half-tube-shaped; labial palps not clearly visible; gena not divided into two lobes (Fig. S11d); tarsi five-segmented, no tarsal plantulae (Fig. S11c); pretarsal claws strong with arolium between them; wings homonomous; venation of acercarian-type with a common stem R+M+CuA and a crossvein cua-cup between CuP and CuA; M re-emerging from R well distal of wing base, forked twice into four branches, M1-M2 and M3-M4; RP forked; radial stem lacking pronounced posterior angle; two anal veins;

pterostigmata present on all wings, but not posteriorly delimited by R; areola postica present, longer than wide; shape of ScP unclear in all wings; presence or absence of abdominal sternum I cannot be verified; first abdominal segment narrower than others, but less than in *Psocorrhyncha*; female abdominal terga IX, X and XI completely developed; cerci present, short and unsegmented (Figs. S11e-f); ovipositor present and well developed; male genital structures unknown.

Alimentation of Permopsocida and Hypoperlidae

The guts of three specimens of *P. burmitica* (specimens SMNS Bu-157, NIGP161473, and SMNS Bu-135) are filled with one morphotype of pollen grains, which are mostly intact and untampered. A fecal pellet extruding from the abdomen of specimen NIGP161473 is also totally composed of the same type of pollen grains (Fig. S5c).

Some grains were extracted from the abdomen of NIGP161473 and examined with SEM (see Material and Methods). The morphology of these grains corresponds with fossil *Nyssapollenites* and extant members of the angiosperm family Nyssaceae³¹. A unique difference is their smaller size (diameter: 11-14 μm for fossil vs ca. 30 μm for extant species of *Davidia*, 40 μm for species of *Camptotheca*, and 46 μm for species of *Nyssa*³²). Presence of intact, unopened pollen grains in the guts and feces of these specimens of *Psocorrhyncha* suggests the pollen wall might have been infiltrated with digestive enzymes, as in extant bees³³.

Thus, imagos of *Psocorrhyncha* fed on entire pollen grains, without masticating them with their well-developed molar plates. Moreover, it appears their elongate mouthparts were not adapted for chewing nyssacean flowers with their short and flat corollae. As these insects belong to hemimetabolous Acercaria, their nymphs certainly had similar mouthpart morphology and diets as the adults.

Extant Nyssaceae only bloom during a brief period in spring (April to June). Mouthparts of Permopsocida are completely different from those of typical modern, exclusive pollen-feeding insects that visit flowers having short corollae (*e.g.*, beetles of the lineages Scarabaeidae, Leiodidae, or Staphylinoidea, in which the mandibles have reduced incisors, but with brush-like hairs on their lacinia and galea³⁴⁻³⁵, and most certainly different from those bees that visit short-corolla flowers). Perhaps adults and nymphs of *Psocorrhyncha* fed upon another food source (*e.g.*, ripened fruits of Nyssaceae, or even small insects) during other periods of the year, or the flowering phenology of fossiliferous Nyssaceae differed from that of their extant representatives. In comparison, the mirid predator *Macrolophus pygmaeus* uses pollen as alternative or supplementary food source, favouring nymphal development³⁶. Also some insectivorous modern Chrysopidae can be found with the gut full of pollen³⁷.

One fossil specimen of *Archipsylla sinica* Huang et al., 2008 also has structures tentatively interpretable as sporangia in its gut (Fig. S7). Among the Permian Permopsocida, *Dichentomum tinctum* and *Stenopsocidium elongatum* have elongate mouthparts, similar to those of *Psocorrhyncha* and *A. sinica*. This would suggest that all of these had similar modes of alimentation. However, if Permian permopsocids fed on pallinomorphs, these must have certainly been of a different type than those eaten by *Psocorrhyncha*, as angiosperms did not exist during the Permian. Krassilov et al.³⁸ found pallinomorphs in the gut of the Middle Permian psocidiid *Dichentomum* (*Parapsocidium*) *uralicum* (Zalessky, 1937). The Permian psocidiid *Dichentomum* (*Parapsocidium*) *uralicum* appeared to have been polylectic³⁸ (pollen grains of seed ferns and of gymnosperms in its gut), while *Psocorrhyncha* was apparently oligolectic on angiosperm Nyssaceae.

Some modern Psocodea, Thripida, and Hemiptera also feed (in part) on pollen grains. While thrips and hemipterans empty the grains of pollen³⁹, booklice ingest whole or crushed grains. Gut contents of extant Psocodea can contain angiosperm and gymnosperm pollen

grains, frequently mixed with fungal spores⁴⁰. Interestingly, Krassilov et al.⁴¹ stated, “In the Kungurian of Tchekarda we found taeniate pollen grains in the gut compressions of *Idelopsocus* (Hypoperlidae), ... , while *Idelopsocus diradiatus* Rasnitsyn fed on both *Lunatisporites* and *Protohaploxylinus*”. These types of pollen grains of these plants are currently assigned to Pteridophyta, plants present in the Lower Permian.

As Hypoperlidae belong to the stem group of Acercaria, and Permopsocida to the stem group of Condylgnatha (Thripida+Hemiptera), palynivory seems to be a ground plan character of Acercaria, which evolved dramatically after the Late Palaeozoic.

(C) SI References

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Supporting Information

• **S1 Fig. Method of preparation of specimens and extraction of pollen grains.**

(a) Amber cut and polished manually. (b) Polished piece heated to boiling in Canada balsam. (c) Amber polished to reach margin of bubble. (d) Surface drilled with thin pin and bubble filled with Canada balsam. (e) Curved pin piercing the abdomen to remove pollen grains from abdominal wall. (f) Drawn tip of Pasteur pipette introduced into abdomen to extract palynomorphs. (g-h) Volume renderings of segmented synchrotron radiation micro-CT scans of specimen SMNS BU-135, pollen gut contents highlighted in orange color (drawings DA).

• **S2 Fig. Head structures of *Psocorrhyncha burmitica* gen. et sp. nov., paratype NIGP161474.**

(a) Right mandible showing molar plate. (b) Right subgena and postgena. (c) Galea and lacinia. (d) Lacinia, photomicrograph under green fluorescence. (e) Right dorso-lateral view of head. (f) General habitus. (g) base of right antenna, arrow: lateral antennifer. (h) Head, ventral view. Ga. galea; Lac. lacinia; Man. mandible; A.g. anterior part of gena; P.g. posterior part of gena; Mo. molar plate; pe. pedicel; Postgn. postgena; Sc. Scape; Subgn. Subgena. Scale bars, 0.1 mm (a, b, c, e, h), 0.2 mm (D), 1.0 mm (g).

• **S3 Fig. *Psocorrhyncha burmitica* gen. et sp. nov., allotype SMNS Bu-157.**

(a) General habitus, lateral view, arrow first abdominal segment. (b) Head, frontal view, arrows paraclypeus. (c) Wings. (d) Female genitalia, latero-ventral view. (e) Head and thorax, dorsal view, arrows ocelli. (f) Female genitalia, lateral view. Epi. epiproct; GoVIII gonocoxite VIII; GoIX gonocoxite IX; GyVIII gonapophyse VIII; GyIX gonapophyse IX; LtVIII laterotergite VIII; LtIX laterotergite IX; Pa. paraproct; T.f. trichobothrial field; TX tergite X. Scale bars, 500 μ m (a, c, e), 0.1 mm (b), 200 μ m (d, f).

- **S4 Fig. *Psocorrhyncha burmitica* gen. et sp. nov., paratype SMNS Bu-135.**

(a) General habitus, lateral view. (b) Head, lateral view. (c) Forewing. (d) Female genitalia. (e) Foreleg. (f) Midleg. (g) Hindleg. Scale bars, 1.0 mm (a), 200 μ m (b, e, f, g), 500 μ m (c).

- **S5 Fig. Morphological structures of Permopsocida.**

(a-c) *Psocorrhyncha burmitica* gen. et sp. nov., holotype NIGP161473. (A) Apical part of first flagellomere, arrow: sensilla. (b) Apical part of second flagellomere, arrow: sensilla. (c) Male genitalia. (d) Tarsi, *Archipsylla sinica* Huang *et al.*, 2008, white arrows: arolia. (e) *Archipsylla sinica* Huang *et al.*, 2008, Specimen NIGP161884, general habitus; A.g. anterior part of gena; P.g. posterior part of gena. Aed. aedeagus; D.e. ductus ejaculatorius; Hy hypandrium; St VIII sternite VIII; St. IX sternite IX; T. VIII tergite VIII; T. IX tergite IX. Scale bars, 0.1 mm (a, b, c, d), 1.0 mm (e).

- **S6 Fig. Morphological structures of Permopsocida.**

(a-b) *Psocorrhyncha burmitica* gen. et sp. nov., paratype NIGP161474. (a) Wing base sclerites. (b) Fore- and hind wings pterostigmata. (c) Holotype NIGP161473, detail of forewing return of ScP from C to RA. (d) *Dichentomum grande* Carpenter, 1933, Holotype MCZ 3358 forewing. BR & 2AX basiradiale and second axillary sclerite; C

costa; CuA cubitus anterior; CuP cubitus posterior; HP & Bsc humeral plate and basisubcostale plate; M median; RA radius anterior; RP radius posterior; ScP subcostal posterior. Copyrights for MCZ 3358 belong to Museum of Comparative Zoology at Harvard University. Scale bars, 0.04 mm (a), 0.1 mm (b, c), 1.0 mm (d).

- **S7 Fig. Specimen NIGP161883, *Archipsylla sinica* Huang *et al.*, 2008 with possible sporangium in gut.**

(a-b) General habitus, print and counterprint. (c-d) enigmatic structures in gut, under normal light and electron scanning microscope. Scale bars, 2.0 mm (a, b), 0.2 mm (c, d).

- **S8 Fig. Details of morphology of *Dichentomum tinctum* Tillyard, 1926.**

(a) Specimen MCZ 3324b, head structures, arrows: maxillary palps. (b) Specimen MCZ 3347b, wings and mid leg, arrows: tarsomeres. (c) Specimen MCZ 3348, habitus, arrows indicate limits of basal flagellomeres. (d) Specimen MCZ 3331b, Head and thorax. Ga. galea; La. labrum; Man. mandible; P.g. posterior part of gena; Par.cl. paraclypeus; Pt pterostigma. Copyrights for the specimens Nos. MCZ 3324b, MCZ 3331b, MCZ 3347b and MCZ 3348 belong to Museum of Comparative Zoology at Harvard University. Scale bars, 1.0 mm (a, b, c, d).

- **S9 Fig. Morphology of Psocidiidae, Fatjanopteridae, and Hypoperlidae.**

(a) *Stenopsocidium elongatum* Tillyard, 1935, holotype NHM In 46397, arrow: elongate mouthparts. (b) *Fatjanoptera mnemonica* Martynova, 1961, holotype PIN 1216/4, forewing. (c) *Hypoperla elegans* Martynov, 1928, holotype PIN 117/968, forewing. (d) *Hypoperla elegans*, PIN 3353/471, hind wing. (e) *Fatjanoptera mnemonica*, holotype PIN 1216/4, forewing reconstruction(drawn AN, JP). (f) ‘*Idelopsocus*’ cf. *splendens*, PIN 1700/3298, habitus. cua-cup crossvein between CuA and CuP; CuA cubitus anterior; CuP cubitus posterior; M median; RA radius anterior;

RP radius posterior; ScP subcostal posterior. Copyrights for NHM In 46397 belong to The Natural History Museum, London. Scale bars, 1.0 mm (a), 2.0 mm (d), 5.0 mm (b, e, f).

- **S10 Fig. Morphology of hypoperlid ‘*Idelopsocus*’ *splendens*, PU 2/129.**

(a) Imprint, general habitus. (b) Counterimprint, general habitus. (c) Fore tarsi. (d) Head, imprint. (e) Imprint, apex of abdomen, arrow: cercus. (f) Conterimprint, apex of abdomen, arrow: cercus. La labrum; Max.palp maxillary palp. Scale bars, 1.0 mm (a, b, c), 500 μ m (d, e, f).

- **S11 Fig. Phylogeny of Acercaria.**

Most parsimonious cladogram, length = 100 steps, CI = 0.730, RI = 0.833; Bremer values indicated (drawn RG).

- **S12 Fig. Paraclypeus and gena in Hemiptera: Lachnidae and Thripida.**

(a) Recent *Stomaphis* species, head, dorsal view. (b) *Moundthrips beatificus* Nel et al., 2007, holotype J2A Azar Coll., head ventro-lateral view. La. labrum; Man. mandible; A.g. anterior part of gena; P.g. posterior part of gena; Par.cl. paraclypeus; Tor. antennal torulus. Scale bars, 0.2 mm (A), 0.01 mm (B).

- **S1 Table. List of species included in Permopsocida**

- **S2 Table. List of taxa used in the phylogenetic analysis**

- **S3 Table. Characters and character states used in the phylogenetic analysis**

- **S4 Table. Data matrix of taxa and characters**

- **S5 Table. Comparison of species numbers in acercarian orders.**

S1 Table. List of species included in Permopsocida

Family	Genus	Species	Age
Archipsyllidae	<i>Eopsylla</i>	<i>E. sojanense</i> (Bekker-Migdisova, 1962)	Upper Permian
	<i>Archipsylla</i>	<i>A. primitiva</i> Handlirsch, 1906	Lower Jurassic
		<i>A. sinica</i> Haung et al., 2008	Middle Jurassic
		<i>A. turanica</i> Martynov, 1926	Upper Jurassic
		<i>A. lata</i> Vishniakova, 1976	Upper Jurassic
		<i>A. similis</i> Vishniakova, 1976	Upper Jurassic
	<i>Archipsyllodes</i>	<i>A. speciosus</i> Vishniakova, 1976	Lower Cretaceous
	<i>Archipsyllopsis</i>	<i>A. baissica</i> Vishniakova, 1976	Lower Cretaceous
	<i>Psocorrhyncha</i>	<i>P. burmitica</i> sp. nov.	Upper Cretaceous
Psocidiidae	<i>Dichentomum</i>	<i>D. tinctum</i> Tillyard, 1926	Lower Permian
		<i>D. complexum</i> Carpenter, 1926	Lower Permian
		<i>D. grande</i> Carpenter, 1933	Lower Permian
		<i>D. latum</i> Carpenter, 1932	Lower Permian
		<i>D. minimum</i> Carpenter, 1932	Lower Permian
		<i>D. parvulum</i> Carpenter, 1932	Lower Permian
		<i>D. arroyo</i> Rasnitsyn, 2004	Lower Permian
	<i>Liassopsocus</i>	<i>L. lanceolatus</i> Ansorge, 1996	Lower Jurassic
	<i>Austropsocidium</i>	<i>A. pincombei</i> Tillyard, 1935	Upper Permian
		<i>A. stigmaticum</i> Tillyard, 1935	Upper Permian

	<i>Megapsocidium</i>	<i>M. australe</i> Tillyard, 1935	Upper Permian
	<i>Stenopsocidium</i>	<i>S. elongatum</i> Tillyard, 1935	Upper Permian
Permopsocidae	<i>Permopsocus</i>	<i>P. latipennis</i> Tillyard, 1926	Lower Permian
	<i>Lithopsocidium</i>	<i>L. permianum</i> Carpenter, 1932	Lower Permian
	<i>Orthopsocus</i>	<i>O. singularis</i> Carpenter, 1932	Lower Permian
	<i>Progonopsocus</i>	<i>P. permianus</i> Tillyard, 1926	Lower Permian

717

718 **Remarks**

719 a) *Archiconiopteryx liasina* (Handlirsch, 1906) (Liassic, Dobbartin, Germany) was
720 originally⁴² included in genus *Archipsylla* Handlirsch, 1906, but later transferred to the genus
721 *Archiconiopteryx* in Neuroptera: Coniopterygidae⁴³, and then revised again⁴⁴ and transferred
722 to the sternorrhynchan family Archiconiopterygidae Ansorge, 1996.

723 b) *Eopsylla sojanense* was originally placed in psocidiid genus *Dichentomum*⁴⁵; Rasnitsyn¹⁵
724 proposed to remove it to the Psocidiidae because of ‘possessing a complete ScP unlike the
725 Mesozoic Archipsyllidae’, which is contradictory to the reconstruction of Vishniakova⁴⁵. This
726 taxon should be revised.

727 c) ?*Dichentomum arroyo* Rasnitsyn, 2004 and ?*Dichentomum* sp., from the Carrizo Arroyo
728 Permian⁴⁶, are only partially preserved with their basal halves of the wings missing, and are
729 too fragmented to safely be attributed to the Permopsocida.

730 d) The phylogenetic position of *Dichentomum* (*Parapsocidium*) *uralicum* (Zalessky, 1937)
731 remains ambiguous, although Carpenter⁴⁷ synonymized the genus *Parapsocidium* Zalessky,
732 1937 with *Dichentomum*, without clear explanation. *Parapsocidium uralicum* shares with
733 *Dichentomum* and the Permopsocida a strong posterior angle of RA below the pterostigma, a
734 sclerotized pterostigma, and the same pattern of branching of RP, M, and CuA in the
735 forewing. It is likely a Permopsocida, although we do not know if it had pterostigmata on the

hind wings. Its areola postica longer than broad suggests a position near or in the Psocidiidae rather than the Permopsocidae.

e) *Liassopsocus lanceolatus* shares with the Permian Psocidiidae a vein ScP terminating into RA, but also shared with the Archipsyllidae a RA strongly angular in the pterostigma, thus its position remains uncertain even if it is a Permopsocida.

f) Following the reconstruction proposed by Tillyard⁴⁸, *Austropsocidium* Tillyard, 1935 strongly differs from Permopsocida in the absence of pterostigma in the hind wings and that RA does not form a deep curve and angle below the forewing pterostigma. The other wing venation characters (areola postica, M forked twice, RP forked) are not apomorphies of the Permopsocida. The base of M+CuA distal of wing base suggests that it is not a psocodean. As all of the body characters are unknown, it is not possible to assert it is a Permopsocida. It could belong to the stem group of the Acercaria. *Austropsocidium stigmaticum* Tillyard, 1935 is based on the distal two-thirds of a wing⁴⁸. The form of the pterostigma with RA not exhibiting a strong posterior angle would exclude this taxon from the Permopsocida, made further complicated as the organization of the bases of M and CuA are unknown. It is probably best considered as ‘Acercaria incertae sedis’.

g) The lack of a strong posterior angle formed below and of the pterostigma with RA would exclude *Megapsocidium* Tillyard, 1935 from the Permopsocida. Furthermore the organization of the bases of M and CuA are unknown and it should likely be placed as ‘Acercaria incertae sedis’.

h) Tillyard’s reconstruction of *Stenopsocidium elongatum* strongly differs from the original wing⁴⁸, and the forewing pterostigma fits well with those of *Psocorrhyncha* and Permopsocida in the presence of a posterior curve of RA below it and presence of a basal vein closing it. The main difference with other Permopsocida is the absence of a crossvein between RA and RP below the pterostigma, which is a rather variable character, even among modern

Psocodea (Fig. S9a). *Stenopsocidium* also shares with *Psocorrhyncha* elongate mouthparts with long mandibles and labrum; Jell⁴⁹ presented a photograph of a complete forewing from the Upper Permian of Australia that is clearly a Permopsocida owing to the shape of the pterostigma, RA, RP, M, CuA, etc. Its ScP terminates on RA closer to the pterostigma than to the base of RP, a character present in Psocidiidae.

i) Nel et al.⁷ re-analysed the pattern of wing venation of *Permopsocus* and determined it to be clearly of acercarian type. Specimen number ‘3992a-b’ depicted in a photograph in Carpenter⁵⁰, of great interest as it has an elongate prognathous head with large compound eyes and long mouthparts, similar to those of other Permopsocida, a constriction between the thorax and abdomen and a long structure corresponding to a large sclerotized spoon-like male hypandrium. Carpenter¹⁹ determined the antenna of specimen number ‘3155’ to have moderately long flagellomeres. The wing venation shows all diagnostic characters of Permopsocida.

j) *Lithopsocidium permianum* is based on isolated wings¹⁹⁻²⁰. Nel et al.⁷ verified its venation to be of acercarian type.

k) *Orthopsocus singularis* is based on an isolated wing¹⁹. Although Nel et al.⁷ could not verify the pattern of venation fits with Acercaria, its great similarity to that of *Permopsocus* strongly supports an attribution to the same group.

S2 Table. List of taxa used in the phylogenetic analysis

Outgroups:

Blattodea: *Periplaneta americana* (Linnaeus, 1758) (extant)

Plecoptera: *Eusthenia costalis* Banks, 1913 (extant)

Zoraptera: *Zorotypus caudelli* Karny, 1927 (extant)

786 Holometabola: *Xyela julii* (Brébisson, 1818) (extant)

787 **Ingroups:**

788 **Hypoperlidae:**

789 *Hypoperla elegans* Martynov, 1928 (based on reexamined photographs of the type wings)

790 (Permian)

791 *Idelopsocus splendens* (Zalessky, 1948) (based on revision of specimens PIN 1700/3298 and

792 PU 2/129) (Permian)

793 **Permopsocida:**

794 *Archipsylla sinica* Huang et al, 2008 (Middle Jurassic)

795 *Dichentomum tinctum* Tillyard, 1926 (based on present revision) (Permian)

796 *Permopsocus latipennis* Tillyard, 1926 (Permian)

797 *Psocorrhyncha burmitica* gen. nov., sp. nov. (Cretaceous)

798 **Psocodea:**

799 *Burmacompsocus perreaui* Nel & Waller, 2007 (Compsocidae) (Cretaceous)

800 *Libanomphientomum nudus* Choufani et al., 2011 (Amphientomidae) (Cretaceous)

801 **Thripida:**

802 *Moundthrips beatificus* Nel et al., 2007 (Cretaceous)

803 *Thrips tabaci* Lindeman, 1889 (extant)

804 **Hemiptera:**

805 *Archescytina* sp. (Archescytinidae, supposed most basal clade of Hemiptera, specimen with

806 body preserved)

807 *Southia opposita* (F., 1803) (Fulgoromorpha: Kinnaridae) (extant)

808

809 **S3 Table. Characters and character states used in the phylogenetic analysis**

810

1. Head: (0) not opisthognathous; (1) opisthognathous, orientated obliquely, with mouthparts pointed backward (Palaeozoic and some Mesozoic Thripida have a prognathous or hypognathous head, while the head is opisthognathous in modern Thysanoptera⁵¹. The opisthognathy cannot be considered a synapomorphy of Thripida and Hemiptera. The Permopsocida have hypognathous heads) (state 0 for *Psocorrhyncha*)
2. Sclerotized ring at base of first antennal flagellomere, inside pedicel: (0) absent; (1) present (a character of Hemiptera and modern Thysanoptera⁵²⁻⁵³) (state 0 for *Psocorrhyncha*)
3. Rupturing mechanism at base of antennal flagellum: (0) absent; (1) present (a character of Psocodea^{11,53}) (state 0 for *Psocorrhyncha*)
4. Flagellomeres annulated with cuticular sculpture: (0) present; (1) absent (annulation is present in Psocodea: Troctomorpha, in some Thripida, Hemiptera: Aphidoidea, Isoptera, Mantophasmatodea, Ephemeroptera, and Plecoptera) (state 0 for *Psocorrhyncha*)
5. Insertion of scape on head capsule by a dicondylar articulation (acute lateral antennifer and weaker median articulation point on head capsule): (0) present; (1) absent (a dicondylar articulation occurs in modern Thysanoptera⁵³, Orthoptera, Phasmatodea, and Thysanura⁵⁴⁻⁵⁶, while other insects have a ball-and-socket joint⁵⁶. Psocodea have a single condyle or no condyle^{53,57}. While Heming⁵³ considered the dicondylar articulation as derived in Thysanoptera, its presence in Thysanura, Orthoptera, and Phasmatodea suggests it could be a plesiomorphy for the Insecta) (state 0 for *Psocorrhyncha*)
6. Position of anterior tentorial pits: (0) frontal side of head; (1) shifted dorsally (the anterior tentorial pits are absent in Anoplura and Rhynchophthirina, not considered

- here; they are shifted dorsally in Hemiptera and modern Thysanoptera, but not in Palaeozoic and Mesozoic Thripida^{11,58}) (state 0 for *Psocorrhyncha*)
7. Dorsal part of head with a sub-horizontal posterior part and a subvertical anterior part bearing the ocelli: (0) no (Psocodea, Thripida); (1) yes (state '0' occurs in outgroups, Psocodea and Thripida, state '1' occurs in Hemiptera: Fulgoromorpha⁵⁸⁻⁶⁰) (state 1 for *Psocorrhyncha*)
8. Ocell-ocular distance < inter-ocellar distance: (0) no ; (1) yes (state '1' occurs in those Hemiptera with a broad clypeo-frons⁶¹) (state 1 for *Psocorrhyncha*)
9. Clypeus divided by a furrow into ante- and postclypeus: (0) no; (1) yes (state '1' in some Hemiptera (e.g. Cicadoidea) but not all (e.g Aphidoidea), Thripida, and some Psocodea⁶²) (state 1 for *Psocorrhyncha*)
10. Postclypeus: (0) not very large and bulbous; (1) large, bulbous, with large cibarial dilator muscles (this character state is currently assigned to the Acercaria⁶²⁻⁶³), but the postclypeus is not as large and bulbous in the Palaeozoic or Mesozoic Thripida nec. Thysanoptera as in Psocodea, extant Thysanoptera, and Hemiptera. Therefore the large postclypeus of Psocodea, extant Thysanoptera and Hemiptera is certainly a convergence. In Psocodea, the frons is well separated from the postclypeus, unlike in modern Thysanoptera, and probably Hemiptera, although terminology for the latter clade is controversial^{59,62,64}) (state 0 for *Psocorrhyncha*)
11. Paraclypeal lobes: (0) not separated and not distinct from median part of (ante)-clypeus; (1) separated and distinct from median part of (ante)-clypeus (Presence of two relatively sclerotized paraclypeal lobes⁶⁵ is an apomorphic character present in recent and fossil Thripida⁵⁸. Hemiptera also have sclerotized sclerites in the same position as the paraclypeal lobes of Thripida and of *Psocorrhyncha*. Some authors confused the mandibular plate (lora) for paraclypeus (see ⁵⁹ for summary of diverse

opinions). Spangenberg et al.⁶⁵ and Spangenberg⁶⁶ confirmed the opinion of Singh⁶⁷ about the fact that the paraclypeus of Hemiptera is a structure different from the mandibular plate. In Coleorrhyncha⁶⁵, the paraclypeal lobes are visible in dorsal view, placed laterally to the anterior part of the anteclypeus while mandibular plates are visible only in lateral view; these structures are fused but separated internally by a ‘distinct crescent-shaped apodeme’⁶⁵. In the aphidoidean *Stomaphis*, the paraclypeal lobes are very broad structures (Fig. S13a). The clypeus of the Psocodea, Hypoperlidae, and other Insecta is not clearly differentiated into paraclypeal lobes and a median part. This character constitutes a potential synapomorphy of a clade comprising Permopsocida, Thripida, and Hemiptera. *Stenopsocidium elongatum* could also have two sclerotized paraclypeal lobes (Fig. S9a). Also *Dichentomum tinctum* has two small rounded sclerites at the base of the labrum corresponding to paraclypeal lobes, see Fig. S8a) (state 1 for *Psocorrhyncha*)

12. Median part of (ante)-clypeus: (0) not membraneous; (1) membraneous (state ‘1’ in Thripida⁵⁸; a potential synapomorphy of Permopsocida and Thripida, modified in Hemiptera in relation to the hyper-development of the clypeus) (state 1 for *Psocorrhyncha*)

13. Labrum: (0) not elongate, less than two times longer than broad; (1) elongate, two times longer than broad or more (state ‘1’ in Hemiptera and Thripida) (state 1 for *Psocorrhyncha*)

14. Left mandible: (0) not stylet-like; (1) stylet-like (state ‘1’ in Hemiptera and Thripida) (state 0 for *Psocorrhyncha*)

15. Right mandible: (0) not stylet-like; (1) stylet-like (state ‘1’ in Hemiptera; the elongate mandibles with a broad base together with the elongate labrum in *Psocorrhyncha* fits well with the “Hypothetical scheme of transformations of chewing mandibles into

- stylets” proposed by Emeljanov³⁰, placing *Psocorrhyncha* between his steps “(1)” (psocodean state) and “(2)”. Nevertheless the mandibles of Permopsocida are clearly plesiomorphic compared to the stylet-like mandibles of Thripida and Hemiptera) (state 0 for *Psocorrhyncha*)
16. Right mandible: (0) present; (1) absent, mouthcone asymmetrical (state ‘1’ in Thripida⁵¹) (state 0 for *Psocorrhyncha*)
17. Maxillary lacinia: (0) in direct contact with stipes; (1) not in direct contact with stipes, probably independently movable (putative apomorphy of Acercaria¹¹, there is an intermediate structure between the lacinia and the stipes in modern Thysanoptera) (state 1 for *Psocorrhyncha*)
18. Lacinia: (0) with at least one subapical tooth; (1) without any subapical tooth (in Orthoptera, Phasmatodea, Plecoptera, and Psocodea, the lacinia has at least one strong subapical tooth, except in few Caeciliidae, while in Thripida and Hemiptera there is only an acute apical tooth) (state 1 for *Psocorrhyncha*)
19. Lacinia: (0) distally broad; (1) stylet-like distally (a broadened distal part of lacinia is a plesiomorphic character state present in Psocodea, compared to the acute and thin lacinia of Thripida and Hemiptera⁵⁷; note the eucinetid beetle *Jentozkus plaumanni* has stylet-like lacinia, plus galea) (state 0 for *Psocorrhyncha*)
20. Lacinia: (0) not elongate; (1) elongate (state ‘1’ in Acercaria, but elongate lacinia cannot be considered as a strict synapomorphy of Acercaria because elongate lacinia occur frequently when the head and mouthparts are elongate (e.g., the mecopteran genus *Panorpodes*) (state 1 for *Psocorrhyncha*)
21. Cardo and stipes: (0) separated by a furrow; (1) fused (The cardo and stipes separated by a furrow is a plesiomorphy relative to their fusion in Psocodea^{11,62}) (state 0 for *Psocorrhyncha*)

22. Gena: (0) not subdivided into two parts, (1) subdivided into two parts by a strong furrow (The gena is subdivided into two parts by a strong furrow in *Psocorrhyncha*. Such a subdivision of the gena is absent in Psocodea and the Hypoperlidae, but visible in *Dichentomum*. There is a controversy about the origin of the maxillary lobe of Hemiptera of genal origin⁶⁸⁻⁶⁹, versus of appendicular origin (maxilla)^{64,66}. Duporte⁷⁰ proposed that the maxillary plate could be of composite origin, due to the fusion of cardo and stipes, and that both latter in turn are fused with the genae and postgenae. Presence of a posterior lobe of gena in *Psocorrhyncha* would support the hypothesis of Bourgoin⁶⁸ because this taxon has a ‘normal’ maxilla not fused with the gena, and in many Hemiptera there is continuity without any maxillary suture between the posterior part of the gena and the maxillary plate. Nevertheless the problem will be really solved using the tools of the genetic of the development. The anterior part of the gena is currently called lora (for non-heteropteran Hemiptera), or mandibular plates (for Heteroptera)^{65,68}. The mid Jurassic Permopsocida appear to also have a subdivision of the gena (Fig. S5e). The Thripida have also a gena subdivided into a long mandibular plate in lateral position in front of the base of the antenna plus a posterior part below the eye (visible in the Cretaceous thripidan *Moundthrips* (Fig. S13b), and present in the early nymphs of modern *Heliothrips* or *Haplothrips*⁷¹⁻⁷². A genal fissure is also present in the modern Tubulifera⁷³. The anterior mandibular plate closes the mouthcone laterally in *Moundthrips* (Fig. S13b), but it appears fused with the maxilla in modern Thysanoptera. Emeljanov³⁰ proposed hypothetical stages of transformation from the ‘psocodean’ head to the ‘hemipteran’ one, with two structures progressively appearing and developing and corresponding to the mandibular and maybe the maxillary lobes, but he misplaced these structures anteriorly to the gena) (state 1 for *Psocorrhyncha*)

23. Maxillary palp: (0) five-segmented; (1) four-segmented, (2) less than four-segmented (Hemiptera and Thripida have state '2') (state 1 for *Psocorrhyncha*)
24. Last maxillary palpomere: (0) inserted normally on penultimate; (1) inserted apically on penultimate, penultimate cut obliquely at its apex (*Psocorrhyncha* unique apomorphy)
25. Last maxillary palpomere: (0) without broad flat sensillar zone; (1) with broad flat sensillar zone (*Psocorrhyncha* unique apomorphy, unknown in other Permopsocida)
26. Mentum: (0) not elongated; (1) elongated (state '0' in Psocodea and Hypoperlidae, the mentum are not elongate; state '1' in Hemiptera and Thripida⁷⁴ (state 1 for *Psocorrhyncha*)
27. Labial palps: (0) with more than two segments; (1) absent or strongly reduced (Presence of three-segmented labial palps in *Psocorrhyncha* is plesiomorphic. Psocodea and Thripida have labial palps one- or two-segmented, while they are lost in Hemiptera) (state 0 for *Psocorrhyncha*)
28. Hypopharynx: (0) not expanded posteriorly; (1) expanded posteriorly (state '0' in Psocodea, state '1' in Hemiptera, modern Thysanoptera, and at least in *Moundthrips* among Mesozoic Thripida^{30,75}) (state unknown for *Psocorrhyncha*)
29. Cibarial water-vapour uptake apparatus: (0) absent; (1) present (state '1' in Psocodea¹¹) (state unknown for *Psocorrhyncha*)
30. Pearman's organ on hind coxa: (0) absent; (1) present (state '1' Psocoptera excl. Liposcelidae) (state unknown for *Psocorrhyncha*)
31. Number of tarsomeres (multistate): (0) five; (1) four; (2) three or less (five-segmented tarsi in the ground plan of Pterygota; three-segmented tarsi in the ground plan of Plecoptera, state '2' in Zoraptera, Psocodea, Thripida, and Hemiptera; five-segmented tarsi in Hypoperlidae, four-segmented tarsi in Permopsocida; it is likely that reduction

- in the number of tarsomeres occurred convergently in Zoraptera, Psocodea, and the clade Thripida + Hemiptera) (state 1 for *Psocorrhyncha*)
32. Paired tarsal plantulae: (0) present; (1) absent (state '1' is a character of Eumetabola = Acercaria + Holometabola; Beutel & Gorb⁷⁶ indicated the presence of 'euplantulae' in some Mallophaga, but these are unpaired structure⁷⁷, probably non homologous⁷⁸ to the euplantulae of the polyneoptera) (state 1 for *Psocorrhyncha*)
33. Claws: (0) not reduced in adult; (1) reduced in adult (state '1' in fossil and modern Thripida) (state 0 for *Psocorrhyncha*)
34. Arolium: (0) broad and fleshy; (1) arolium broad but retractile; (2) arolium reduced, only a pulvillus inserted at base of claw (state '0' in *Psocorrhyncha*, Xylelidae, many Polyneoptera, Hemiptera; state '1' in Thripida⁵⁸; state '2' in Psocodea¹¹)
35. In wing articulation, humeral plate (HP) and basisubcostale (BSc): (0) separated; (1) united (state '1' apomorphy of Acercaria⁷⁹) (state 1 for *Psocorrhyncha*)
36. In wing articulation, BSc and second axillary sclerite (2Ax): (0) separated; (1) fused (state '1' in Hemiptera⁷⁹; state unknown in Thripida) (state 0 for *Psocorrhyncha*)
37. Fringe on posterior edge of wing: (0) absent; (1) present. (state '1' in Thripida⁷) (state 0 for *Psocorrhyncha*)
38. Forewings: (0) not more sclerotized than hind wings; (1) at least slightly more sclerotized than hind wings (state '1' in some modern Hemiptera⁸) (state 0 for *Psocorrhyncha*)
39. Wings: (0) hind wings not much smaller than forewings; (1) hind wings much smaller than forewings (state '1' in Psocodea but also in Hemiptera: Aphidoidea⁸) (state 0 for *Psocorrhyncha*)
40. A common stem R+M+CuA: (0) absent; (1) present (state '1' convergently present in Archaeorthoptera and Acercaria^{7,23}) (state 1 for *Psocorrhyncha*)

- 986 41. M (plus CuA if fused basally with radius) separates from R: (0) well distal of wing
987 base; (1) very close to wing base (state '1' is proper to the Psocodea, fossil and
988 modern, except some Troctomorpha⁷) (state 0 for *Psocorrhyncha*)
- 989 42. A neutral crossvein cua-cup between concave CuP and convex CuA, weaker than
990 CuA: (0) absent; (1) present (state '1' in Acercaria⁷) (state 1 for *Psocorrhyncha*)
- 991 43. Radial stem at point of re-emergence of CuA and M: (0) not displaying a pronounced
992 posterior angle; (1) displaying a strong posterior angle (Such an angle appears to be
993 present in the hemipteran ground plan, as it can be observed in Archescytinidae and
994 many Fulgoromorpha, but not in Psocodea or Thripida) (state 1 for *Psocorrhyncha*)
- 995 44. Areola postica: (0) absent; (1) present, longer than high; (2) present, higher than long
996 (States '1' or '2' in Acercaria, CuA-fork is reduced in Thripida and few Psocodea)
997 (state 2 for *Psocorrhyncha*)
- 998 45. Vein M: (0) forked into many branches; (1) forked twice into four branches M1-M2
999 and M3-M4; (2) forked into three pectinate branches (hemipteran ground plan?); (3)
1000 only forked once into two branches or less (State '1' in Permopsocida; the three states
1001 '1', '2', and '3' are present among various taxa in Psocodea and Hemiptera; state '3'
1002 in Thripida)
- 1003 46. RP: (0) forked; (1) unforked (State '1' in the majority of Hemiptera, but not all) (state
1004 0 for *Psocorrhyncha*)
- 1005 47. Pterostigma in forewing: (0) absent; (1) present but not limited by costal wing margin
1006 and vein RA, more sclerotized than rest of wing; (2) present, limited by costal wing
1007 margin and vein RA, more sclerotized than rest of wing (State '2' in psocodean
1008 ground plan; Thripida have no pterostigmata; Hemiptera have forewing pterostigmata
1009 in their ground plan, present in Archescytinidae and some Fulgoromorpha, Aphididae,
1010 etc.) (state 2 for *Psocorrhyncha*)

- 1011 48. Pterostigma in hind wing: (0) absent; (1) present but not limited by costal wing margin
 1012 and vein RA, more sclerotized than rest of wing; (2) limited by costal wing margin
 1013 and a deep posterior curve of vein RA, more sclerotized than rest of wing (State 2 for
 1014 Permopsocida, autapomorphy; similar hind wing pterostigmata are also present in
 1015 holometabolous Raphidioptera; Hemiptera Archescytinidae also have pterostigmata in
 1016 their fore- and hind wings, but of different shape)
- 1017 49. Forewing ScP: (0) parallel to radius and fusing with it far from wing base; (1) fused
 1018 with costa near wing base but re-emerging distally to end in radius; (2) fused with
 1019 costa near wing base and not re-emerging (homoplastic character states as the two
 1020 situations ‘0’ and ‘2’ can occur in the same family of Psocodea, and in different taxa
 1021 of Permopsocida; state ‘1’ occurs also in the psocodean family Lepidopsocidae but
 1022 with ScP only fused for a short length with costa)
- 1023 50. Anal veins in fore wings: (0) more than two free anal veins; (1) two free anal veins or
 1024 less (state ‘1’ in Acercaria) (State 1 for *Psocorrhyncha*)
- 1025 51. Coupling of fore- and hind wings with stigmapophysis in rest (a blunt chitinous
 1026 projection at base of pterostigma of forewing): (0) absent; (1) present (State ‘1’ in
 1027 winged Psocodea) (state 0 for *Psocorrhyncha*)
- 1028 52. Jugal ‘bar’: (0) absent; (1) present (State ‘1’ in Eumetabola; definitely not present in
 1029 Zoraptera according to Grimaldi & Engel⁶³ and Friedemann et al.¹¹; contra Wheeler et
 1030 al.⁸⁰); not discernable in any of the studied fossils)
- 1031 53. Abdominal sternite 1: (0) present and fully developed; (1) reduced or absent (State ‘0’
 1032 in Zoraptera; state ‘1’ in modern Acercaria, except Thysanoptera; Friedemann et al.¹¹)
 1033 (state 1 for *Psocorrhyncha*)
- 1034 54. Abdominal segment I: (0) not very narrow and reduced; (1) very narrow and reduced
 1035 (Character state ‘1’ present in all Permopsocida; the hypoperlid *Idelopsocus* has a

1036 narrow segment I but less narrow than in Permopsocida; nevertheless some Burmese
 1037 amber specimens and extant Psocodea (e.g. *Lachesilla*) have a similar constriction,
 1038 thus this character is subject to homoplasy in Acercaria)

1039 55. Female with reduced abdominal tergites IX and X (thripidan type): (0) no; (1) yes
 1040 (state ‘1’ in Thripida⁵⁸) (state 0 for *Psocorrhyncha*)

1041 56. Cerci: (0) long and multi-segmented; (1) short and one-segmented; (2) absent (State
 1042 ‘1’ in Zoraptera; state ‘2’ in Acercaria, except in Hypoperlidae; in Hymenoptera there
 1043 are ‘cerci’ but it is unclear if they belong to the 10th or the 11th segment⁸¹) (state 2 for
 1044 *Psocorrhyncha*)

1045 57. Ovipositor: (0) present and well developed; (1) reduced, of psocodean type (State ‘1’
 1046 Psocodea; state ‘0’ in the ground plan of Thripida, a character described by
 1047 Bourgoin⁸². The female anal appendages of *Psocorrhyncha* are similar to those of
 1048 Hemiptera: Fulgoromorpha of raking type⁸², viz. in the presence of gonapophyses VIII
 1049 with a raking structure, gonapophyses IX weaker and less sclerotized and broad
 1050 weakly sclerotized gonoplags. These anal appendages do not correspond to female
 1051 anal appendages of thripidan type⁵⁸ because *Psocorrhyncha* has reduced tergites IX
 1052 and X. *Psocorrhyncha* differs from those of the female Psocodea in the strong
 1053 gonapophyses VIII with raking apparatus⁶⁰)

1054 58. Female gonangulum: (0) not fused with tergum IX; (1) fused with tergum IX (State ‘1’
 1055 in Acercaria; after Friedemann et al.¹¹, ‘The gonangulum is fused with tergum IX in
 1056 Acercaria and Odonata’, and ‘the situation is unknown for Enicocephalomorpha,
 1057 Dipsocoromorpha, and Phthiraptera’) (state unknown for *Psocorrhyncha*).

1058 59. Gonostyli: (0) present; (1) absent, lost (state ‘1’ in Acercaria, Zoraptera, Embioptera)
 1059 (state 1 for *Psocorrhyncha*)

60. Male anal appendages more sclerotized, especially with large and strongly sclerotized spoon-like hypandrium: (0) yes; (1) no (State ‘1’ in modern Psocodea⁶⁰. The male anal appendages of *Psocorrhyncha* are more sclerotized than in modern Psocodea, especially in the presence of a large and strongly sclerotized spoon-like hypandrium) (state 0 for *Psocorrhyncha*)

61. Abdominal ganglia: (0) more than two separate ganglia; (1) two separate ganglia; (2) one single ganglionic mass. Two separate abdominal ganglionic complexes are found in Zoraptera. A single ganglionic mass is a possible autapomorphy of Acercaria¹¹.

62. Lateral hypopharyngeal arm (0) present; (1) absent. The lateral hypopharyngeal arm is absent in Psocodea and Zoraptera. It is present in Thysanoptera, Auchenorrhyncha, Aphidoidea, Psylloidea, Pentatomomorpha, Enicocephalomorpha, Dipsocoromorpha, and Coleorrhyncha. The situation is unknown for Aleyrodidae, and Coccoidea¹¹.

Remark. Grimaldi and Engel⁶³ proposed that the presence of abdominal trichobothria in winged forms is a synapomorphy of Acercaria. The most ‘basal’ extant Thysanoptera (Merothripidae, some Aeolothripidae) have a pair of trichobothria on the tergum X⁸³. The Psocodea have a trichobothrial field on the paraprocts⁸⁴, supposedly corresponding to a ‘reduced cercus’ of the segment XI. *Psocorrhyncha* has the same structure, at least in the female allotype. Hemiptera have no such trichobothrial field on their reduced paraprocts, and Thripida have no visible paraproct (as a remnant of segment XI). Many Hemiptera have pairs of trichobothria on several abdominal sternites. Therefore, there is no clear reason to consider diverse abdominal trichobothria are homologous between Psocodea, Hemiptera, and Thripida. Because of this ambiguity we preferred to not include the trichobothrial character proposed by Grimaldi and Engel⁶³ in our matrix.

S4 Table. Data matrix of taxa and characters

[illegible]

S4 Table. Data matrix of taxa and characters (continue)

Taxa/Characters	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Eusthenia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zorotypus</i>	1	0	2	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	1	0	0	0	0	0	1	1	?	1	1
<i>Xyela</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	3	1	2	0	0	1	0	1	0	0	0	?	0	0	0	0
<i>Hypoperla</i>	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	1	1	0	1	?	?	?	?	?	?	?	?	?	?
<i>Idelopsocus</i>	1	0	0	?	?	0	0	0	1	0	1	0	1	1	0	1	1	0	1	?	?	?	?	0	0	1	0	?	?
<i>Psocorrhyncha</i>	1	0	0	1	0	0	0	0	1	0	1	1	1	1	0	2	2	1	1	0	?	1	1	0	2	0	?	1	0
<i>Archipsylla</i>	1	0	0	?	?	0	0	0	1	0	1	1	1	1	0	2	2	1	1	0	?	?	1	0	2	0	?	?	?
<i>Dichentomum</i>	1	0	?	?	?	0	0	0	1	0	1	1	1	1	0	2	2	0	1	?	?	?	1	0	2	0	?	?	?
<i>Permopsocus</i>	?	?	?	?	?	0	0	0	1	0	1	1	2	1	0	2	2	0	1	?	?	?	1	?	2	?	?	?	0
<i>Burmacompsocus</i>	1	0	2	1	0	0	0	1	1	1	1	0	2	2	0	2	0	0	1	1	1	1	0	0	2	1	1	1	1
<i>Libanomphientomum</i>	1	0	2	1	0	0	0	1	1	1	1	0	2	2	0	2	0	0	1	1	1	1	0	0	2	1	1	1	1
<i>Thrips</i>	1	1	1	1	?	1	0	0	1	0	1	0	0	3	1	0	0	2	1	0	0	1	0	1	2	0	1	1	0
<i>Moundthrips</i>	1	1	1	?	?	1	0	0	1	0	1	0	0	3	1	0	0	2	1	0	0	1	0	1	2	0	1	1	0
<i>Archescytina</i>	?	?	?	?	?	0	0	0	1	0	1	0	1	2	1	2	0	2	1	0	?	?	0	0	2	0	?	?	?
<i>Southia</i>	1	0	0	1	1	0	1	0	1	0	1	0	1	2	1	2	0	2	1	0	1	1	0	0	2	0	1	1	0
<i>Periplaneta</i>	0	0	0	0	0	0	1	0	0	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0	0	0

1110 **S5 Table. Comparison of species numbers in acercarian orders.**

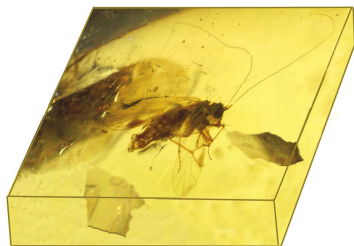
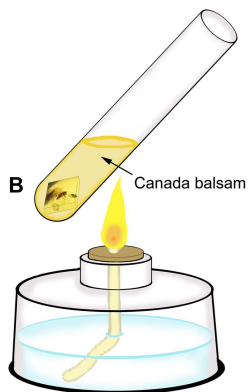
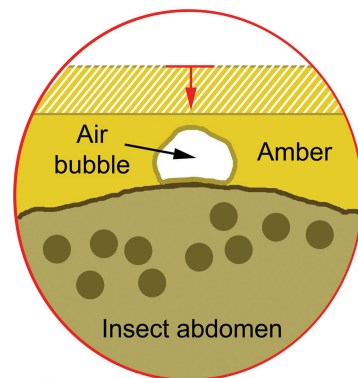
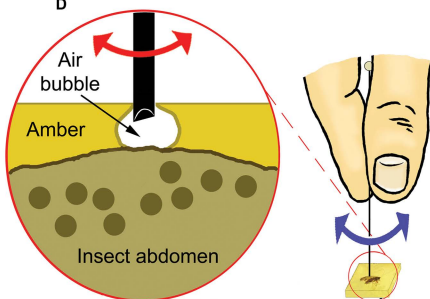
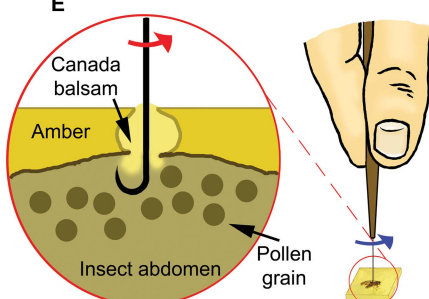
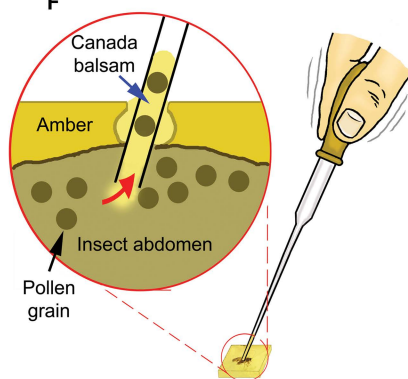
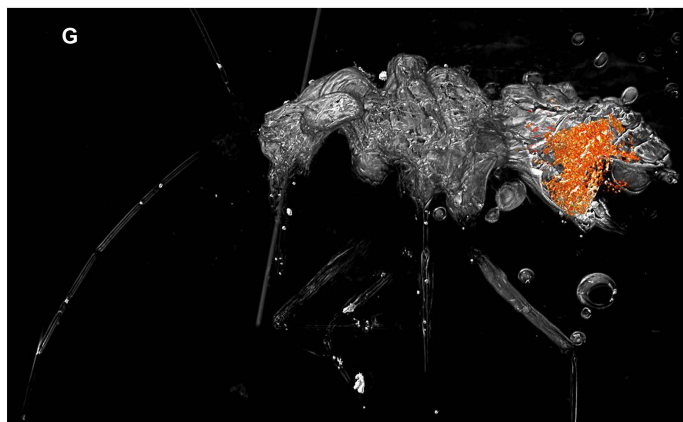
1111 Remark. Within Psocodea-Phthiraptera sucking-piercing mouthparts evolved at least three
 1112 times in convergence: in Anoplura and in the two humming bird parasites *Trochiloectes* and
 1113 *Ricinus* (= *Trochiliphagus*) *jimenezi* (Amblycera)⁸⁵.

1114

Order	Stratigraphic range	Feeding mode	Species number
Hypoperlidae	307 mya – 254 mya	chewing	13
Psocodea	315(–307) mya – Recent	chewing or sucking- piercing	11.000
Permopsocida	290(–283) mya – 99 mya	chiseling	25
Thripida (incl. Thysanoptera)	323(–315) mya – Recent	chiseling	6.000
Hemiptera	315(–307) mya – Recent	sucking-piercing	82.000

1115

1116

A**B****C****D****E****F****G****H**