

cies differ in the degree of reduction of the eighth tergite: the eighth tergite is well-developed in species with an elongate ovipositor (*E. daensis* and *E. petri* sp. nov.), small but distinct (possibly clearly visible due to extension of the abdomen) in *E. rohdendorphi* with a short ovipositor, and inconspicuous in *E. transbaicalica*, *E. abbreviata*, *E. karatavica*, and *E. baisica*.

The sex of the specimens assigned to *E. karatavica* and *E. baisica* is not certain. They were previously considered to be females with markedly shortened cerci. However, as their presumed cerci are too widely spaced, it has been speculated (Lukashevich, 1993) that these could be males with small terminalia apparently withdrawn into the preceding abdominal segments, so that the abdomen gradually tapers apically and the gonocoxites and gonostyles are not easy to see. These species have paired structures of an unknown nature, which are shaped like rounded dark spots with a truncate posterior margin, at the level of the fourth abdominal segment (Lukashevich, 1993, text-fig. 1a).

It is interesting that the males of some living *Ptychoptera* species possess a setiferous glandular pouch on the third abdominal sternite, which is used in some not yet fully understood way during copulation (Alexander, 1927). In addition, males of some Limoniidae (*Teucholabis* Osten-Sacken, Eriopterinae) show an entirely similar sternal pouch with stiff setae on the fifth (sometimes also sixth) abdominal sternite (Alexander, 1927; Savchenko, 1989). However, these structures are unpaired, unlike the paired spots on the abdomen of *Eoptychoptera* species.

Unusual external structures are sometimes observed in females as well. For example, in the limoniid genus *Tasiocera* Skuse (subgenus *Dasymolophilus* Goetgh.), two types of ovipositor are found (elongated and short) and, moreover, in the species with shortened cerci, two pairs of transverse brushes consisting of thick modified setae directed caudally are situated on the sixth and seventh abdominal tergites (Savchenko, 1989, text-fig. 112). Unfortunately, no complete analogy has been revealed (in males, the segmental position is similar but the structures are unpaired; in females, paired brushes are situated more caudally), so these structures do not aid in determining sex in *Eoptychoptera*.

The above structures in *Eoptychoptera* seem to be internal (despite having originally been described as

situated on sternites), as, in the holotype of *E. baisica* (Fig. 4f), they seem to be placed on tergites (due to poor preservation, it is difficult to describe their shape). In another specimen of the same species with the abdomen preserved almost laterally, they lie much nearer to the dorsum (PIN, no. 4210/5397; Fig. 4e), while in the paratype of *E. karatavica* (PIN, no. 2239/2240), these spots extend beyond the posterior margin of the fourth sternite and tergite. They are situated too far from the abdominal apex to be spermathecae (the latter usually observed in the seventh, eighth, or, at most, sixth segment); moreover, these spots seem to be densely covered with microtrichia, which is more characteristic of external structures (Pl. 9, fig. 4). Although in some chironomids of the subfamily Orthoclaadiinae, both spermathecae are hairy and similar in shape, with a truncate posterior margin (Saether, 1977), hairy and glabrous spermathecae are found in congeneric species (glabrous ones would be inconspicuous in fossils). In several primitive blackflies (some species of *Prosimulium* Roubaud and *Twinnia* Stone et Jamnback), the sole large spermatheca is also similarly shaped, i.e., hemispherical with a truncate posterior margin (Peterson, 1981). However, in all specimens of *E. karatavica*, the dark spots are strictly symmetrical relative to the longitudinal body axis, whereas the spermathecae usually form an arbitrary group. Among eoptychopterids, undoubted spermathecae are only recorded in *Proptychoptera evecta* Lukashevich, 1993 from Karatau—two dark structures in the seventh segment (presence of the third spermatheca figured in dashed line is doubtful; Lukashevich, 1993, text-fig. 6c).

Interesting paired internal structures of the fourth abdominal segment are known in primitive families of other mecopteroid orders (caddis flies and moths: Ivanov and Melnitsky, 1999). These are sternal pheromone glands often occurring in either sex, sometimes, only in females, and rarely, only in males. For example, in the family Nepticulidae (Lepidoptera), large glands of the fourth segment are placed near the midline and, at least in their position, closely resemble the structures in question of *Eoptychoptera* (S.I. Melnitsky, personal communication). However, nothing similar is known in other Diptera.

The sole undoubted male *Eoptychoptera* (*E. ?daiensis*, Fig. 3c) is fragmentarily preserved, allowing no detailed study of pregenital and genital segments. The

Explanation of Plate 10

Morphological details of *Eoptychoptera baisica* Kalugina, 1989, specimen PIN, no. 4210/5397, male:

Fig. 1. Ommatidia, $\times 140$.

Fig. 2. Mouthparts, $\times 140$.

Fig. 3. Head and legs, $\times 30$.

Fig. 4. Dark spots of the abdomen, $\times 85$.

Fig. 5. Pterostigmal area of the wing, $\times 50$.

Figs. 6 and 7. Last tarsomeres of foreleg (part and counterpart), to show (6) claw and (7) empodium, $\times 85$.

Designations: (*clw*) claw, (*emp*) empodium, (*lbl*) labella, (*lbr*) labrum, (*plp*) maxillary palp, (*pt*) pterostigma, (*sen pit*) sensory pit, (*spt*) dark spots of the abdomen, and (*spur*) tibial spur.

abdomen is preserved in profile, the second segment is elongated, and the third to sixth segments are sequentially shortened; however, it remains uncertain whether the abdomen gradually tapers towards the apex (although the hypopygium is hardly wider than the pregenital segments); the elongate structures that lie across the abdominal axis are presumably small simple gonostyles. There are no dark spots at the fourth segment (but this is not an argument against interpreting the above specimens of *E. karatavica* and *E. baisica* as males, because glandular pouches, e.g., in living *Ptychoptera*, are characteristic of only some species).

E. karatavica and *E. abbreviata*, described as closely related species from the same locality (the former represented by many specimens, while the latter is represented by one), can possibly provide a clue to this problem. These species are hardly distinguishable by their wing characters (the differences are explainable by the wing being folded in the *E. abbreviata* holotype and individual variation). In all *E. karatavica* specimens, the genitalia look uniformly withdrawn, despite the abdomen being more or less (sometimes strongly) extended; in the *E. abbreviata* holotype, the genitalia are clearly protruding, despite the pregenital segments being not extended; therefore, these seem to be two types of abdomen that were differently deformed in burial due to dissimilar internal structures. It would appear reasonable to interpret *E. abbreviata* as a female and *E. karatavica* as males of the same species (*E. karatavica* = *E. abbreviata*, syn. nov.). Although there are still no ironclad arguments, it is most plausible to consider all the specimens of *E. karatavica* and *E. baisica* with dark spots to be males.

Another unresolved problem is the mouthpart structure and feeding mode of *Eoptychopterina* (incidentally, feeding in living *Ptychopteridae* is still a live question.) Many scholars believe they are aphagous, which seems dubious taking into account the well-developed labella (homologous to the paraglossa (Peterson, 1916) or to the labial palps (Alexander, 1927)) and the maxillary palps. At least, a "potential ability to ingest liquid food intensively" in the *Ptychopteridae* is evidenced by the well-developed cibarial dilator, the contraction of which in normally feeding dipterans forces them to ingest food through the canal between the mouthparts (Panov, 2001).

Owing to the find of a uniquely preserved specimen of *E. baisica*, it became possible to compare in detail the mouthpart structures of *Eoptychopterina* and *Ptychoptera*. The mouthparts of these two genera show many characters in common (Fig. 5): a large clypeus and labella and very long five-segmented maxillary palps with the terminal segment longest and narrowest. Notably, the palp surface is covered with two types of setae in the same way as in the living *Ptychopteridae* and *Limoniidae*: "large macrotrichia on well-developed annular setiferous pores and small microchetae... on the terminal segment, the microchetae are mounted on special transverse sclerites shaped like narrow, slightly

wavy pigmented plates, giving the segment surface a crimped appearance" (Savchenko, 1983, p. 23). In addition, a stout unpaired sclerotized hook is found that curves upward at an almost right angle relative to the clypeus (Pl. 9, fig. 2); this is most probably the labrum, which, in living *ptychopterids* does not appear so stiff and is a small transparent membranous structure that is slightly suffused subapically (Fig. 5c).

It is unclear why the labrum is so strong and acute in *Eoptychopterina*. It is well known that the labrum is toothed in bloodsucking *Ceratopogonidae* and *Simuliidae*, the denticles being directed upward and serving to raise the host's skin when inserting the stylets (Peterson, 1916; Wenk, 1962). This raises the question of possible bloodsucking of *Eoptychopterina*. This seems to have been further confirmed by the presence of a sensory pit on the third segment of the maxillary palps of *Eoptychopterina* (Pl. 9, fig. 2). This structure is absent in the living *Ptychopteridae* but present in many nematoceros bloodsuckers (in some families, it is called Lutz's organ or Lauterborn's organ) and plays an important role in perceiving the stimuli that attract insects to the host. However, the sensory pit occurs not only in bloodsuckers, but also in some other groups, such as the *Anisopodidae* (McAlpine, 1981).

Earlier, the possibility of bloodsucking in *Eoptychopterina* was discussed by Kalugina (1989, 1991), but this assumption resulted from misinterpretation of the mouthparts' structure. She interpreted the edge of the large labellae as being curved segments of the maxillary palps and the basal segments of these palps, which lie in straight line, as stylets; she laid them out them (Figs. 5e–5f; Kalugina, 1989, p. 70, text-fig. 3a) and concluded that the mouthparts were possibly piercing in nature.

Judging from the mouthparts' structure alone, it is difficult to confirm a bloodsucking habit beyond doubt; however, it is often possible to discard such an assumption. Among living *Nematocera*, there are no bloodsuckers without a complete set of mouthparts (Snodgrass, 1943): though the presence of mandibles does not prove bloodsucking, their absence argues unambiguously for a different feeding mode.

Studying the mouthparts of the above-mentioned specimen of *Eoptychopterina* from Baissa, we found a pair of rather wide sclerotized stripes that are slightly rounded apically and terminate short of reaching the apex of the downward directed labrum (Fig. 5a). If a second pair also existed, they, due to their shape, could plausibly be interpreted as mandibles. However, there are no other stylets, while mandibles are often lost in dipterans; thus, maxillae seem to be a more probable homology. Unfortunately, the bloodsucking hypothesis cannot be discarded at this stage, because the specimen in question is regarded as male.

Furthermore, even speculation on the presence of maxillae raises some doubts. In living *Ptychopteridae*, both stylet pairs, the mandibles and maxillae, are absent. When studying isolated mouthparts of *Pty-*

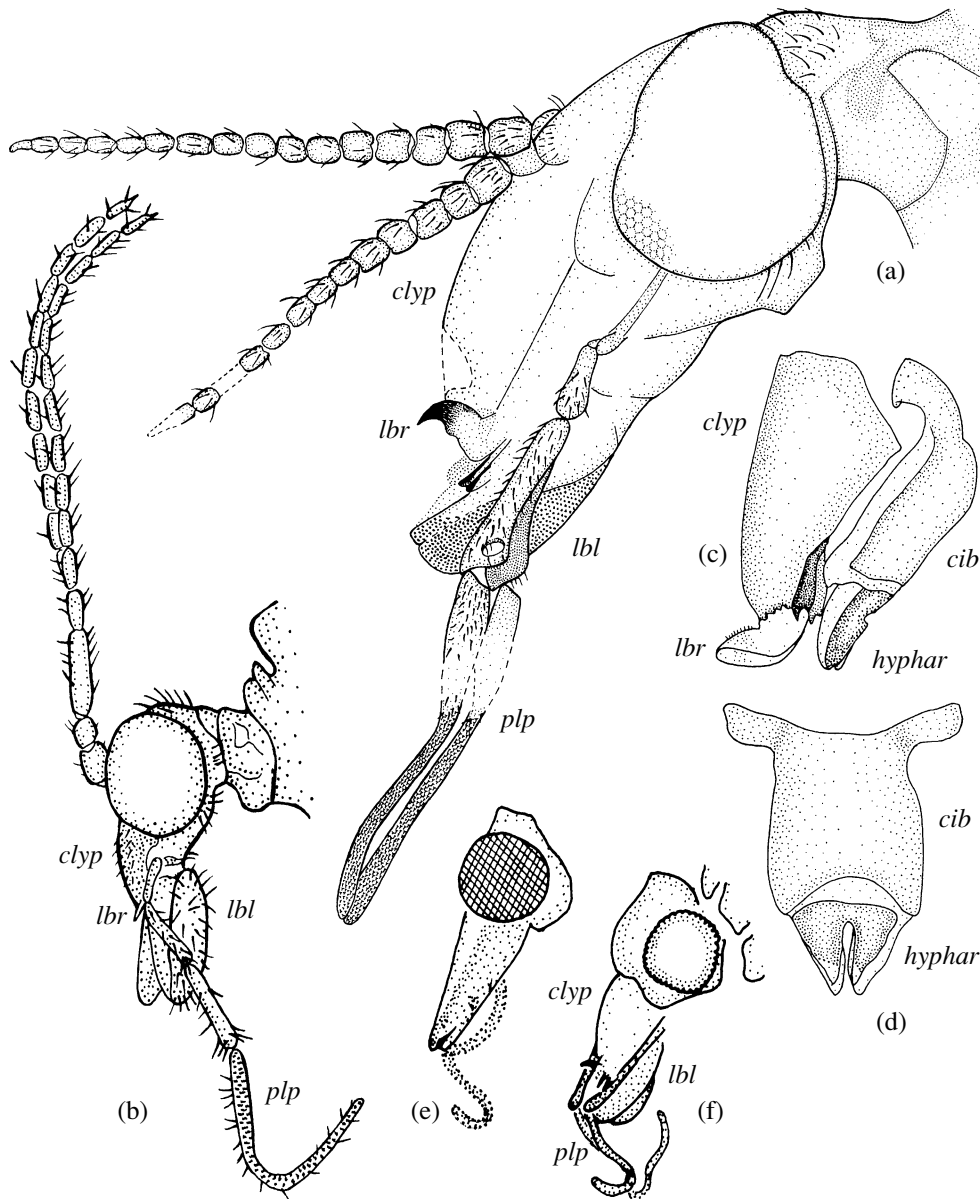


Fig. 5. Head structure in *Eoptychopterina* and *Ptychoptera*: (a) *E. basica* Kalugina, specimen PIN, no. 4210/5397; (b–d) *P. contaminata* (L.): (b) female head, (c) mouthparts in lateral view, and (d) hypopharynx in dorsal view; (e–f) *E. basica* Kalugina; holotype: (e) schematized figure from Kalugina (1989), (f) new interpretation. Designations: (cib) cibarium, (clyp) clypeus, (hyphar) hypopharynx, (lbl) labella, (lbr) labrum, and (plp) maxillary palp.

choptera, we noted that, in the absence of stylets, an illusion of their presence could be created in the lateral view due to the complicated shape and uneven sclerotization of the hypopharynx (Figs. 5c, 5d). Apparently, the stylets are likewise completely absent in *Eoptychopterina*. However, the difference in sclerotization is clearly pronounced. In *Eoptychopterina*, only the labrum and distal part of the hypopharynx are sclerotized. In *Ptychoptera*, the most sclerotized element is the clypeus (laterally provided with complicated, stout, and sharp ribs), while the hypopharynx is very unevenly sclerotized and the labrum is transparent. Despite the different degree of sclerotization (and therefore of stiff-

ness), the labrum in both cases is identically bent upward and, in profile, resembles an acute hook (although *Ptychoptera* in reality lacks any sharp point).

Unfortunately, nothing like such a stout labrum is known in the living Nematocera, and its function in the absence of all stylets remains one more mystery of *Eoptychopterina*. Members of the nominotypical subfamily of the Eoptychopteridae that were preserved in Lebanese and Burmese amber also show nothing similar. The labrum of *Leptychoptera* Lukaszewich et Azar, 2003 is transparent and unsclerotized like that of living *Ptychoptera*.

The conclusion of the complete absence of the stylets is important for reconstructing not only the feeding mode of the genus, but also its relationships. Kalugina (1989, 1991) hypothesized that the Jurassic *Eoptychopterina* may have been ancestral to blackflies (Simuliidae; known since the Early Cretaceous or, possibly, Late Jurassic) on account of the mouthparts and antennal structure of *Eoptychopterina*, their habitual similarity to blackflies, and the derivability of the simuliid venation from that of *Eoptychopterina*. On the strength of this alleged relationship, Kalugina tentatively assigned the pupa *Simulimima grandis* Kalugina, 1985 (uppermost Lower Jurassic, Ichetui Formation) to the Eoptychopteridae, despite its striking similarity to simuliid pupae (arborescent gills and arrangement of abdominal hooks). This conclusion was supported by the early age of this find, the gradual (rather than abrupt) apical tapering of the abdomen, and, especially, by the large size (the pupa, exclusive of gills, is 12 mm long), which is atypical of living and fossil blackflies, whereas eoptychopterids (which, incidentally, are recorded in the Ichetui Formation) are often very large.

Reexamination of the holotype of *S. grandis* has shown that it is a pupal exuvium with the extended abdomen, so that intersegmental membranes are in places longer than the tergites themselves, resulting in the shape of the abdomen being modified and its length increased by more than 1.5 times relative to the vital length. The arrangement of the abdominal hooks (onchotaxy) follows in detail that of living blackflies: the tergal hooks on the second to fourth segments and the sternal hooks on the fifth to seventh segments are situated nearer to the posterior segment margin (the presence of hooks on the first tergite is doubtful), the spine combs are at the anterior margin of the fifth to eighth tergites, and the tail hook is on the ninth tergite. Therefore, Crosskey (1990) with confidence transferred this genus to the Simuliidae and placed it close to the extant genus *Prosimulium*, something with which we agree, despite the gap in the record of blackflies, which have not been found in any undoubtedly Jurassic locality. Pupae that are known to be eoptychopterids, although belonging to the genus *Crenoptychoptera* Kalugina, 1985 from another subfamily, are completely dissimilar to *Simulimima*, but surprisingly resemble those of living Ptychopteridae (Lukashevich, 1995).

The new interpretation of the *E. baisica* mouthparts weakens the hypothesis about the relationship between *Eoptychopterina* and the Simuliidae. It is difficult to derive blackflies with a complete set of mouthparts directly from *Eoptychopterina*, with its reduced and apparently strongly specialized mouthparts (although *E. baisica* comes from the Lower Cretaceous and, consequently, it is not inconceivable that the stylets were retained by its Jurassic congeners). Relationships between the Eoptychopterinae and Simuliidae remain possible, but we can, at most, hypothesize that they had some common ancestors rather than one having directly descended from another.

As for immature Eoptychopterinae, the sole pretender left after *S. grandis* being transferred to blackflies is *Bolboia mira* Kalugina, 1989. Unfortunately, the ten larval specimens from the Bolboi locality (eastern Transbaikalia; Upper Jurassic or Lower Cretaceous, Byankino Formation) do not allow us to determine their taxonomic position precisely, and nothing similar is known in the fossil record. Among the few dipterans collected in Bolboi, there are no Eoptychopteridae or any other large adults that might be associated with these larvae (although the collection cannot be considered representative). Kalugina tentatively placed the genus *Bolboia* in the Eoptychopteridae, close to *Eoptychopterina*, and her arguments seem quite sound. It was assigned to the ptychopteroid larval type on account of the well-developed head capsule, presence of the slender caudal region, and ability of strong longitudinal contraction; the finely granulate integument could also be noted. However, the absence of conspicuous external segmentation, prolegs, and additional caudal processes distinguish these larvae from those of the living Ptychopteridae. Therefore, until receiving new data, we provisionally assign *Bolboia* to the subfamily Eoptychopterinae.

The specimens mentioned below are stored at the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN); Maidstone Museum and Art Gallery, Great Britain (MNEMG); and Capital Normal University, Beijing, China (CNU).

SYSTEMATIC PALEONTOLOGY

Family Eoptychopteridae Handlirsch, 1906

Subfamily Eoptychopterinae Lukashevich, 1995

Genus *Eoptychopterina* Kalugina, 1985

Eoptychopterina: Kalugina and Kovalev, 1985, p. 37.

Type species. *E. rohdendorphi* Kalugina, 1985.

Diagnosis. Massive gnats of medium and large size. Eyes large and glabrous; ommatidia uniform in size. Mouthparts large, elongate; clypeus well-developed; labella large; maxillary palps long with terminal segment longest (about third of total length). Antennae short, with segments (about 20) rounded, gradually diminished, with numerous short macrotrichia. Mesothorax with scutal and transepimeral sutures, anepisternal suture incomplete. Wing often wide, with costal area broadened; wing membrane either densely pubescent or with sparse short hairs, pterostigma large and either dark or pale, respectively. Rs stem about midlength curved toward medial stem; R_{4+5} stem angulate at junction with r-m; M stem weak and often desclerotized; three branches of M (M_1 , M_2 , M_{3+4}); im connecting M_{1+2} and M_{3+4} ; CuA beyond m-cu feebly sigmoidal or straight. Alular incision deep; alula sometimes developed. Legs densely covered with fine setae; tarsi additionally covered with rows of stronger setae; tibial spurs large, pubescent except for acuminate tip (at least middle leg, with two spurs); first tarsomere

longest, no longer than remaining combined; claws relatively small, simple; empodium apparently present. Abdomen compact, 1.5–2.5 times shorter than wing and longer than thorax; ovipositor sclerotized or not, sometimes shortened.

Species composition. Fifteen species from the uppermost Lower Jurassic–Lower Cretaceous of Europe and Asia.

Key to Species of *Eoptychopterina* Based on Wings

- 1 (4) R_4 continuing direction of dR_{4+5} (Fig. 6a)
- 2 (3) $r-m$ joining proximal part of glabrous discal cell (bM_{1+2} much shorter than mM_{1+2}); R_{4+5} fork three times as long as dR_{4+5} (wing 8.6 mm long).....*E. demissa*
- 3 (2) $r-m$ joining midlength of hairy discal cell ($bM_{1+2} = mM_{1+2}$); R_{4+5} fork five times longer than dR_{4+5} (wing ca. 7 mm long).....*E. dimidiata*
- 4 (1) R_{4+5} forked symmetrically
- 5 (6) Sc terminating at $r-m$ level (wing ca. 5 mm long).....*E. undensis*
- 6 (5) Sc terminating distal to $r-m$
- 7 (18) Wing glabrous or covered with small sparse hairs; pterostigma pale or inconspicuous
- 8 (9) im joining very close to M_{1+2} bifurcation (wing ca. 10 mm long, Fig. 6d).....*E. kaluginae* sp. nov.
- 9 (8) im joining M_{1+2} at some distance (not shorter than $r-m$) from its bifurcation
- 10 (13) R_3 curved
- 11 (12) Sc terminating proximal to im ; dR_{4+5} four times longer than bR_{4+5} ; mM_{3+4} longer than dM_{3+4} (wing 4.4 mm long, Fig. 6b).....*E. camura*
- 12 (11) Sc terminating at level of junction of im and M_{3+4} ; dR_{4+5} only slightly longer than bR_{4+5} ; mM_{3+4} not longer than dM_{3+4} (wing 5 mm long, Fig. 3a).....*E. petri* sp. nov.
- 13 (10) R_3 straight
- 14 (15) dM_{1+2} six times shorter than mM_{1+2} and four times shorter than im (wing 7 mm long).....*E. rohdendorphi*
- 15 (14) dM_{1+2} two to four times shorter than mM_{1+2} and at most half as long as im
- 16 (17) dR_{4+5} slightly longer than bR_{4+5} ; R_{4+5} forked proximal to im ; discal cell four times as long as wide (wing 6.3 mm long, Fig. 3b).....*E. daiensis*
- 17 (16) dR_{4+5} three times as long as bR_{4+5} ; R_{4+5} forked at im level; discal cell 2.5–3 times as long as wide (wing 6–9 mm long).....*E. glabra*
- 18 (7) Wing densely pubescent, especially anteriorly and apically; pterostigma dark
- 19 (24) im joining close (just proximal or distal) to M_{1+2} bifurcation
- 20 (21) Smaller (wing 6.5 mm long, Fig. 6c)....*E. omissa* sp. nov.
- 21 (20) Larger (wing 8–14 mm long)
- 22 (23) M_1 proximally angulate; R_{4+5} fork 4–4.5 times longer than dR_{4+5} (wing 9.5–14 mm long, Figs. 6e, 6f).....*E. angularis*
- 23 (22) M_1 smoothly curved; R_{4+5} fork six times longer than dR_{4+5} (wing 8.2–10.2 mm long).....*E. elenae*
- 24 (19) im joining M_{1+2} at some distance (not shorter than $r-m$) from its bifurcation
- 25 (26) R_{4+5} fork four to five times longer than dR_{4+5} ; $r-m$ equal to dM_{1+2} (wing 7.5–12 mm long).....*E. karatavica* (= *E. abbreviata*, syn. nov.)
- 26 (25) R_{4+5} fork 3–3.5 times longer than dR_{4+5} ; $r-m$ twice shorter than dM_{1+2}
- 27 (28) Smaller (wing 6.5 mm long); dM_{1+2} about four times shorter than mM_{1+2} ; $r-m$ 5 times shorter than im*E. transbaicalica*
- 28 (27) Larger (wing 7–9 mm long); dM_{1+2} two to three times shorter than mM_{1+2} ; $r-m$ two to three times shorter than im*E. baisica*

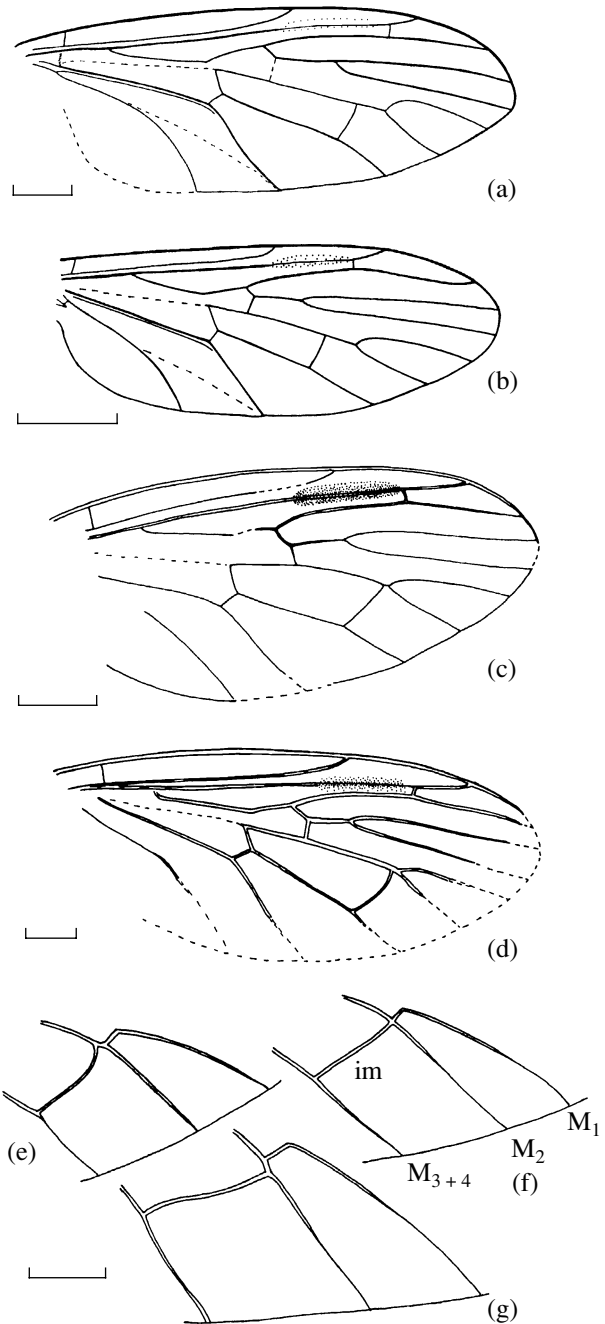


Fig 6. Wings of *Eoptychopterina* (pubescence not shown): (a) *E. demissa* Lukashевич *et al.*, holotype; (b) *E. camura* Lukashевич *et al.*, holotype; (c) *E. omissa* sp. nov., holotype; (d) *E. kaluginae* sp. nov., holotype; and (e–g) *E. angularis* Lukashевич, medial branches: (e) holotype, (f) paratype PIN, no. 2997/787, and (g) paratype PIN, no. 2997/4186. Scale bar, 1 mm.

- 26 (25) R_{4+5} fork 3–3.5 times longer than dR_{4+5} ; $r-m$ twice shorter than dM_{1+2}
- 27 (28) Smaller (wing 6.5 mm long); dM_{1+2} about four times shorter than mM_{1+2} ; $r-m$ 5 times shorter than im*E. transbaicalica*
- 28 (27) Larger (wing 7–9 mm long); dM_{1+2} two to three times shorter than mM_{1+2} ; $r-m$ two to three times shorter than im*E. baisica*

Eoptychopterina rohdendorphi Kalugina, 1985

E. rohdendorphi: Kalugina and Kovalev, 1985, p. 39, text-fig. 4, pl. 1, fig. 1; Lukashevich, 1999, p. 75, text-fig. 16.

The species is represented by the holotype (PIN, no. 3000/1251, well-preserved female, Fig. 4b) from the Novospasskoe locality (Transbaikalia; uppermost Lower or lowermost Middle Jurassic, Ichetui Formation). The collection number of the holotype was incorrectly cited in the original description. In addition, a poorly preserved impression of a female (PIN, no. 3000/1626) was originally assigned to this species, its counterpart being determined in the same paper as ?Procramptonomyiidae incertae sedis by Kovalev (p. 122). We agree with the latter opinion and exclude this specimen from consideration.

Eoptychopterina transbaicalica Kalugina, 1985

E. transbaicalica: Kalugina and Kovalev, 1985, p. 39, text-fig. 5; Kalugina, 1989, p. 70, text-fig. 3c.

The species is known from the holotype (PIN, no. 3053/880, satisfactory preserved female, head and tarsi missing, Fig. 4c) from the Uda locality (Transbaikalia; uppermost Lower or lowermost Middle Jurassic, Uda Formation).

Eoptychopterina glabra Lukashevich, 1993

E. glaber: Lukashevich, 1993, p. 110, text-fig. 2a.

The species is known from the holotype (PIN, no. 1255/1501, incomplete imprint of a satisfactory preserved adult) and paratypes (PIN, nos. 1255/1502 and 1255/1503, adult and wing) from the Kubekovo locality (southern Siberia; Middle Jurassic, Itat Formation).

Eoptychopterina elenae Ren et Krzemiński, 2002

E. elenae: Ren and Krzemiński, 2002, p. 209, text-figs. 5–7, pl. 3.

The species is known from the holotype (CNU, BCD 2013, well-preserved female) from the Daohugou locality (China; Middle or Upper Jurassic, Jiulongshan Formation).

Eoptychopterina angularis Lukashevich, 1993

E. angularis: Lukashevich, 1993, p. 106, text-fig. 1k.

The species is known from the holotype (PIN, no. 2784/74) and paratypes (PIN, nos. 2997/787, 4186, wings, Figs. 6e–6g) from the Karatau locality (Kazakhstan; Upper Jurassic, Karabastau Formation).

Eoptychopterina karatavica Lukashevich, 1993

E. karatavica: Lukashevich, 1993, p. 106, text-figs. 1a–1f; Lukashevich *et al.*, 1998, p. 317, text-fig. 2; Lukashevich, 1999, p. 77, text-fig. 22.

E. abbreviata: Lukashevich, 1993, p. 107, text-figs. 1i and 1j; Lukashevich, 1999, text-fig. 21 (syn. nov.).

The species is known from the type series from the Karatau locality (Kazakhstan; Upper Jurassic, Karabastau Formation): holotype (PIN, no. 2066/1988, well-preserved male) and paratypes (PIN, nos. 2066/1692,

Fig. 4d; 2239/2240, 2239/2603, 2997/3032, males; and 2554/942, wing). Specimens PIN, nos. 2384/1238 and 2384/2323 (adults) probably belong to this species as well. The *E. abbreviata* holotype (PIN, no. 2066/1459, well-preserved female, Fig. 4a) is assigned to this species. Specimen PIN, no. 2997/3533, originally assigned to this species, is described below as a separate species.

Eoptychopterina omissa Lukashevich, sp. nov.

E. karatavica (part.): Lukashevich, 1993, p. 107.

E t y m o l o g y. From the Latin *omissus* (overlooked).

H o l o t y p e. PIN, no. 2997/3533, satisfactory preserved adult; Kazakhstan, Chimkent Region, Chayanskii District, near the village of Mikhailovka, Karatau locality; Upper Jurassic, Karabastau Formation.

D e s c r i p t i o n (Fig. 6c). The body is dark; the abdomen is somewhat shorter than the wings. The wing is about twice as long as it is wide. The wing blade is densely pubescent, especially anteriorly and apically; the pterostigma is dark. Sc terminates distal to r–m at the level of junction of im and M_{3+4} . The R_{4+5} stem is forked symmetrically. The R_{4+5} fork is 3.6 times longer than dR_{4+5} . The im crossvein joins almost the M_{1+2} bifurcation. The discal cell is three times as long as wide. CuA is curved distal to the junction with m–cu.

M e a s u r e m e n t s, mm: antennal length, 1.4; thoracic length, 1.9; abdominal length, ca. 5.3; wing length, 6.5; wing width, 2.8; foreleg, length of: femur, 1.8, tibia, 2.2, first tarsomere, 1.3; hind leg, length of: femur, 2.5, tibia, 2.9, tarsomeres, 1.5 : 0.7 : 0.5 : 0.25 : 0.2.

M a t e r i a l. Holotype.

Eoptychopterina kaluginae Lukashevich, sp. nov.

E t y m o l o g y. In memory of the dipterologist N.S. Kalugina.

H o l o t y p e. PIN, no. 4270/232, well-preserved incomplete wing (part and counterpart); Mongolia, Gobi-Altai Aimak, southeast of the Adzh-Bogd Mountain Range, 5 km west of Shara-Teg Mountain, Shara-Teg locality; Upper Jurassic.

D e s c r i p t i o n (Fig. 6d). The wing blade bears only small hairs anteriorly and apically; the pterostigma is distinct. Sc terminates distal to r–m at the level of junction of im and M_{3+4} . R_3 is straight. The R_{4+5} stem is forked symmetrically. The R_{4+5} fork is about 4.5 times longer than dR_{4+5} . The im crossvein joins almost the M_{1+2} bifurcation. The discal cell is 2.5 times as long as it is wide. CuA is curved distal to the junction with m–cu.

M e a s u r e m e n t s, mm: reconstructed wing length, about 10.

M a t e r i a l. Holotype.

Eoptychopterina undensis Kalugina, 1989

E. undensis: Kalugina, 1989, p. 66, text-fig. 1.

The species is known from the type series: holotype PIN, no. 3015/146(177) (satisfactorily preserved incom-

plete adult, genitalia missing) and paratype PIN, no. 3015/1442 (male) from the Unda locality (Transbaikalia; Upper Jurassic or Lower Cretaceous, Glushkovo Formation). The paratype was described as a female; however, the terminalia of this specimen are similar to those of *E. karatavica*, so it is interpreted as being male.

Eoptychopterina daiensis Kalugina, 1989

E. daiensis: Kalugina, 1989, p. 68, text-fig. 2; Lukashevich, 1993, p. 105, text-figs. 1g and 1h.

The species is known from the holotype (PIN, no. 3063/878, well-preserved female, Fig. 3b) from the Daya locality (Transbaikalia; Upper Jurassic or Lower Cretaceous, Glushkovo Formation). A male (specimen PIN, no. 3063/1428; Fig. 3c) and a female (specimen PIN, no. 3063/1426) from the same locality apparently also belong to this species on account of their size, straight R_3 , proportions of discal cell, and wing shape; however, it is impossible to conclude this with certainty because of the incomplete preservation of the wing.

Eoptychopterina petri Lukashevich, sp. nov.

E t y m o l o g y. In honor of P. Kuznetsov, who collected the specimen.

H o l o t y p e. PIN, no. 3063/1425, well-preserved female (head missing); Transbaikalia, Chita Region, Shelopuginskii District, left bank of the Daya River, 2 km upstream of the Shiviya Creek, Daya locality; Upper Jurassic or Lower Cretaceous, Glushkovo Formation.

D e s c r i p t i o n (Fig. 3a). The body is dark; the abdomen is somewhat shorter than wings. The wing is nearly twice as long as wide. The wing blade is glabrous; no pterostigma is observed. Sc terminates distal to r-m at the level of the junction of im and M_{3+4} . R_3 is curved. The R_{4+5} stem is forked symmetrically. The R_{4+5} fork is five times longer than dR_{4+5} , which is only slightly longer than bR_{4+5} . The r-m crossvein is situated at the midlength of the wide discal cell, which is 2.2 times as long as wide. The im crossvein is almost equal to dM_{1+2} , which is only 1.3 times shorter than mM_{1+2} ; mM_{3+4} is no longer than dM_{3+4} . CuA is straight distal to the junction with m-cu. The eighth abdominal segment and sclerotized ovipositor are well-developed.

M e a s u r e m e n t s, mm: thoracic length, 1.4, abdominal length, 3.4 (including ovipositor, 0.4), wing length, 5; foreleg, length of: femur, 1.2, tibia, 1.6, tarsomeres: 0.8 : 0.37 : 0.24 : 0.2 : 0.2; hind leg, length of: femur, 1.7, tibia, 1.6, first tarsomere, 0.85.

R e m a r k s. Taking into account the possibility of rock distortion, which sometimes results in a different width-to-length ratio of the right and left wing of the same specimen (such case was described for *E. elenae*), one might assume that *E. petri* sp. nov. is conspecific to *E. daiensis* from the same locality. However, *E. daien-*

sis is distinguished by the following characters: R_3 is straight, dM_{1+2} nearly 2.5 times longer than mM_{1+2} , mM_{3+4} is longer than dM_{3+4} , and the length of the discal cell is 4.4 times greater than its maximum width; these features cannot be explained by the wing distortion. Therefore, *E. petri* is considered to be a separate species.

M a t e r i a l. Holotype.

Eoptychopterina demissa Lukashevich, Coram et Jarzembowski, 2001

E. aff. glaber: Coram and Jarzembowski, 1998, p. 137, text-fig. 4.

E. demissa: Lukashevich *et al.*, 2001, p. 455, text-fig. 4.

The species is known from the holotype (MNEMG 1998.16, well-preserved wing, Fig. 6a) from the Durlston Bay locality (England; Upper Berriasian, Durlston Formation).

Eoptychopterina dimidiata Lukashevich, Coram et Jarzembowski, 2001

E. aff. undensis: Coram, Jarzembowski, 1998, p. 137, text-fig. 5.

E. dimidiata: Lukashevich *et al.*, 2001, p. 456, text-fig. 5.

The species is known from the holotype (MNEMG 1998.17, well-preserved incomplete wing) from the Durlston Bay locality (England; Upper Berriasian, Durlston Formation).

Eoptychopterina camura Lukashevich, Coram et Jarzembowski, 2001

E. camura: Lukashevich *et al.*, 2001, p. 456, text-fig. 6.

The species is known from the holotype (MNEMG 2000.49, well-preserved wing, Fig. 6b) from the Clockhouse locality (England; Upper Hauterivian, Lower Weald Clay).

Eoptychopterina baisica Kalugina, 1989

E. baisica: Kalugina, 1989, p. 68, text-figs. 3a and 3b.

The species is known from the Baissa locality (Transbaikalia; Lower Cretaceous, Zaza Formation): the holotype (PIN, no. 1989/3175, satisfactory preserved male, Figs. 4f, 5e, 5f) and additional specimens were collected in the type locality after the first description: an excellently preserved male (part and counterpart, PIN, no. 4210/5397, Figs. 2, 4e, 5a, Pl. 9, figs. 1-7) and wings (specimens PIN, nos. 3064/8632, 4210/7518, parts and counterparts, and 3064/8671, wing).

Eoptychopterina spp.

The collection housed at the PIN contains several *Eoptychopterina* specimens that do not belong to any of the above species; however, they cannot be formally described because of poor preservation. These are isolated wings from the Karatau and Baissa localities (specimens PIN, nos. 2997/675 and 4210/3342; in the latter, the reconstructed wing is ca. 16 mm long) and the body (wings missing) from Karatau (specimen PIN, no. 2239/2608, body is ca. 14 mm long).

ACKNOWLEDGMENTS

The study was supported by the Russian Foundation for Basic Research, project no. 01-05-64741.

REFERENCES

1. C. P. Alexander, "Family Ptychopteridae," *Genera Insectorum. F. 188* (L. Desmet-Verteneuil, Brussels, 1927).
2. R. Coram and E. A. Jarzembowski, "Insect-Bearing Horizons in the Type Purbeck and New Purbeck/Wealden Flies (Diptera)," *Proc. Dorset Nat. Hist. Archeol. Soc.* **119**, 135–140, 1998 (1997).
3. R. W. Crosskey, *The Natural History of Blackflies* (Wiley, Chichester, 1990).
4. V. D. Ivanov and S. I. Melnitsky, "The Structure of Sternal Pheromone-Secreting Glands of Caddisflies (Trichoptera)," *Entomol. Obozr.* **78** (3), 505–526 (1999).
5. J. P. Just, "Die Anatomie der Postabdomina von *Phlebotomus garnhami* Heisch, Guiggberg und Teesdale, *Pericoma palustris* Meigen und *Liriope lacustris* Meigen (Diptera, Nematocera)," *Zool. Jb. Anat.* **91**, 305–388 (1973).
6. N. S. Kalugina, "New Psychodomorphic Dipteran Insects from the Mesozoic of Siberia (Diptera: Eoptychopteridae, Ptychopteridae)," *Paleontol. Zh.*, No. 1, 65–77 (1989).
7. N. S. Kalugina, "New Mesozoic Simuliidae and Leptonopidae and the Origin of Blood-Sucking Habit in the Lower Dipteran Insects," *Paleontol. Zh.*, No. 1, 69–80 (1991).
8. N. S. Kalugina and V. G. Kovalev, *Jurassic Dipteran Insects of Siberia* (Nauka, Moscow, 1985) [in Russian].
9. N. P. Krivosheina, A. I. Zaitsev, and V. K. Mohrig, "A Contribution to the Biology of the Dipteran Fungus Gnats (Diptera, Sciaridae)," in *Ecology and Morphology of Insects Inhabiting Mushroom Substrates* (Nauka, Moscow, 1987), pp. 6–24 [in Russian].
10. W. Krzemiński, "Ptychopteridae of Poland (Diptera, Nematocera)," *Polskie Pismo Entomol.* **56**, 105–131 (1986).
11. E. D. Lukashevich, "New Eoptychopteridae (Diptera: Psychodomorpha) from the Jurassic of Asia," *Paleontol. J.* **27** (1A), 103–123 (1993).
12. E. D. Lukashevich, "First Pupae of the Eoptychopteridae and Ptychopteridae from the Mesozoic of Siberia (Insecta: Diptera)," *Paleontol. J.* **29** (4), 164–170 (1995).
13. E. D. Lukashevich, "Mesozoic Ptychopteroidea (Diptera: Nematocera): The Stages of a Long Way," in *Proc. First Int. Palaeoentomol. Conf., Moscow, 1998* (AMBA project AM/PFICM98/1.99., Bratislava, 1999), pp. 73–79.
14. E. D. Lukashevich, J. Ansorge, W. Krzemiński, and E. Krzemińska, "Revision of Eoptychopterinae (Diptera: Eoptychopteridae)," *Polskie Pismo Entomol.* **67**, 311–343 (1998).
15. E. D. Lukashevich, R.A. Coram, and E. A. Jarzembowski, "New True Flies (Insecta: Diptera) from the Lower Cretaceous of Southern England," *Cretaceous Res.* **22**, 451–460 (2001).
16. O. M. Martynova, "Phylogenetic Relationships between Insects of the Mecopteroide Complex," *Tr. Inst. Morfol. Zhivotn. Akad. Nauk SSSR*, No. 27, 221–230 (1959).
17. J. F. McAlpine, "Morphology and Terminology: Adults," in "Manual of Nearctic Diptera," Ed. by J. F. McAlpine *et al.* (Res. Branch Agric. Can., Ottawa, 1981), Vol. 1, pp. 9–63.
18. W. Mohrig and E. Kauschke, "New Sciarid Flies from the Italian Province of Apulia," *Boll. Soc. Entomol. Ital.* **126** (2), 175–185 (1994).
19. A. A. Panov, "The Histological Structure of the Alimentary Canal in the Adult Head of Nematocera (Diptera): 1. Limoniidae, Tipulidae, Trichoceridae, Ptychopteridae, and Psychodidae," *Zool. Zh.* **80** (2), 188–200 (2001).
20. A. Peterson, "The Head-Capsule and Mouth-Parts of Diptera," *Ill. Biol. Monogr.* **3** (2), 1–112 (1916).
21. B. V. Peterson, "Simuliidae," in *Manual of Nearctic Diptera*, Ed. by J. F. McAlpine *et al.* (Res. Branch Agric. Can., Ottawa, 1981), Vol. 1, pp. 355–391.
22. F. Peus, "Liriopeidae," *Die fliegenden palaearktischen Region*, Ed. by E. Lindner (1958), Lief. 200, pp. 10–44.
23. D. Ren and W. Krzemiński, "Eoptychopteridae (Diptera) from the Middle Jurassic of China," *Ann. Zoologica* **52** (2), 207–210 (2002).
24. O. A. Saether, "Female Genitalia in Chironomidae and Other Nematocera: Morphology, Phylogenies, Keys," *Bull. Fish. Res. Board Can.*, No. 197, 1–210 (1977).
25. E. N. Savchenko, "Crane Flies of the Family Tipulidae: General Considerations and Systematic Paleontology (First Part): Subfamily Dolichozeinae and Subfamily Tipulinae (First Part)," in *Fauna of the USSR: Nov. Ser. No. 127. Dipteran Insects* (Nauka, Leningrad, 1983), Vol. 2, Issues 1–2 [in Russian].
26. E. N. Savchenko, *Limoniid Mosquitoes in the Fauna of the USSR: A Guide for Identification of Genera and Higher Taxa with a Checklist of Species* (Naukova Dumka, Kiev, 1989) [in Russian].
27. D. E. Shcherbakov, E. D. Lukashevich, and V. A. Blagoderov, "Triassic Diptera and Initial Radiation of the Order," *Int. J. Dipterol. Res.* **6** (2), 75–115 (1995).
28. R. E. Snodgrass, "The Feeding Apparatus of Biting and Disease-Carrying Flies: A Wartime Contribution to Medical Entomology," *Smiths. Misc. Coll.* **104** (1), 1–51 (1943).
29. P. Wenk, "Anatomie des Kopfes von *Wilhelmia equina* L. (Simuliidae syn. Melusinidae, Diptera)," *Zool. Jb. (Anat.)* **80**, 81–134 (1962).
30. B. P. Yong, "Attachment of the Abdomen to the Thorax in Diptera," *Mem. Corn. Univ. Agric. Exp. Stn.*, No. 44, 255–306 (1921).