

New *Eoptychoptera* (Insecta: Diptera, Ptychopteridae) from the Lower Cretaceous of Spain



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ABSTRACT

A new species, *Eoptychoptera cantabrica* sp. nov. is described from the Albian El Soplao amber-bearing deposits based on a single male with an elongated proboscis, unknown among extant members of Ptychopteridae. It represents the youngest record of the species-diverse genus *Eoptychoptera*. A pupa of *Eoptychoptera* sp. with a long respiratory horn, typical of extant ptychopterids, is described from Las Hoyas limestones, where adult fossil ptychopterids have yet to be discovered. A key to species of *Eoptychoptera*, based on wing venation, and a distribution map of Cretaceous Ptychopteridae are provided. The climatic preferences and mouthparts of Mesozoic and recent Ptychopteridae are discussed.

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1. Introduction

Ptychopteridae is a small, but rather widespread and ancient nematoceran family, in the recent fauna clearly relict, represented by only three genera of two subfamilies, Ptychopterinae and Bitacomorphinae. The adults occur on wet meadows, in swales, at lake shores, and in shady forests, usually near running water. The immature stages dwell in shallow water and waterlogged soil of the same habitats (Alexander, 1927).

In the Mesozoic, the family was considerably more diverse, with at least 11 genera of five subfamilies (including two extant ones, known since the Early Cretaceous) and over 70 species described to date from Eurasian and South American deposits (Eskov & Lukashevich, 2015; Lukashevich, 2008, 2012). During the Early Cretaceous, members of the extinct and extant subfamilies co-occurred, as evidenced by their adults (e.g. in England and Transbaikalia; Kalugina, 1989; Lukashevich, Coram, & Jarzembowski, 2001) and pupae (Lukashevich, 1995) being found in the same localities, sometimes on the same rock slabs.

Surprisingly, ptychopterids have not yet been found in Upper Cretaceous amber deposits of France, Hungary, Taimyr, Canada and

USA, with the only possible record known from Burmese amber, dated now as the late Albian–early Cenomanian, ca. 99 Ma (Shi et al., 2012). In the Cenozoic, the extinct subfamilies of Ptychopteridae are absent, whereas both extant subfamilies are rare, known as several impressions and inclusions from deposits of Eurasia and North America (Evenhuis, 2015).

Eoptychoptera Handlirsch is the most species-diverse and widespread extinct ptychopterid genus, diagnosed mainly by its wings with comparatively long Sc, R₁ and R_s, with four medial veins, and with crossvein *im* between M₂ and M₃ (Kalugina & Kovalev, 1985; Lukashevich, Ansorge, Krzemiński, & Krzemińska, 1998). To date, 19 certain and one questionable species of this genus have been recorded from half of the Eurasian Mesozoic localities bearing ptychopterid impressions. A member of *Eoptychoptera* is known also from the Santana Formation in Northeastern Brazil (late Aptian, ca.112–115 Ma), which is the only record of the family from the South America and the only Mesozoic record of the family from the southern hemisphere (Krzemiński, Kania, & Lukashevich, 2015). However, the genus has not been found in Cretaceous amber, where only *Leptychoptera* Lukashevich et Azar was recorded (Lukashevich & Azar, 2003; Lukashevich & Grimaldi, 2004).

In the present paper, a new species of *Eoptychoptera* is described, based on a single male found in El Soplao amber. Additionally, a pupa from Las Hoyas lacustrine limestones is described and placed in *Eoptychoptera* based on the venation of its wing

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sheaths. Ptychopterid immature stages occur in the fossil state much more rarely than adults. Up to now, undoubted pupae have been described only for three genera from three Asian Mesozoic localities; among these, the pupae of *Crenoptychoptera* Kalugina (extinct Eoptychopterinae) and *Zhiganka* Lukashevich (extant Bitacomorphinae) are remarkably similar to pupae of the recent ptychopterids (Lukashevich, 1995). A single incompletely preserved pupa of *Eoptychoptera*, without respiratory horns and the abdomen, has been described so far (Lukashevich et al., 1998).

Because the number of known species of *Eoptychoptera* is now half as much again as in the only revision of the genus (Lukashevich et al., 1998), an updated identification key is given herein.

El Soplao outcrop, early Albian in age (ca. 110 Ma), was recently discovered in northern Spain near the municipality of Rábago (Autonomous Community of Cantabria), on the northwestern margin of the Basque-Cantabrian Basin. It is one of the largest sites of insectiferous fossil resins found in Spain so far. The El Soplao amber-bearing deposits are included within the Las Peñasas Formation in a unit of heterolithic sandstones-siltstones and carbonaceous mudstones related to broadly coastal delta-estuarine environments (Najarro et al., 2009, 2010; Peñalver & Delclòs, 2010). The highly diverse entomofauna of El Soplao amber includes members of 12 orders: Blattodea, Isoptera, Psocodea, Thysanoptera, Hemiptera, Raphidioptera, Neuroptera, Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, and Diptera, with predominance of beetles and flies. The study of Diptera has just begun, and only several Ceratopogonidae and Zhangsolvidae have been described (Arillo et al., 2015; Pérez-de la Fuente, Delclòs, Peñalver, & Arillo, 2011).

The Las Hoyas outcrop, late Barremian in age (ca. 126 Ma), belongs to the Las Hoyas sub-basin of the Iberian Basin, which is located in the southern part of the Serranía de Cuenca (southwestern Iberian Mountain Range, east-central Spain). The laminated limestone of the La Huérguina Formation, to which the beds of Las Hoyas belong, is famous for superb preservation of soft-bodied organisms. Numerous and diverse fishes, some amphibians, turtles, lacertilians, crocodylomorphs, dinosaurs, and birds all occurred in the subtropical seasonal wetland reconstructed for Las Hoyas (Buscalioni & Fregenal-Martínez, 2010). Continental deposits of the La Huérguina Formation have yielded over 2500 insect specimens from 12 orders: Odonata, Ephemeroptera, Orthoptera, Blattodea, Isoptera, Hemiptera, Neuroptera, Coleoptera, Trichoptera, Hymenoptera, Mecoptera, and Diptera. The assemblage is dominated by aquatic Heteroptera (Martínez-Delclòs, Nel, & Popov, 1995) and terrestrial beetles and neuropterans. Dipterans are rare, with only few species hitherto described or mentioned (Mostovski & Martínez-Delclòs, 2000; Ribeiro & Lukashevich, 2014). In 2013, the senior author found neither adults nor immature stages of Ptychopteridae in the collection of Museo de las Ciencias de Castilla-La Mancha in Cuenca. The pupa described below was found during excavation in the same year.

2. Material and methods

The male CES 059 from El Soplao (north Spain, Basque-Cantabrian Basin, the Las Peñasas Formation, 43°18'N, 4°25'W, Fig. 1) is preserved in a piece of amber with the following syninclusions: one Staphylinidae (Coleoptera), one Scelionidae (Hymenoptera) and a small fragmentary wing of Diptera. The specimen was embedded in a high quality casting epoxy (Epotek 301) according to protocols in Corral, López del Valle, and Alonso (1999) and Nascimbene and Silverstein (2000). It was photographed with a camera mounted on an Olympus BX51 compound microscope, and will be housed at the El Soplao museum in Cantabria.

The pupa LH 35084 ± from the La Huérguina Formation, Las Hoyas (east-central Spain, Iberian Basin, 40°5'N, 1°29'W; Fig. 1) is

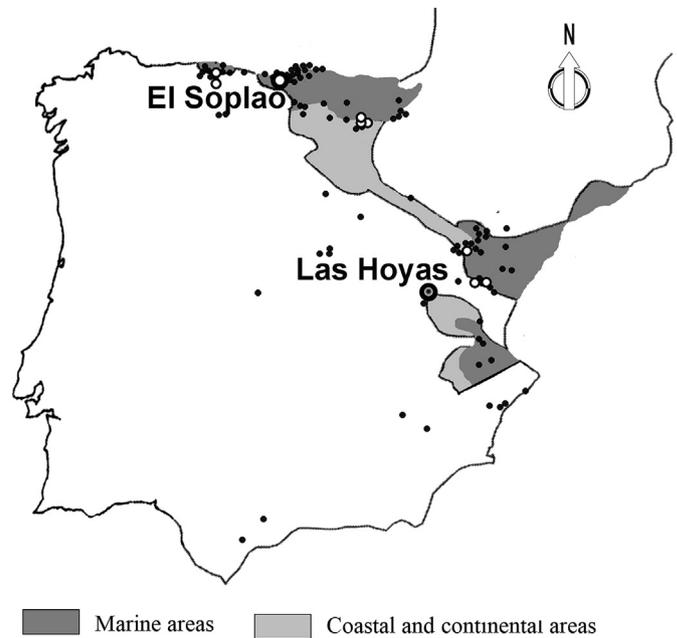


Fig. 1. Map of the Iberian Peninsula showing the location of the lower Albian marine and continental areas and the distribution of Lower Cretaceous amber outcrops (open circles – arthropod-bearing amber) and Las Hoyas outcrop (redrawn from Peñalver & Delclòs, 2010).

housed in Museo de las Ciencias de Castilla-La Mancha. It was photographed with a Nikon D3100 digital camera attached to a Nikon stereomicroscope. Drawings were made with a drawing tube attached to a stereomicroscope.

For comparison, we used ethanol-preserved adults of recent Ptychopteridae, Tanyderidae and Blephariceridae from the personal collection of the senior author. Photographs of recent midges were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera, Z-stacked using Helicon Focus 4.10 Pro and adjusted in Adobe Photoshop® CS3 10.0.

3. Systematic paleontology

Family Ptychopteridae Osten Sacken, 1862.
Subfamily Eoptychopterinae Handlirsch, 1906.

Genus *Eoptychoptera* Handlirsch, 1906.
Type species. *Eoptychoptera simplex* Handlirsch, 1906.

Range and localities. Lower Jurassic (Sogyuty and probably Charmouth, Sinemurian) up to Lower Cretaceous (El Soplao, lower Albian).

Key to species of *Eoptychoptera* based on wing venation.

- 1 (4) *r-m* about midlength of R_{4+5} (Fig. 2A)
- 2 (3) R_1 tip distal to M_{1+2} furcation, M_4 clearly shorter than M_{3+4}
E. aequidistans Lukashevich et al., 1998 (J₁, Kyrgyzstan, Sogyuty)
- 3 (2) R_1 tip level with M_{1+2} furcation, M_4 subequal to M_{3+4}
E. britannica Lukashevich, Coram et Jarzembowski, 2001 (K₁, Great Britain, Clockhouse)
- 4 (1) *r-m* close to R_s fork, distal, interstitial or proximal to it (Figs. 2B, E, H)
- 5 (20) wing with small dark spots at crossveins and furcations.
- 6 (7) M_4 subequal to M_{3+4} (Fig. 2B)
E. longifurcata Lukashevich, Coram et Jarzembowski, 2001 (K₁, Great Britain, Durlston Bay)
- 7 (6) M_4 clearly shorter than M_{3+4}

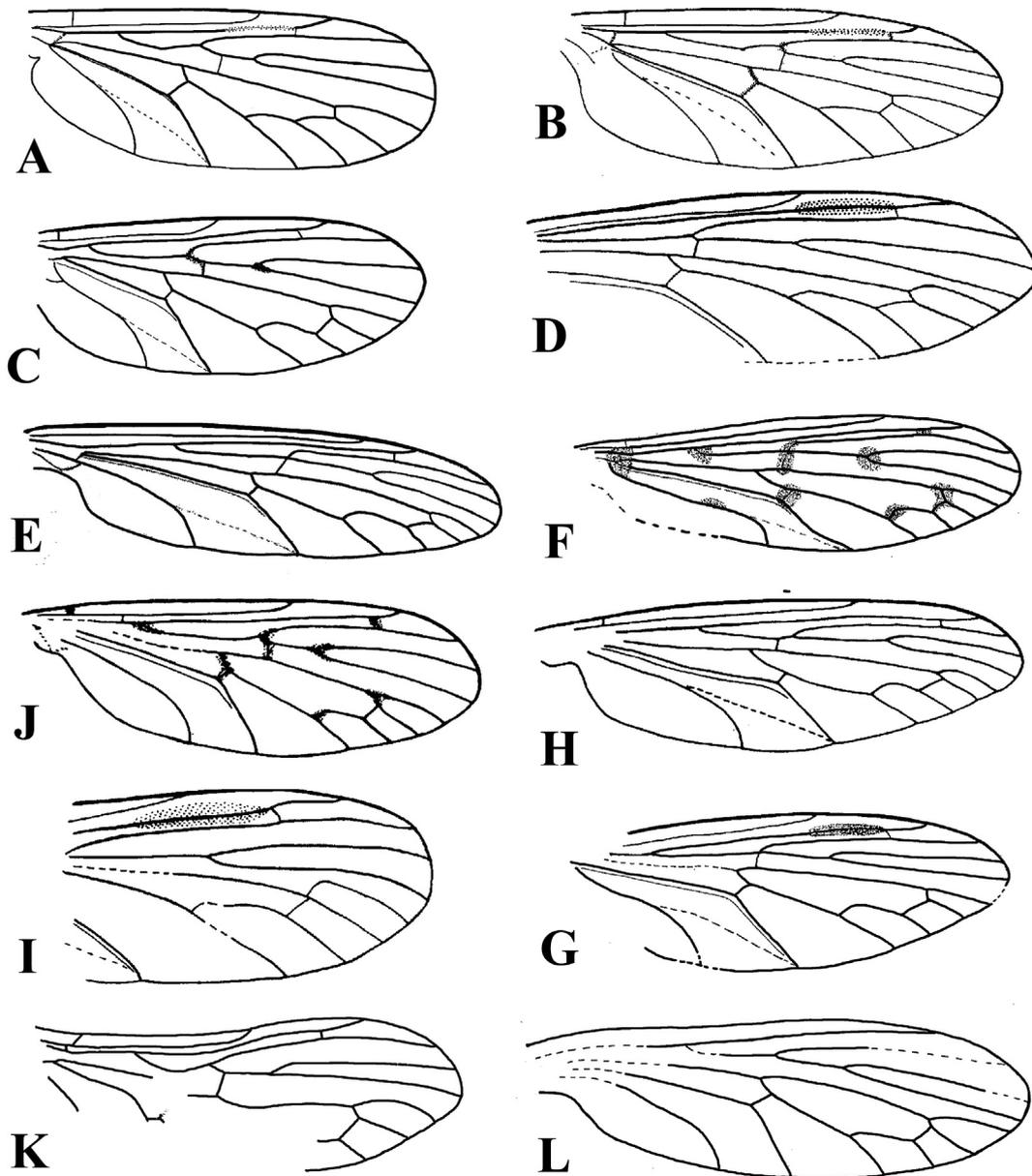


Fig. 2. Wing venation of *Eoptychoptera* (after Lukashevich, 1993; Lukashevich et al., 1998; Lukashevich, 2000; Lukashevich et al., 2001 and orig.): A, *E. britannica*, holotype, Clockhouse, K₁; B, *E. longifurcata*, holotype, Durlston Bay, K₁; C, *E. simplex*, holotype, Dobbertin, J₁; D, *E. shurabica*, holotype, Sagul, J₁; E, *E. eximia*, specimen LD 1194/1, Dobbertin, J₁; F, *E. tempestilla*, holotype, Shar Teg, J₃; J, *E. asiatica*, holotype, Karatau, J₂₋₃; H, *E. magna*, holotype, Karatau, J₂₋₃; I, *E. elevata*, holotype, Kempendyay, J₃–K₁; G, *E. vitrea*, holotype, Sogyuty, J₁; K, *E. cantabrica* sp.nov., holotype, El Soplao, K₁; L, *Eoptychoptera* pupa, specimen LH 35084, venation on wing sheath, Las Hoyas, K₁. Without scale.

8 (9) Rs origin at about 15% wing length, R_{2+3} subequal to R_3 (Fig. 2C)

E. simplex Handlirsch, 1906 (J₁, Germany, Dobbertin, Hondelage, Grassel)

9 (8) Rs shorter, R_{2+3} no less than 1.5 times longer than R_3 (Fig. 2F)
10(17) R_{4+5} furcation proximal to that of M_{3+4} , bas M_{3+4} 3–4 times longer than *m-cu*, R_{4+5} fork 2 times longer than R_{4+5}

11(12) Sc tip level with R_{4+5} furcation and proximal to that of M_{3+4}
E. altaica (Kalugina, 1988) (J₂₋₃, Mongolia, Bakhar)

12(11) Sc tip distal to R_{4+5} furcation and level with that of M_{3+4}
13(14) med M_{1+2} 4 times longer than bas M_{1+2} , CuA straight beyond *m-cu*

E. paramaculata (Kalugina & Kovalev, 1985) (J₂, Siberia, Kubekovo)

14(13) med M_{1+2} в 6.5 раза longer than bas M_{1+2} , CuA sigmoidal beyond *m-cu*

15(16) wing medium-sized (length about 10 mm; Fig. 2F)

E. tempestilla Lukashevich et al., 1998 (J₃, Mongolia, Shara Teg)

16(15) wing large-sized (length about 17 mm)

E. ansorgei Ren et Krzeminski, 2002 (J₂₋₃, China, Daohugou)

17(10) R_{4+5} furcation distal to that of M_{3+4} , bas M_{3+4} subequal to *m-cu*, R_{4+5} fork 3 times longer than R_{4+5}

18(19) dark spot near Rs midlength

E. aucta (Lukashevich, 1993) (J₂₋₃; Kazakhstan, Karatau)

19(18) no such spot (Fig. 2J)

E. asiatica (Lukashevich, 1993) (J₂₋₃; Kazakhstan, Karatau)

20(5) wing with only one spot: pale, elongate pterostigma (Fig. 2D)

21(26) R_{4+5} furcation proximal to that of M_{3+4} , R_{4+5} fork 3 times longer than R_{4+5}

22(23) Sc tip level with R_{4+5} furcation; R_2 level with M_{1+2} furcation; *r-m* before Rs furcation; med M_{1+2} 11 times longer than bas M_{1+2} , wing length 10 mm

- E. modica* (Lukashevich, 1993) (J₂, Siberia, Kubekovo)
23(22) Sc tip proximal to R₄₊₅ furcation; R₂ proximal to M₁₊₂ furcation; *r-m* interstitial or beyond Rs furcation; med M₁₊₂ 6–7 times longer than bas M₁₊₂, wing smaller
- 24(25) Rs stem straight, aligned with R₄₊₅, wing length 7 mm (Fig. 2G)
- E. vitrea* Lukashevich et al., 1998 (J₁, Kyrgyzstan, Sogyuty)
25(24) Rs stem curved, forking symmetrically, wing length 4 mm (Fig. 2K)
- E. cantabrica* sp. nov. (K₁, Spain, El Soplao amber)
26(21) R₄₊₅ furcation distal to that of M₃₊₄, R₄₊₅ fork no more than 2.5 times longer than R₄₊₅
- 27(28) bas M₃₊₄ 3 times longer than *m-cu* (Fig. 2H)
- E. magna* (Lukashevich, 1993) (J_{2–3}; Kazakhstan, Karatau)
28(27) bas M₃₊₄ slightly longer than *m-cu* (unknown for *E. maxima* and *E. elevata*)
- 29(32) *im* at M₁₊₂ furcation
- 30(31) M₁₊₂ forking symmetrically, wing length 15 mm
- E. maxima* (Kalugina & Kovalev, 1985) (J₂, Siberia, Kubekovo)
31(30) M₁₊₂ stem aligned with M₂, wing length 10 mm (Fig. 2I)
- E. elevata* Lukashevich, 2000 (J_{3–K1}, Yakutia, Kempendyay)
32(29) *im* meeting M₂
- 33(34) med M₁₊₂ 19 times longer than bas M₁₊₂
- E. cretacea* (Kalugina, 1989) (K₁, Transbaikalia, Baissa)
34(33) med M₁₊₂ 3–8 times longer than bas M₁₊₂
- 35(40) Sc tip distal to M₃₊₄ furcation; *r-m* interstitial or distal to Rs furcation, wing smaller than 10 mm
- 36(39) Sc tip proximal to R₄₊₅ furcation
- 37(38) d cell 4–5 times longer than M₂ (Fig. 2E)
- E. eximia* (Bode, 1953) (J₁, Germany, Hondelage, Dobbertin)
38(d) d cell 3 times longer than M₂
- E. braziliana* Krzemiński, Kania et Lukashevich, 2015 (K₁, Brazil, Santana)
39(36) Sc tip distal to R₄₊₅ to furcation (Fig. 2D)
- E. shurabica* Lukashevich, 2000 (J₁, Kyrgyzstan, Sagul = Shurab III)
40(35) Sc tip proximal to M₃₊₄ furcation; *r-m* proximal to Rs furcation, wing length 14 mm
- E. jurassica* Ren et Krzeminski, 2002 (J_{2–3}, China, Daohugou)

Eoptychoptera cantabrica sp. nov.

(Figs. 2K, 3, 4, 5A–C)

Derivation of name. The species name is derived from Cantabria, the province of Spain, where the specimen was found.

Material examined. Holotype CES 059, entire male; north Spain, El Soplao, Las Peñasas Formation, lower Albian, Lower Cretaceous.

Diagnosis. Small midge; head, thorax (mesonotum and large mediotergite), and legs with long bristles; wing without spots, with Sc terminating near midlength, Rs stem short, forking symmetrically, R₂₊₃ subequal to R₃ and *r-m* close to Rs furcation; male pregenital abdominal segments modified, shortened, hypopygium probably broader than preceding segment.

Description. Male. Small midge. Head: (Figs. 3A, 4A, B, 5A–C) with long bristles. Eyes large, bare; facets of equal size. Clypeus produced; maxillary palps elongate, 1.3 mm long; last palpomere gofferred, subequal to remainder of palpus; proboscis elongated, labrum long (longer than clypeus), labella densely pubescent, medium-sized (shorter than prementum), with pseudotracheae. Antenna (Fig. 4C) 1.5 mm long, shorter than abdomen, 21-segmented, with scape and pedicel moderately large, 18 flagellomeres bacilliform, subequal, each with a whorl of few (4–5) long setae and dense, short pubescence, terminal flagellomere very short.

Thorax (Fig. 4A): 1.2 mm long, 1.0 mm tall, mesonotum and large mediotergite with long bristles and short delicate hairs.

Wing (Figs. 2K, 3B, 4A) transparent, without spots, entirely covered with macrotrichia, 3.5 mm long, 1.2 mm wide. Sc, R₁ and Rs not very short: Sc terminating near wing midlength, R₁ terminating beyond 3/4 wing length, Rs originating at approximately 1/4 of wing length, R₂₊₃ subequal to R₃, tip of R₃ level with tip of M₁, R₄₊₅ fork 3 times as long as R₄₊₅ stem, *r-m* close to Rs furcation. Prehalter (Fig. 4A) long, subequal to halter stem, capitulum of halter and tip of prehalter with short dense pubescence. Legs (Figs. 3A, 4A, D–F): long; coxae elongate; tibial spurs (1:2:?) large and hairy. Fore femur/tibia/tarsus 1.0/1.3/1.5 mm long, middle femur/tibia/tarsus 1.2/1.7/1.8 mm, hind femur/tibia + tarsus 1.2/2.6 mm. Tarsomere I slightly shorter than all others combined; tarsomeres I–IV each with apical pair of pseudospurs. Tarsomere IV without basal swelling bearing tufts of setae opposite to tarsal claws (clasp organ of Hennig, 1968). Empodium and pulvilli absent; claws simple, small.

Abdomen (Figs. 3A, 4A): moderately elongate, shorter than wing, 1.6 mm preserved. Segments apparently modified: anterior ones elongate and pregenital one strongly shortened. Male hypopygium not preserved entirely but seems to be broader than preceding segment.

Remarks. Due to incomplete preservation we cannot exclude the presence of three medial veins, which occur in combination with visible *im* only in *Crenoptychoptera* Kalugina. However, *Crenoptychoptera* have longer male abdomen and straight Rs (Kalugina & Kovalev, 1985: Fig. 9a).

Only two entire *Eoptychoptera* males have previously been described, *E. asiatica* and *E. aucta*, both having a short compact abdomen with pregenital segments not modified, gradually narrowing towards a compact hypopygium, not wider than the preceding segment (Lukashevich, 1993: Figs. 3a, 4e). Such shape is different from the abdomen we describe here, but a similar difference has been recorded between two subgenera of *Leptychoptera* (Lukashevich & Grimaldi, 2004). Despite the diversity of *Eoptychoptera*, all attempts to divide the genus into subgenera failed so far (Lukashevich, 2012). Since the Early Jurassic, two wing types can be recognized: (1) wider, with spots at most bifurcations and crossveins, often with longer Rs, and (2) usually more elongate, without spots, often with shorter Rs. Both Asian males have spotted wings, whereas the Spanish male belongs to the second group, in which only females were previously known.

The moderately elongate male abdomen with modified pregenital segments has previously been known only in the subgenus *Burmptychoptera* Lukashevich of *Leptychoptera* (Lukashevich & Grimaldi, 2004). Due to incomplete preservation of the Spanish male, it is unclear if its hypopygium is broader than the preceding segment (as in *Burmptychoptera*) or not (as in other known *Eoptychoptera*), but the first condition appears to be more probable. In spite of this uncertainty, the new species is attributed to *Eoptychoptera* based on its wing venation, with long R₁ and Rs. In contrast, in all *Leptychoptera* R₁ terminates before 2/3 and Rs originates near 1/3 of the wing length. Additionally, the new species has a longer labrum, longer last maxillary palpomere, and 19 flagellomeres (instead of 21 in *Leptychoptera*); however these characters may vary at the level of species.

The prehalter (a basal appendage of the halter) is a trait unique of Ptychopteridae. Prehalteres have been described in the subfamily Eoptychopterinae in both subgenera of *Leptychoptera*; their presence was one of the main arguments for synonymization of Eoptychopteridae under Ptychopteridae (Lukashevich, 2008). The new find confirms the hypothesis (Lukashevich & Azar, 2003) that the prehalter is a synapomorphy of, at least, Eoptychopterinae plus Ptychopterinae and Bittacomorphinae.



Fig. 3. Photos of *Eoptychoptera*: A–B, *E. cantabrica* sp. nov., holotype CES 059, male: A, total view; B, wing; C–D, *E. sp.*, specimen LH 35084, pupa: C, total view; D, portion of wing sheath, arrows mark M_{1+2} and M_{3+4} furcations. Scale bar, 1 mm.

***Eoptychoptera* sp.**
(Figs. 2L, 3 C, D)

Material examined. Pupa LH 35084±; east-central Spain, Las Hoyas, La Huérguina Limestone Formation, upper Barremian, Lower Cretaceous.

Description. Small pupa. Total length 7.9 mm; wing sheath length 2.5 mm, width 0.8 mm; respiratory horn length no less than 2.6 mm (broken). Respiratory horns (at least one) well-developed, long and slender. Wing sheaths with typical *Eoptychoptera* venation (four medial veins, short M_{3+4} fork), extending to posterior margin of abdominal segment II. Leg sheaths extending to

midlength of abdominal segment III, apparently only sheaths of two pairs lying side by side, with third tarsus overlapping. All tergites transversely wrinkled, tergites II–VII each with transverse band of small tubercles along posterior margin. Pleurites II–V with 7 longitudinal bands of large tubercles on posterior margin. Genital sheaths short, not pointed, probably male.

Remarks. Neither colour pattern nor the positions of Sc tip and crossvein *r-m* are visible, thus the specimen can be identified only to genus. The sternites are poorly visible, due to the lateral position of the pupa, and it is unclear if they possess the transverse chitinized bands of tubercles along the posterior margin and 2 pairs of tubercles in the middle, as observed in the pupae of

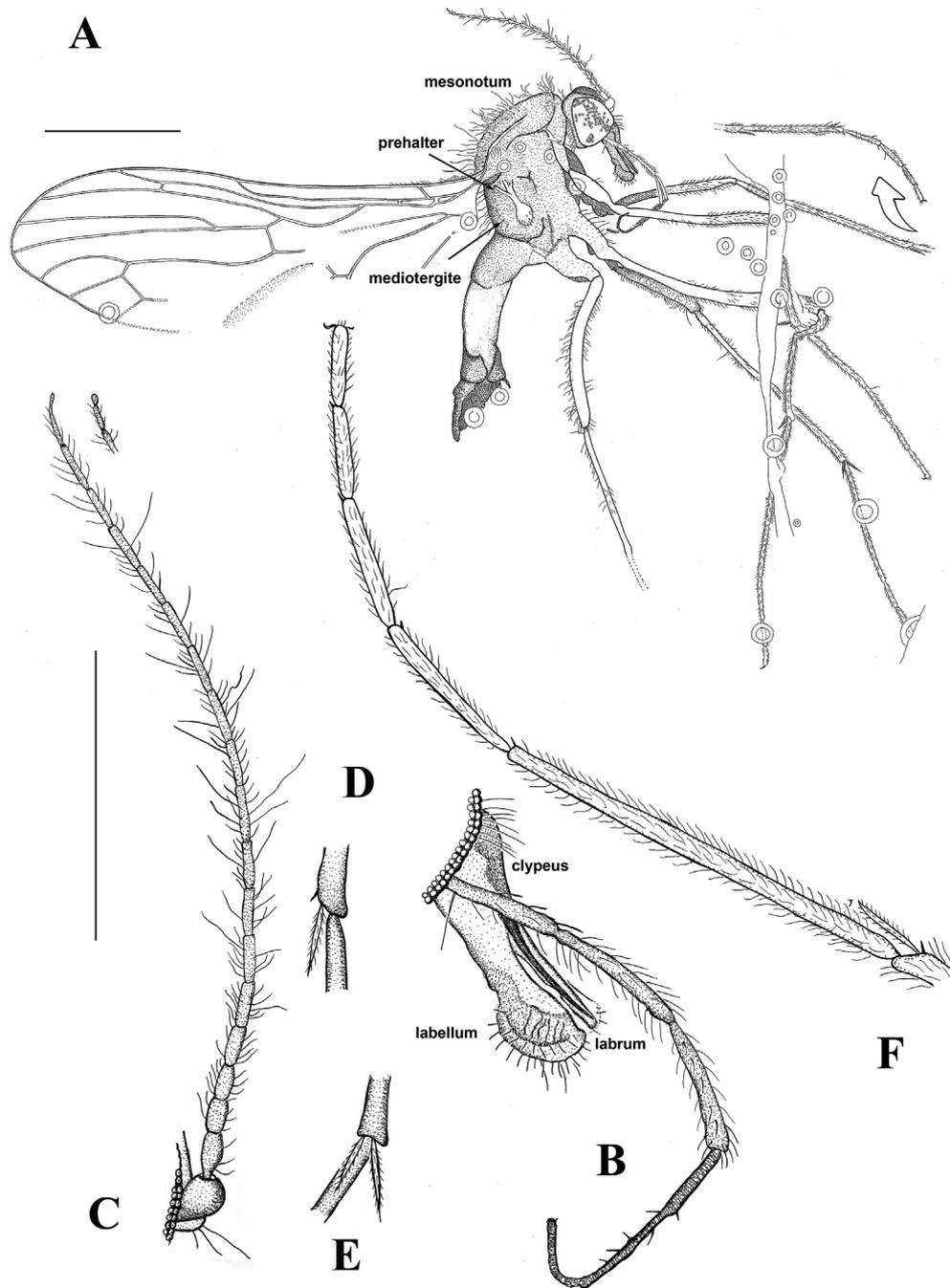


Fig. 4. Structures of *Eoptychoptera cantabrica* sp.nov., holotype CES 059, male: A, total view; B, mouth parts; C, antenna; D, tibial spur of foreleg; E, tibial spurs of middle leg; F, tarsus of foreleg. Scale bars, 1 mm (A) and 0.5 mm (B–F).

Crenoptychoptera gronskayae Kalugina. A similar long respiratory pupal horn, typical of extant ptychopterids, was described in *Crenoptychoptera conspecta* Lukashevich (Lukashevich, 1995).

Since a ptychopterid wing is approximately twice as long as its sheath (Lukashevich, 1995), the estimated wing length of this midge is ca. 5 mm.

4. Discussion

4.1. Climatic preferences

It is now evident that *Eoptychoptera* occurred in all three climatic belts of the Early Cretaceous (Fig. 6). The tropical-equatorial hot arid

climate, as in today's savannah regions, has been confidently reconstructed only for the Aptian Santana in Brazil (Chumakov et al., 1995). The Albian deposits in Spain also correspond to a hot arid belt, but sediments in the surroundings of El Soplao indicate non-xeric coastal and interdistributary bay environments (Najarro et al., 2009). Other European Cretaceous *Eoptychoptera* are known from Purbeck (Durlston Bay; lower Berriasian) and Wealden (Clockhouse; upper Hauterivian), representing mid-latitude warm humid belts with an essentially Mediterranean seasonality, with recurrent droughts reconstructed for Wealden Clay times (Allen, 1998). However, due to the archipelagic setting of the Purbeck-Wealden facies, their close analogues may not exist today. A similar seasonal subtropical wetland has been reconstructed for Las Hoyas

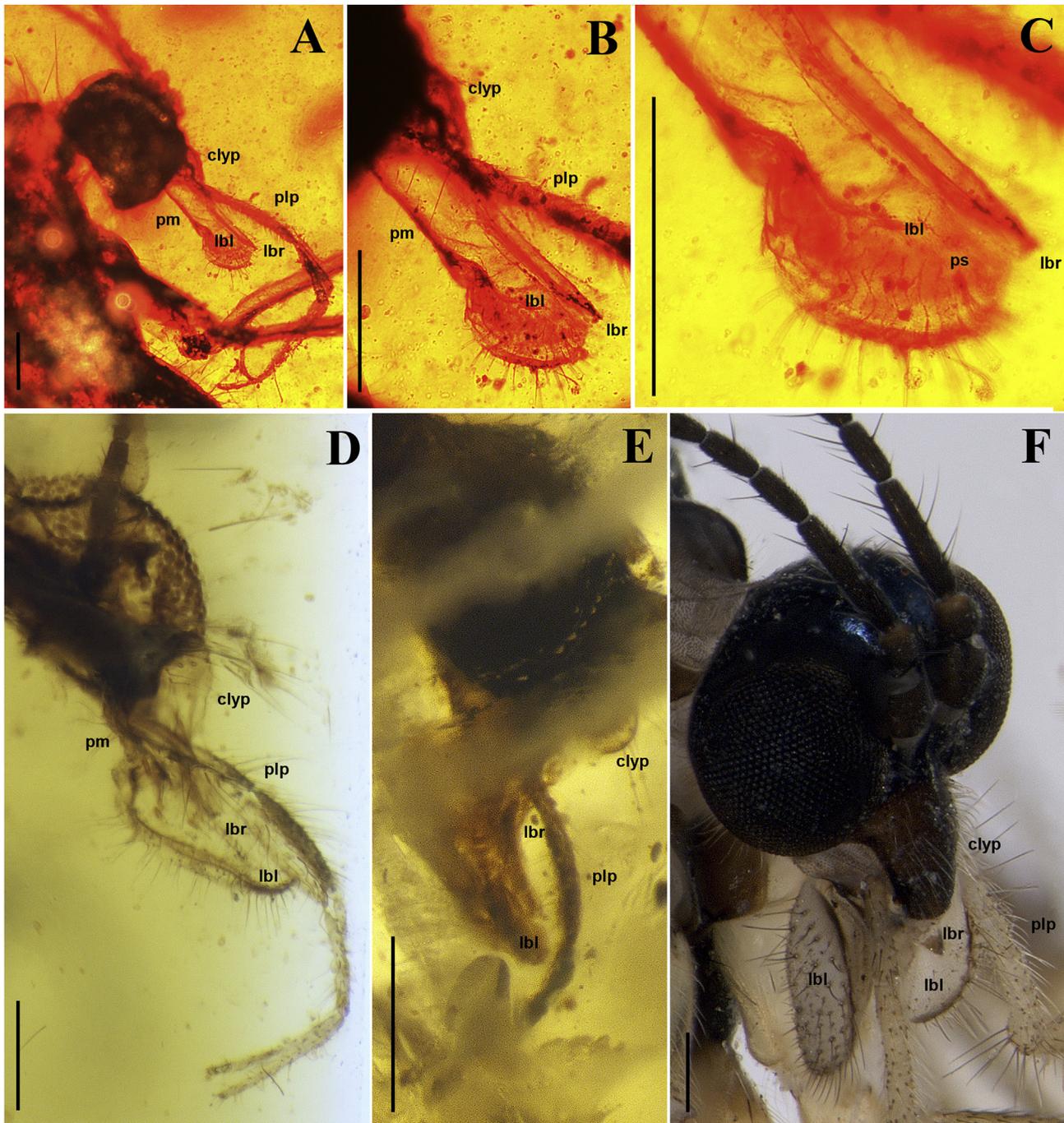


Fig. 5. Photos of ptychopterid heads: A–C, *Eoptychoptera cantabrica* sp. nov. holotype, male (El Soplao, K₁); D, *Leptychoptera* (*Burmaptychoptera*) *reburra*, holotype, male (Kachin, K₁₋₂); E, *Leptychoptera* (*Burmaptychoptera*) *calva*, holotype, male (Kachin, K₁₋₂); F, *Ptychoptera*, female (Russia, Moscow, Fili park, recent). Scale bar, 0.2 mm. Abbreviations: clyp – clypeus, lbl – labellum, lbr – labrum, plp – maxillary palpus, pm – prementum, ps – pseudotracheae.

(Buscalioni & Fregenal-Martínez, 2010), situated during the Barremian near a supposed boundary between the hot and the humid belts. The Asian localities of Cretaceous *Eoptychoptera*—Zhigansk, Bolboy (both of debatable age near J₃/K₁ boundary), and Baissa (Berriasian-Valanginian)—represent high-latitude temperate humid belts, although in the latter locality the genus was found only in the “warm” layers (Zherikhin, Mostovski, Vrsansky, Blagoderov, & Lukashevich, 1998).

The wide climatic tolerance of Cretaceous *Eoptychoptera* may be partly explained by the global climate being at that time significantly

more equable than at present, i.e., its climatic zones being not so drastically different (Chumakov et al., 1995). Moreover, wide climatic ranges are also known among extant ptychopterids: members of *Ptychoptera* Meigen occur from the subarctic zone down to the equatorial one (Andersen, Hagenlund, Haland, Kvitte, & Skartveit, 2013; Eskov & Lukashevich, 2015; Freeman, 1959; Krzemiński & Zwick, 1993) and the commonest American species, *Bittacomorpha clavipes* (Fabricius), widely distributed in eastern North America, extending north to Newfoundland and Quebec (Alexander, 1916), was recently discovered in Costa Rica (Fasbender, 2014).

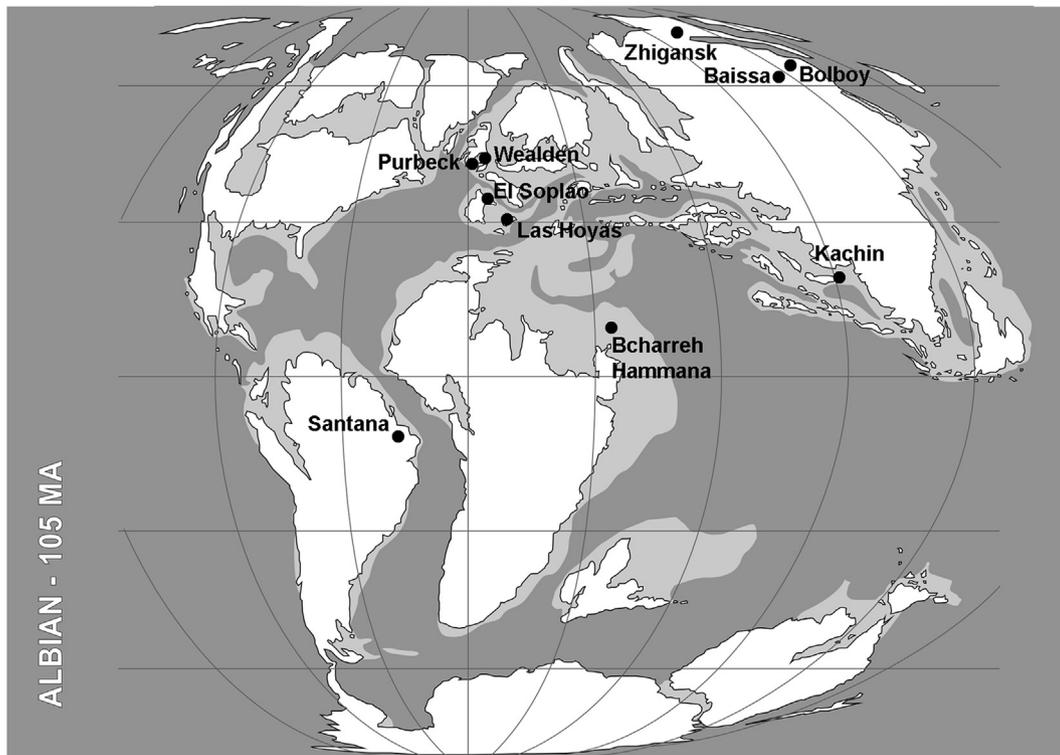


Fig. 6. Cretaceous localities of Ptychopteridae shown on a palaeogeographic map (middle Albian, ~105 Ma; redrawn from Blakey, 2011). **Bolboi**, Siberia (J₃-K₁): *Bolboia mira*. **Zhitgansk**, Siberia (K₁): *Crenoptychoptera gronskayae*, *Zhitganka comitans*. **Purbeck**, Great Britain (Berriasian): *Brodilka mitchelli*, *Eoptychoptera longifurcata*, *Eoptychoptera demissa*, *E. dimidiata*. **Wealden**, Great Britain (upper Hauterivian): *Eoptychoptera britannica*, *Eoptychoptera camura*, *Zhitganka woolgari*. **Baissa**, Transbaikalia (Berriasian-Valanginian): *Doptychoptera baisica*, *Eoptychoptera cretacea*, *Eoptychoptera baisica*, *Ptychoptera mesozoica*. **Bcharreh**, **Hammana**, Lebanese amber (Barremian): *Leptychoptera dimkina*, *L. vovkina*. **Las Hoyas**, Spain (upper Barremian): *Eoptychoptera* sp. **Santana**, Brazil (upper Aptian): *Eoptychoptera braziliana*. **El Soplao**, Spanish amber (lower Albian): *Eoptychoptera cantabrica* sp. nov. **Kachin**, Myanmar amber (upper Albian–Cenomanian): *Leptychoptera (Burmaptychoptera) reburra*, *L. (B.) calva*.

4.2. Mouthparts of Eoptychoptera

The male of *E. cantabrica* sp. nov. demonstrates an elongated proboscis (Figs. 5A–C), unknown in recent members of the family. In contrast, recent *Ptychoptera* have a powerful elongated clypeus, very short unsclerotized labrum with chitinized tip, and huge (much longer than the prementum = *theca* of Peterson and Snodgrass), fleshy, pubescent labella with numerous pseudotracheae (Fig. 5F). Pseudotracheae are small chitinized troughs serving as conduits for liquid food (Peterson, 1916). The elongated, convex clypeus, obviously housing well developed cibarial dilator muscles, also indicates that these midges were able to take up liquid food (Panov, 2001). Indeed, adult males and females of *Ptychoptera* have been observed licking solidified droplets of honeydew (Shcherbakov & Lukashevich, 2005). In *Leptychoptera* (Fig. 5D, E) from Cretaceous Burmese amber (only males are known) the clypeus is also convex and the labella are huge, longer than the prementum, fleshy and pubescent, with pseudotracheae, but the labrum is not so small, subequal to the clypeus, yet ending well before tips of the labella (Lukashevich & Grimaldi, 2004). Such morphology suggests that the trophic association of ptychopterids with honeydew-producing homopterans may be quite ancient. The male *Eoptychoptera cantabrica* sp. nov. (Fig. 5A–C) also demonstrates a convex clypeus, but its labrum is longer than the clypeus, and the pubescent labella with pseudotracheae are medium-sized, shorter than the prementum. We suggest a possible evolutionary sequence starting with *Eoptychoptera*, where a short clypeus and moderate labella are combined with an elongated labrum. In Cretaceous *Leptychoptera*, the labella and clypeus became enlarged parallel to shortening of the labrum. Finally, in recent *Ptychoptera*

the labrum becomes tiny, almost atrophied, whereas the labella and clypeus become huge.

Unfortunately, the mouthparts of *E. cantabrica* sp. nov. are difficult to interpret. In particular, it is not clear whether the sclerotized stripe is the median portion of the otherwise unsclerotized labrum, the salivary duct of the hypopharynx, or the stylets (mandibles or/and maxillae) inside the proboscis. However, the considerable length of the labrum, ending just before tips of the labella, appears quite informative by itself and allows constructing a chain of assumptions.

As a starting point, we can compare mouthparts of two closely related families, non-biting phantom midges (Chaoboridae) and frog-biting midges (Corethrellidae), so closely related that *Corethrella* was once even considered to be a member of Chaoborinae. In the former family the clypeus is longer than the labrum, and in the latter it is vice versa (Borkent, 2008; Cook, 1956). Indeed, mouthparts with an elongated labrum (not clypeus) being the most pronounced structure are typical of biting flies, blood-sucking (e.g. Simuliidae) as well as insectivorous (e.g. Blephariceridae, Figs. 7A, B). Also, all biting flies possess a complete set of movable mouthparts, sometimes without mandibles in the male (Peterson, 1916; Snodgrass, 1944). Hematophagy and entomophagy in orthorhaphous dipterans are impossible without the full set of mouthparts, but such completeness does not necessarily indicate hematophagy; additional morphological characters are important (Lukashevich & Mostovski, 2003). The proboscis of *Eoptychoptera cantabrica* sp. nov. resembles intermediately developed piecing-and-sucking mouthparts of biting midges (Ceratopogonidae) and sand flies (Psychodidae). It is certainly relatively shorter than the sucking apparatus of mosquitoes (Culicidae) but longer than the

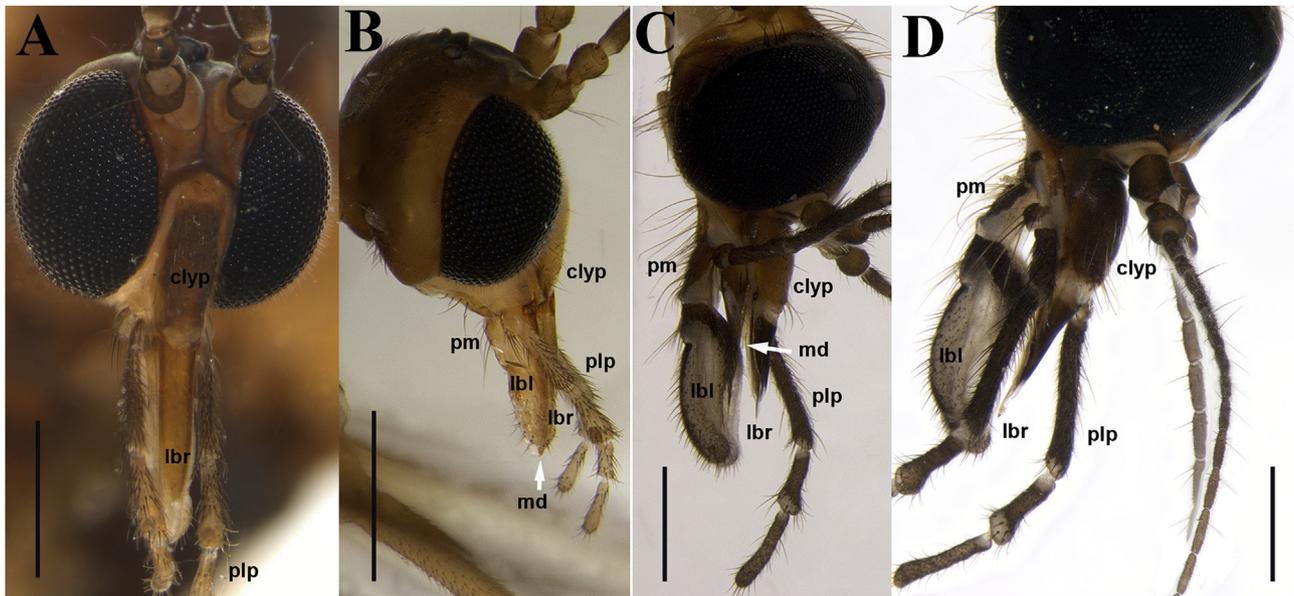


Fig. 7. Photos of heads of recent midges: A, B, male and female of *Edwardsina* (Blephariceridae; Chile, Puyehue National Park, Anticura River, 16.01.2014, leg. E.D. Lukashevich); C, D, male and female of *Araucoderus* (Tanyderidae, Chile, Alerce Andino National Park, Lenca River, 12.01.2015, leg. E.D. Lukashevich; Peres Rosales National Park, Peulla River, 17.01.2015, leg. D.E. Shcherbakov). Scale bar, 0.5 mm. Abbreviations: clyp – clypeus, lbl – labellum, lbr – labrum, md – mandible, plp – maxillary palpus, pm – prementum.

one of black flies (Simuliidae) (Snodgrass, 1944; Szadziewski, 1996). No visible feature prevents one from suggesting that *E. cantabrica* sp. nov. had a biting habit and stylets, the latter looking like the sclerotized stripe under the labrum. However, in extant Ptychopteridae neither mandibular, nor maxillary stylets are present. The hypothesis will, therefore, remain speculative until one discovers a fossil specimen with clearly visible well-developed stylets.

If the above hypothesis is true and the sclerotized stripe indeed marks the mandibles and/or maxillae, then the stylets of the male are subequal to the labrum. As a rule, mouthparts of the non-biting nematocerans are not sexually dimorphic, whereas among the biting taxa the male has a shorter and less complete set of mouthparts due to a different feeding habit (e.g. non-biting *Araucoderus* Alexander and insectivorous *Edwardsina* Alexander, Fig. 7). However, in some recent biting midges, the overall size proportions of the mouthparts are similar between sexes, with the sexual dimorphism being manifested only in the number and size of stylet teeth (sometimes developed as setae), the degree of stylet sclerotization and, in most but not all species, the absence of mandibles in the male (Brinson, McKeever, & Hagan, 1993; McKeever, 1986; Peterson, 1916; Silva & Grunewald, 2000). Thus, if *Eoptychoptera* had the biting habit, the females either had the mandibles longer than the sclerotized labrum, as in the blepharicerid *Edwardsina* (Fig. 7B), or their labium with apical labella was the shortest part of the proboscis, as in the psychodid *Phlebotomus* Loew, or their proboscis was similar to that of the males and had no protruding parts, as in the ceratopogonid *Culicoides* Latreille (Snodgrass, 1944). Unfortunately, the only female of the genus which shows a well-preserved head in the lateral position, *Eoptychoptera braziliiana*, is an impression, not an amber inclusion. Its overlapping maxillary palps prevent an accurate estimation of the length of the labrum (Krzemiński et al., 2015: fig. 5A), but the latter is not longer than the moderately developed labella, and the mandibles appear to not protrude beyond the tips of the labella. Therefore, the mouthpart structure and the feeding habit of female *Eoptychoptera* remain unclear.

The discovery of the extinct male with an elongated proboscis in the ancient relict family Ptychopteridae, with exclusively non-biting extant members, is intriguing. Elongated proboscises of the biting type, with toothed mandibles, were found among recent

primitive crane flies (Tanyderidae; undescribed yet) and two recent genera of non-biting midges (Chironomidae) (Cranston, Edward, & Colless, 1987; Cranston, Edward, & Cook, 2002; Downes & Colless, 1967). Among recent non-biting midges this trait is exceptionally rare, but several Mesozoic chironomid genera from Jurassic deposits and Cretaceous Lebanese amber just turned out to be mandibulate (Azar, Veltz, & Nel, 2008; Azar & Nel, 2012; Lukashevich & Przhiboro, 2011). As one can see, elongated mouthparts of the piercing-and-sucking type were widespread during the Early Cretaceous, being common even in the families with almost exclusively non-biting extant members.

5. Conclusions

The male of *Eoptychoptera cantabrica* sp. nov. from the Lower Cretaceous El Soplao amber-bearing deposits demonstrates an elongated proboscis, unknown in the extant Ptychopteridae. We suggest a possible evolutionary sequence starting with *Eoptychoptera*, where a short clypeus and moderate labella are combined with an elongated labrum. In Cretaceous *Leptychoptera*, the labella and clypeus became enlarged parallel to shortening of the labrum. Finally, in recent *Ptychoptera*, the labrum becomes tiny, almost atrophied, whereas the labella and clypeus become huge. The *Leptychoptera* pattern suggests that the trophic association of extant ptychopterids with honeydew-producing homopterans may be quite ancient, but no visible feature prevents one from suggesting that *E. cantabrica* sp. nov. had biting habit and stylets. However the hypothesis will remain speculative until one discovers a specimen with clearly visible well-developed stylets.

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