

# Lygistorrhinidae (Diptera: Bibionomorpha: Sciarioidea) in early Eocene Cambay amber

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One new genus and three new species of Lygistorrhinidae in early Eocene Cambay amber from India are described, which significantly increases our knowledge about this group in the Eocene. *Lygistorrhina indica* n. sp. is the oldest fossil known from this extant genus. *Indorrhina sahnii* n. gen. et sp. shows morphological similarities to each of the two extant genera *Lygistorrhina* and *Asiorrhina*. *Palaeognoriste orientale* is the third species known from a group that has only been recorded from Eocene Baltic amber before. The latter finding reveals faunal links between Cambay amber and the probably slightly younger Baltic amber, adding further evidence that faunal exchange between Europe/Asia and India took place before the formation of Cambay amber.

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## 9 ABSTRACT

10 One new genus and three new species of Lygistorrhinidae in early Eocene Cambay amber from  
11 India are described, which significantly increases our knowledge about this group in the Eocene.  
12 *Lygistorrhina indica* n. sp. is the oldest fossil known for this extant genus. *Indorrhina sahnii* n.  
13 gen. et sp. shows morphological similarities to each of the two extant genera *Lygistorrhina* and  
14 *Asiorrhina*. *Palaeognoriste orientale* is the third species known from a group that has only been  
15 recorded from Eocene Baltic amber. The latter finding reveals faunal links between Cambay  
16 amber and the probably slightly younger Baltic amber, adding further evidence that faunal  
17 exchange between Europe/Asia and India took place before the formation of Cambay amber.

## 18 INTRODUCTION

19 Lygistorrhinidae is a small dipteran group within the superfamily Sciaroidea (fungus gnats) of the  
20 infraorder Bibionomorpha. The monophyly of the latter two groups has been recently confirmed  
21 with high support by molecular analysis (Ševčík et al., 2016). Within the same analysis  
22 relationships of Lygistorrhinidae amongst other Sciaroidea indicates the inclusion of  
23 Lygistorrhinidae in the family Keroplatidae. Relationships within Lygistorrhinidae are well  
24 explored, with *Parisognoriste* and *Palaeognoriste*, both Eocene in age, being the sister groups to  
25 the remaining recent genera, consensus relationships of which are *Asiorrhina* (*Lygistorrhina*  
26 (*Labellorhina* + *Blagorrhina* + *Gracillorhina*) + (*Matileola* (*Loyugesia* + *Seguyola*))) (e.g.,  
27 Blagoderov, Hippa & Nel, 2010).

28 Members of Lygistorrhinidae can be found in tropical to temperate warm forests today (Grimaldi  
29 & Blagoderov, 2001). They can be easily recognized by the distinct wing venation, with a lack of  
30 the stem and sometimes also the base of the fork of M veins, and generally an elongate proboscis,  
31 which is presumably for feeding from flowers (*Seguyola* lacks this as a derived condition)  
32 (Grimaldi & Blagoderov, 2001). Apart from that however, ecology (e.g., life histories) and  
33 distributions of the species remains largely unknown. It has been concluded that rareness of this  
34 group in recent collections is due a lack of sampling, which is in turn related to poor knowledge  
35 about its biology and distribution (Grimaldi & Blagoderov, 2001). Further, tropical regions like  
36 the Neotropics and Asia generally are still poorly collected and probably harbor a huge number of  
37 undiscovered species. This is supported by the increase of described genera (number more than  
38 tripled) and species (number more than doubled) in the past 15 years, particularly of recent  
39 genera from southern Asia (Grimaldi & Blagoderov, 2001; Hippa, Mattsson & Vilkamaa, 2005;  
40 Blagoderov, Hippa & Ševčík, 2009) and from fossil taxa (Blagoderov & Grimaldi, 2004;  
41 Blagoderov, Hippa & Nel, 2010; Grund, 2012).

42 To date there are 15 genera, seven fossil and eight extant, and 48 species described (Pape,  
43 Blagoderov & Mostovski, 2011; Fungus Gnats online, 2016). The fossil record of  
44 Lygistorrhinidae dates back to the Cretaceous, with the oldest records from Lebanon (125-129  
45 Ma, Maksoud et al., 2016) (†*Lebanognoriste* Blagoderov & Grimaldi, 2004), Myanmar (98-99  
46 Ma, Shi et al., 2012) (†*Archaeognoriste* Blagoderov & Grimaldi, 2004; †*Protognoriste*  
47 Blagoderov & Grimaldi, 2004; †*Leptognoriste* Blagoderov & Grimaldi, 2004), Taimyr  
48 (Santonian, e.g., Rasnitsyn et al., 2016) (†*Plesiognoriste* Blagoderov & Grimaldi, 2004) and  
49 Canada (76-80 Ma, e.g., Borkent, 2000) (†*Plesiognoriste* Blagoderov & Grimaldi, 2004). There  
50 is then a large gap in the fossil record, with the next oldest members known from early Eocene  
51 Oise amber (ca. 53 Ma, Brasero, Nel & Michez, 2009) (†*Parisognoriste* Blagoderov, Hippa &  
52 Nel, 2010), amber from the Baltic Region (35-43 Ma, e.g., Standke, 2008) (†*Palaeognoriste*  
53 Meunier, 1904) and Dominican amber (15-20 Ma, Iturralde-Vinent, 2001) (*Lygistorrhina* Skuse,  
54 1890; see Grund, 2012).

55 Findings of fossil Lygistorrhinidae in Eocene Cambay amber from India now fill a gap in the  
56 spatial fossil record of the Palaeogene. Cambay amber occurs in active lignite mines in the state  
57 of Gujarat, in western India. The amber-bearing sediments have been dated to 52-55 Ma (Clemetz  
58 et al., 2011; Garg et al., 2008; Puneekar & Saraswati, 2010; Sahni et al., 2006). More precisely,  
59 vertebrate remains from between the two major amber layers in Vastan mine have been estimated  
60 at 54.5 Ma (Smith et al., 2016), suggesting an age of ca 54 Ma for the amber.

61 Thus Cambay amber is slightly older than Baltic amber and contemporaneous with Oise amber  
62 from France and Fushun amber from China (50-53 Ma, Wang et al., 2014). Cambay amber has  
63 been formed at a climatically pivotal period: namely during the Early Eocene Climatic Optimum  
64 (EECO). Further, the time of formation of this amber (or at least its burial) is most likely around  
65 the time of collision of the Indian subcontinent with Asia, which, according to most recent  
66 stratigraphic results, took place around 59 Ma (Hu et al., 2015) and led to the uplift of the  
67 Himalaya. In previous studies, investigation of fossils from Cambay amber have proven to be of  
68 major significance for the reconstruction of India's past diversity and geological history (e.g.,  
69 Rust et al., 2010; Stebner et al., 2017).

70 Until now, eight fossil Lygistorrhinidae belonging to three species in three different genera have  
71 been discovered in Cambay amber. These findings add further evidence that these flies are much  
72 more abundant and diverse in past ecosystems than is commonly known, as it has also been  
73 suggested for modern faunas. The fossils represent one species that is very similar to fossils of  
74 the archaic Baltic amber genus *Palaeognoriste*, as well as two species that belong to more  
75 derived, living lineages. Together with known fossil and recent species, and the highly congruent  
76 phylogenetic analyses published so far, the finding of fossils in the early Eocene from India  
77 provides interesting information for divergence-time estimations of this family, and eventually for  
78 biogeographic studies.

79 Interestingly, to date no faunal connections between contemporaneous Cambay amber from India  
80 and Oise amber from France have been found, though numerous affinities of fossils in Cambay  
81 amber to Baltic amber have been recorded (Rust et al., 2010; Engel et al., 2011, 2013; Grimaldi  
82 & Singh, 2012; Stebner et al., 2017). Whether this is a consequence of the relatively nascent state  
83 of investigation of the first two amber deposits, compared to the well-known Baltic amber, may  
84 eventually be determined by additional future studies on Oise and Cambay amber.

85

**METHODS AND MATERIALS**

86 The present study is based on eight fossil Lygistorrhinidae in early Eocene Cambay amber from  
87 India. The specimens derive from the Tadkeshwar lignite mine (N 21° 21.400, E 073° 04.532) in  
88 Gujarat, India. Screening of rough amber pieces was done at the Steinmann Institute, Bonn,  
89 Germany and the American Museum of Natural History (AMNH), New York, USA. Holotypes  
90 are deposited in the Birbal Sahni Institute of Palaeosciences (BSIP), Lucknow India; paratypes  
91 retained in the AMNH.

92 Amber pieces were ground using a Buehler Phoenix Beta grinding machine and Buehler wet-  
93 lapidary wheel. For taxonomic identification and investigation a Leica MZ 12<sub>s</sub> stereoscope and  
94 Nikon SMZ1500 were used. Photographs were taken with an AXIO Zoom.V16 stereomicroscope  
95 (Carl Zeiss, Jena) equipped with an AXIOCam HRc digital camera (Zeiss), using the extended-  
96 depth-of-focus function, and in New York with a Nikon SMZ1500 stereoscope, digital camera,  
97 and Nikon NIS-Elements software.

98 Photo-plates were edited using Photoshop CS5.1 and Adobe Illustrator CS6.

99 General morphological terms and abbreviations follow those given in the Manual of Nearctic  
100 Diptera (McAlpine, 1981) and in Blagoderov & Grimaldi (2004). The spur formula refers to the  
101 number of tibial spurs on fore-, mid-, and hind legs. Wing veins are abbreviated as follows: CuA  
102 = anterior branch of cubital vein; CuP = posterior branch of cubital vein; h = humeral crossvein;  
103 M<sub>1</sub> - M<sub>4</sub> = branches of medial vein; R<sub>1</sub>, R<sub>5</sub> = branches of radial vein; r-m = radial-medial  
104 crossvein; Sc = subcostal vein.

105 The morphological matrix is based on the matrix of Blagoderov et al., 2010. The data matrix was  
106 created and edited in Mesquite ver. 2.6 (Maddison & Maddison, 2009). Strict consensus  
107 cladograms were obtained by using TNT (Goloboff et al., 2008) based on 60 adult morphological  
108 characters (after Blagoderov et al., 2010) (matrix shown in Table S1). It was searched by the  
109 “implicit enumeration” option with “auto-collapse searches” off. The consensus trees were  
110 calculated by “strict (=Nelson)” using all trees and all taxa.

**111 Nomenclatural Acts**

112 The electronic edition of this article conforms to the requirements of the amended International  
113 Code of Zoological Nomenclature, and hence the new names contained herein are available under  
114 that Code from the electronic edition of this article. This published work and the nomenclatural  
115 acts it contains have been registered in ZooBank, the online registration system for the ICZN.  
116 The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information

- 117 viewed through any standard web browser by appending the LSID to the prefix  
118 “<http://zoobank.org/>”. The LSID for this publication is: urn:lsid:zoobank.org:pub:DD2F5D2A-  
119 C3EE-4F5C-B068-C9E541D9B70C.

120

## SYSTEMATICS

121

**Genus *Palaeognoriste* Meunier**

122 **Type species:** *Palaeognoriste sciariforme* Meunier, 1904: 88, by monotypy. In Baltic amber.  
123 Matile 1990a: 360; Matile 1990b: 366, 373-376, 383, 409, 421, 554; Hoffeins and Hoffeins 1996:  
124 311; Grimaldi and Blagoderov 2001: 55; Hippa, Mattsson & Vilkamaa 2005: 5, 11; Blagoderov  
125 Hippa & Ševčík 2009: 32, 33, 35, 37, 45; Blagoderov, Hippa & Nel 2010: 79-81, 83-89.  
126 **Diagnosis** after Blagoderov, Hippa & Nel (2010) and Grimaldi & Blagoderov (2001): Head with  
127 proboscis no longer than 2.5X head height, palpus one-segmented; wing with complete basal  
128 portion of fork of  $M_1$ - $M_2$ , vein Rs and crossvein r-m present.

129

***Palaeognoriste orientale* Stebner and Grimaldi, new species**

130

LSID urn:lsid:zoobank.org:act:122BEB14-EDDA-45D7-9973-3898B609F39C

131

**Figs 1 A-E, 2 A-C, 3 A-E, 4 A, B**

132 **Diagnosis:** Very similar to the two *Palaeognoriste* species in Baltic amber, except that *P.*  
133 *orientale* has a broader, shorter wing; the stem of M and base of M forks are absent (vs. faint);  
134 apex of vein CuA is more acutely bent; gonostylus is more curved; apex of the labellar lobes are  
135 blunt, not narrowly tapered; clypeus projecting forward,  $\Omega$ -shaped; antenna is much longer than  
136 proboscis (vs. approximately the same length).

137 **Material:** Holotype, male Tad-887, complete inclusion in early Eocene Cambay amber from  
138 India; deposited in the BSIP, Lucknow India. Paratypes, 1 male: Tad-587, 2 females: Tad-37A,  
139 Tad-324; deposited in the AMNH.

140 **Locality:** Cambay Formation (early Eocene), Tadkeshwar lignite mine, Tadkeshwar, Gujarat,  
141 India, 21°21.400'N, 73°4.532'E.

142 **Etymology:** Specific name refers to the origin of the species from the Oriental Region.

**DESCRIPTION:**

144 **Measurements:** Male. Head height: 0.24mm; body without head: 1.8mm; wing measured from  
145 humeral vein: 1.06mm; antenna: 0.8mm; proboscis: 0.23mm; palpus: 0.13mm.

146 **Head** (Fig. 1 E): Globular, occipital setae short, postocellar and frontal setae erect and stronger.  
147 Eyes: dichoptic in male and female, medial margins well separated by frons; anterior part  
148 extending to base of antenna. Facets round, equal in size (no differentiation), postocular setae  
149 present, interocular setae very fine, short, sparse. Number of ocelli three, forming triangle, middle  
150 ocellus slightly smaller than lateral ocelli. Palp one-segmented, evenly setose, ca. 0.55-0.6X

151 length of proboscis. Proboscis short, about as long as head high, significantly shorter than  
152 profemur; almost bare, with fine hairs on lower surface; apex blunt, not narrowly tapered.  
153 Labrum narrowly triangular, without setae, length 0.25-0.30X that of proboscis. Antenna with 14  
154 flagellomeres, none laterally flattened. Scape with a slim pedicel/stem and bulbous apical part;  
155 pedicel bulbous, 1.8X wider than flagellomeres. Flagellomere 1 subcylindrical; flagellomeres 2-  
156 13 cylindrical, about 1.6X longer than broad. Terminal flagellomere elongate, evenly tapered to  
157 rounded apex, about 1.5X length of proximal articles and 2.4X longer than broad.

158 **Thorax:** Scutum moderately convex, not dome-shaped or arched, evenly covered with short  
159 setae, longer setae on posterolateral surfaces. Anterior margin of thorax slightly anterior to level  
160 of procoxae. Laterotergite only slightly produced, not lobate, with row of 4-5 fine setae on  
161 posterior margin. Scutellum with long, stiff setae on posterior margin.

162 **Legs:** Coxae nearly equal in length (fore coxa nearly equal in length to other two); fore coxa  
163 sparsely setose anteriorly, mid coxa sparsely setose anteriorly on apical half, hind coxa bare  
164 (holotype) or with very sparse, minute setae (paratype Tad-587). Hind coxa without concavity on  
165 lateral surface. Tibiae and tarsi (Fig. 1 B, C) evenly covered with small setulae, arranged in  
166 longitudinal rows. Mid tibia with six thick, erect, evenly-spaced setae. Tibial spurs 1:2:2, length  
167 0.1: (0.2, 0.1): (0.46, 0.26). Fore and hind tibiae slightly expanded towards apex. Short  
168 transverse comb of thick setae on apex of hind tibia. All claws with pointed (none with blunt)  
169 apex.

170 **Wing** (Fig. 1 A, right wing): length of wing about 2.2X width, apex of wing not broadly rounded.  
171 R<sub>1</sub> and R<sub>5</sub> with row of minute setae, other veins bare. Costa extending beyond R<sub>5</sub> tip to 2/3  
172 distance between tips of R<sub>5</sub> and M<sub>1</sub>. Sc ending at C. R<sub>1</sub> ending slightly before middle of wing,  
173 slightly curved posteriorly. Rs distinct, oblique. Crossvein r-m present. R<sub>5</sub> slightly curved in basal  
174 third. Stem of M and base of M<sub>1+2</sub> fork lost. M<sub>2</sub> extends more basally than M<sub>1</sub>. M<sub>1</sub> and M<sub>2</sub> straight  
175 and parallel posteriorly, apices of M<sub>1</sub> and M<sub>2</sub> on each side of wing apex. M<sub>3+4</sub> and CuA curved  
176 posteriorly, CuA apex in paratype Tad-587 at nearly a right angle to CuA stem, more oblique in  
177 holotype (possibly due to fold in the anal area). CuP very close and parallel to stem of CuA.

178 **Abdomen:** Male terminalia (Fig. 1 D): Visible only from posterior in holotype; ventrally in  
179 paratype Tad-587. Tergite 9 short and rounded apically, covered with short setae. Gonocoxites  
180 wide in basal half, setose, mesal margin with dense small setae. Gonostylus cylindrical, slightly  
181 curved; apex beveled, with two large setae - one on each apical edge (these not observed in  
182 paratype Tad-587), a patch of thick, short setae between those, and with one subapical lobe-like  
183 tooth.

184 **Additional remarks:**

185 **Tad-887** (Fig. 2 A-C): Holotype male; preservation: Complete, well displayed, with good  
186 preservation, although there is a fracture running straight through the amber matrix. Eyes  
187 contorted and sunken by fossilization. Right antenna with flagellomeres 6+7 and 10+11 not  
188 visibly/distinctly separated, probably due to fossilization processes. Anal lobe of right wing  
189 turned down, therefore margin not entirely visible.

190 **Tad-587** (Fig. 3 A-E): Paratype male; preservation: Complete, well displayed, with good  
191 preservation, although the fly is encircled by a milky fracture. This, along with compression and  
192 some distortion of the thorax, obscures pleural structure. Details of the head, legs, and genitalia  
193 are very well preserved. The fly is viewed from its left side only, the right side obscured by an  
194 internal translucent fracture plane close to the fly. The area of the head vertex close to the  
195 antennae is obscured, so eye emarginations cannot be viewed.

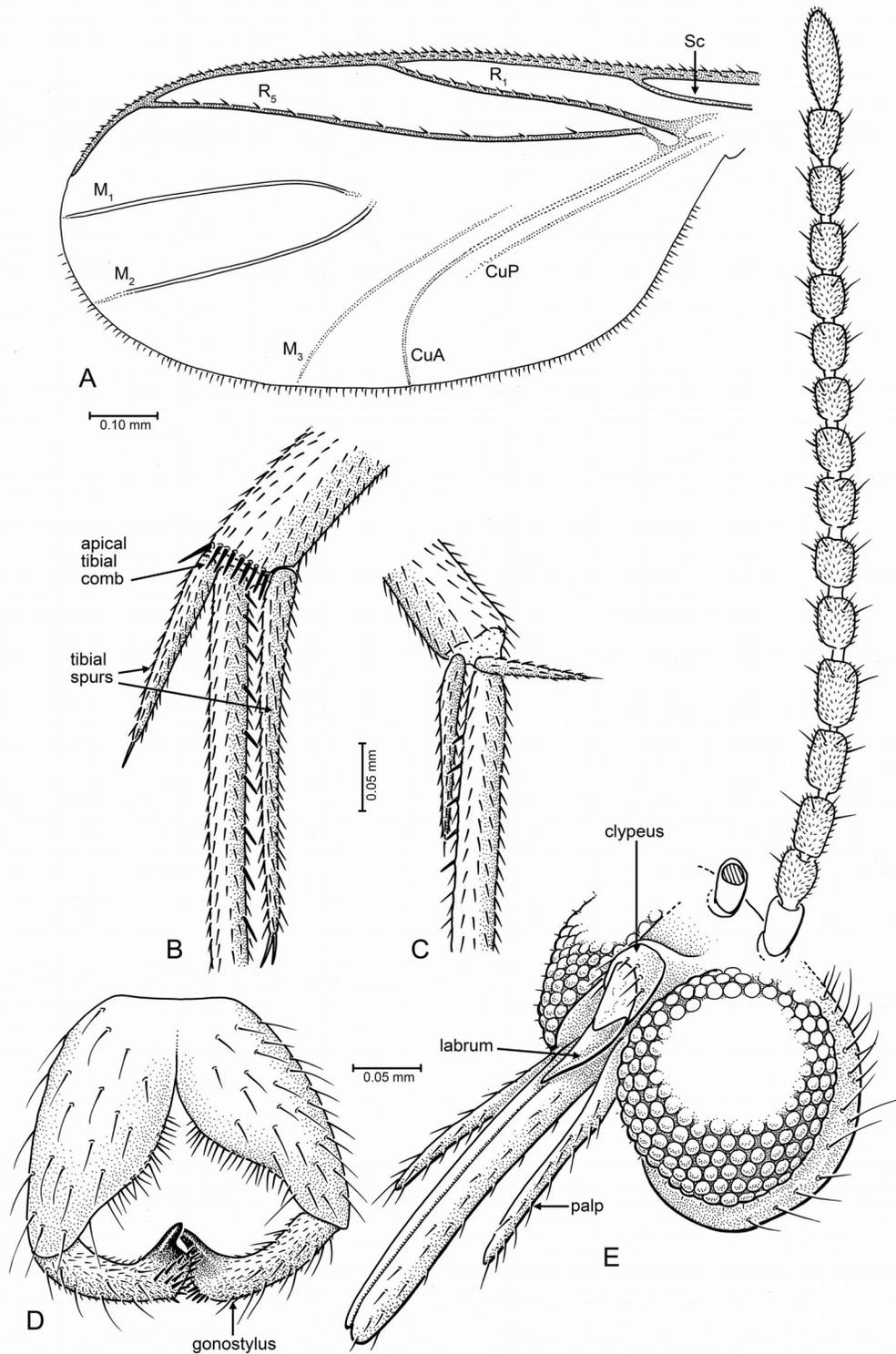
196 Measurements: Head height: not observable; proboscis length: 0.30 mm; palpus length: 0.20  
197 mm; antenna length: 0.75 mm; body length without head: 1.76 mm; wing length from humeral  
198 vein: 1.10 mm.

199 **Tad-37A**: Paratype female; preservation: Fair preservation, with legs and antennae well  
200 displayed but anterior portion of left wing lost at surface of the amber. Head is partially cleared  
201 (dorsum too poorly preserved to observe ocellar area); the fly straddles 3 fractures, which obscure  
202 some structures. The amber required trimming, embedding, and more trimming to obtain  
203 reasonable views.

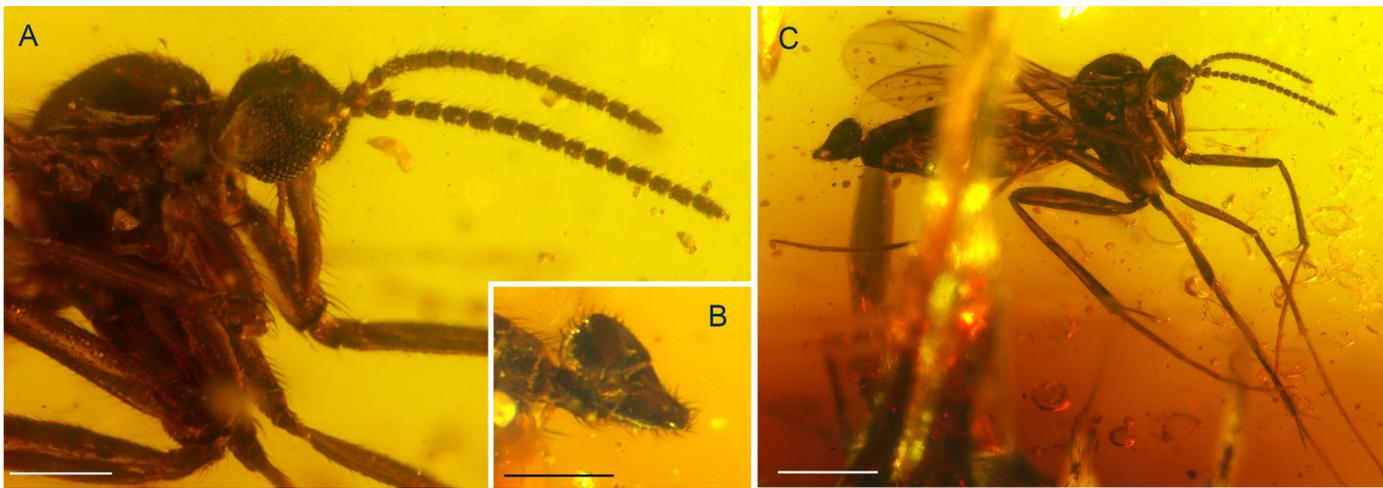
204 Measurements: Head height: 0.23 mm; proboscis length: 0.31 mm; palpus length [not  
205 observable]; antenna length: 0.63 mm; body length without head: ca. 1.6 mm; wing length from  
206 humeral vein: 1.50 mm.

207 **Tad-324** (Fig. 4 A-B): Paratype female; preservation: Fair preservation, appendages (including  
208 mouthparts and antennae) well exposed, but some legs (especially prolegs) distorted by  
209 stretching. Wings intact but partly obscured by fracture over them; terminalia obscured. The  
210 amber required considerable trimming, then was embedded prior to more trimming.

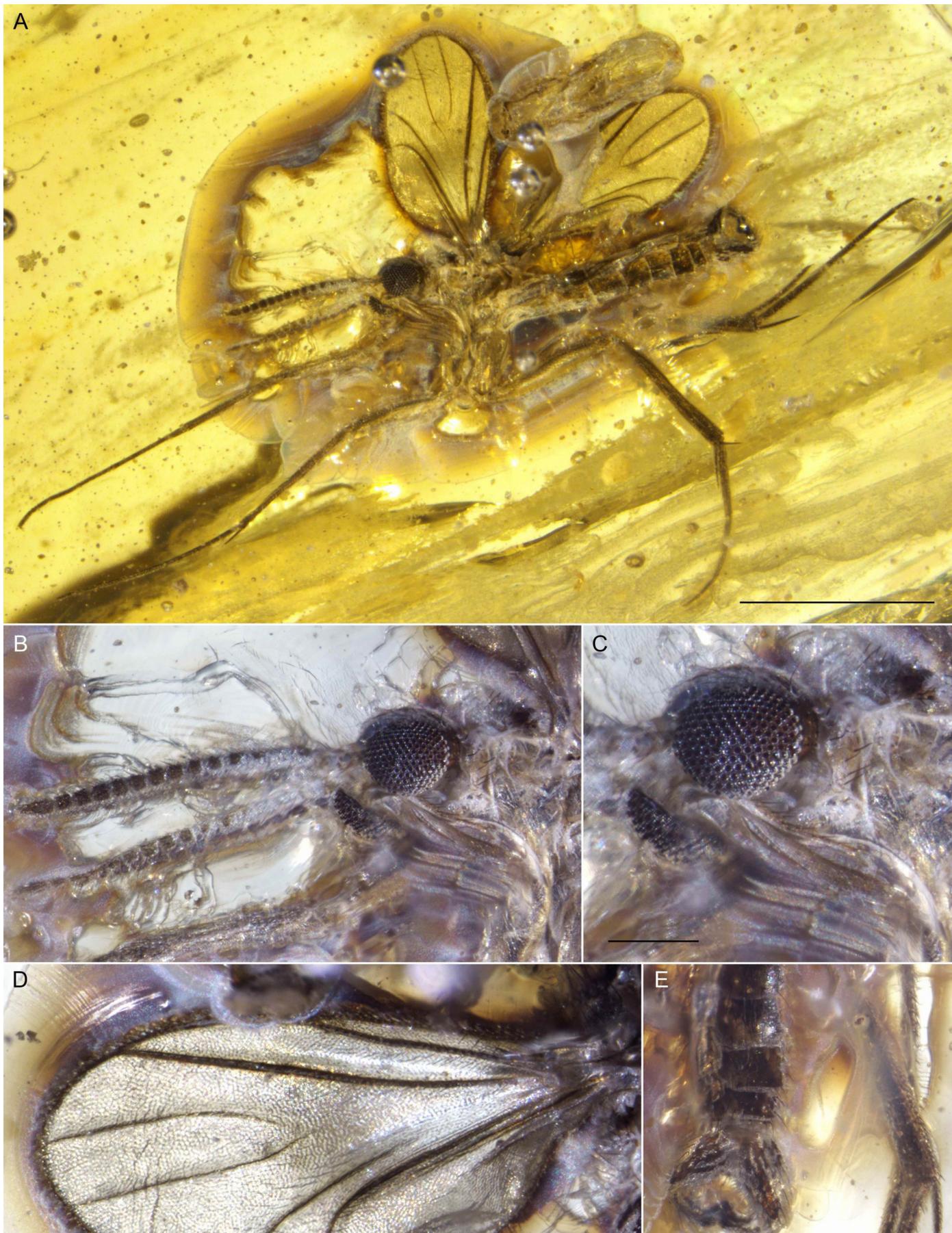
211 Measurements: Head height: 0.29 mm; proboscis length: 0.37 mm; palpus length 0.21 mm;  
212 antenna length: 0.43 mm; body length without head: 1.77 mm; wing length from humeral vein:  
213 1.37 mm.



214 Fig. 1. Drawings of *Palaeognoriste orientale* n. sp., paratype male Tad-587. A. Wing. B, C. Tibial  
 215 spurs (B, hind; C, mid). D. Male terminalia, ventral. E. Head, fronto-lateral.



216 Fig. 2. Photographs of *Palaeognoriste orientale* n. sp., holotype male Tad-887. A. Thorax and  
217 head, lateral. B. Male terminalia. C. Habitus, lateral view. Scale bars: A. 0.2 mm, B. 0.2 mm, C.  
218 0.5 mm



219 Fig. 3. Photographs of *Palaeognoriste orientale* n. sp., paratype male Tad-587. A. Habitus. B.  
220 Head. C. Eyes. D. Wing. E. Male terminalia. Scale bars: A. 1 mm, C. 0.1 mm, D. 0.1 mm, E. 0.1  
221 mm.



222 Fig. 4. Photographs of *Palaeognoriste orientale* n. sp., paratype female Tad-324. A. Habitus. B.  
223 Head. Scale bars: A. 0.5 mm, B. 0.1 mm.

224

### **Genus *Lygistorrhina* Skuse**

225 **Type species:** Type species: *Lygistorrhina insignis* Skuse, 1890: 600, by monotypy.  
226 Williston 1896: 261; Johannsen 1909: 62; Edwards 1912: 203, 204; Senior-White 1922:197;  
227 Edwards 1925: 530; Edwards 1926: 245, 246; Tonnoir 1929: 590; Edwards 1932: 139; Okada  
228 1937: 46; Lane 1946: 345; Shaw & Shaw 1951: 16; Hennig 1954:309; Lane 1958: 209, 210;  
229 Henning 1966: 50; Tuomikoski 1966: 254-260; Thompson 1975: 434-444; Matile 1979: 251-255;  
230 Matile 1986: 286-288; Matile 1990a: 359-362, 364-370; Matile 1996: 30; Huerta & Ibañez-  
231 Bernal 2008: 44-51; Evenhuis 2008: 13-19; Grimaldi & Blagoderov 2001: 43-45, 47, 48, 52-54,  
232 56; Papp 2002: 135,138-140; Papp 2005: 151-154; Hippa, Mattsson & Vilkamaa 2005: 2 - 6, 8,  
233 10, 11, 13, 16, 19; Blagoderov, Hippa & Ševčík 2009: 31-33, 35, 37; Grund 2012: 639-642;  
234 Blagoderov, Papp & Hippa 2013: 1, 2, 4-11.

235 **Diagnosis** after Grimaldi & Blagoderov (2001): Head with proboscis >4X length of head,  
236 including palps; wing with vein Sc incomplete or complete, basal portion of fork of M<sub>1</sub>-M<sub>2</sub> lost,  
237 CuA<sub>1</sub> and CuA<sub>2</sub> not connected in distal fork. Thorax with laterotergite expanded outward, flap-  
238 like, with fringe of long setae on edge.

239

### ***Lygistorrhina indica* Stebner and Grimaldi, new species**

240 LSID urn:lsid:zoobank.org:act:C787AB55-78E4-4E19-940D-29BEAD5A2ABE

241

### **Figs 5 B, 6 C, D, 7 B, 8 A-D, 9 A, B**

242 **Diagnosis:** Very similar to recent and Neogene species of *Lygistorrhina* by the very long, slender  
243 proboscis and palpi; anterior ocellus small to minute; laterotergite lobate and setose; stem of M  
244 and bases of M<sub>1</sub>-M<sub>2</sub> fork absent; R<sub>5</sub> without setae. Differing from other species of the genus by  
245 lack of concavity on lateral surface of metacoxa, and setae on laterotergite not in a row on  
246 posterior margin.

247 **Material:** Holotype, female Tad-442, complete inclusion in early Eocene Cambay amber from  
248 India; deposited in the BSIP. Paratypes, 1 female: Tad-492, 1 incomplete specimen of unknown  
249 sex: Tad-888, deposited in the AMNH.

250 **Locality:** Cambay Formation (early Eocene), Tadkeshwar lignite mine, Tadkeshwar, Gujarat,  
251 India, 21°21.400'N, 73°4.532'E.

252 **Etymology:** Specific name refers to the origin of the amber from India.

253 **DESCRIPTION:**

254 **Measurements:** Measurements: Head height: 0.29 mm; proboscis length: 0.90 mm; palpus  
255 length: 0.61 mm; antenna length: 0.58 mm; body length without head: 2.17 mm; wing length  
256 from humeral vein: 1.32 mm. Only female known.

257 **Head** (Fig. 5 B): Subspherical, occiput and vertex short setose. Eyes with facets round and equal  
258 in size, ommatidia very densely set. Postocular setae not present or not visible, interocular setae  
259 short, sparse, very fine. Eyes emarginate just lateral to antennal base; emarginate area bare of ca.  
260 one row of facets. Number of ocelli three, nearly in a transverse line, middle ocellus significantly  
261 smaller than lateral ocelli. Frons and face broad; extensive membranous area ventral and lateral to  
262 antennal bases, with small sclerotized condyle. Clypeus slightly crescentic, with marginal setae.  
263 Palpi one-segmented, long, 0.7X the length of proboscis, tapered apicad to fine tip, with a single  
264 row of setae. Proboscis evenly curved (of medium length), (very long in Tad-442, Tad-492) about  
265 2.2X (3.3X) as long as head high, with fine short setae. Oral margin slightly protruding; deeply  
266 incised, with clypeus nestled fully within. Labrum long triangular, with rounded apex, without  
267 setae. Antenna with 14 flagellomeres. Scape bulbous; pedicel subcylindrical, broadened apically,  
268 1.8X wider than flagellomeres. Flagellomeres 1-13 cylindrical, about 1.2X longer than broad.  
269 Terminal flagellomere evenly tapering to rounded apex, only slightly longer than previous ones  
270 and 1.5X longer than broad.

271 **Thorax** (Fig. 6 D): Scutum dome-shaped, strongly arched, entirely covered with setae of medium  
272 length; acrostichals long, longer setae on posterolateral surface of scutum. Scutellum with a row  
273 of long setae on posterior margin. Thorax in lateral view short (anterior to posterior margins),  
274 tall/deep (dorsal to ventral margins). Laterotergite well produced posteriad into a lobe, with long  
275 setae over broad surface (not in marginal row).

276 **Legs:** Coxae virtually equal in length. Fore coxae setose anteriorly, mid and hind coxae with  
277 sparse setae laterally. Fore tibia evenly covered with short setae, with one tibial spur, not  
278 expanded towards apex, approximately equal in length to fore femur. Tibiae and tarsi with  
279 microtrichia in longitudinal rows. Tibial spurs 1 : 2 : 2; anterior midtibial spur 0.3X length of  
280 other spur. Hind tibia with apico-lateral comb of thick, short setae (presence/absence of  
281 depression here not observable). Hind coxa without lateral concavity. Tips of all claws pointed,  
282 none blunt.

283 **Wing** (Fig. 7 B): Fairly short and broad, length/width 2.13, apex rounded but not extensively so.  
284 R<sub>1</sub> setose, R<sub>5</sub> without setae, other veins bare. Costa extending to approximately 2/3 distance

285 between  $R_5$  and  $M_1$ . Sc ending at C.  $R_1$  slightly curved posteriorly, apex ending beyond middle of  
286 wing.  $R_5$  moderately sinuous in apical third. M stem and bases of  $M_{1+2}$  fork lost.  $M_2$  extends  
287 slightly more basally than  $M_1$ . CuP very close and parallel to stem of CuA; apex of CuA strongly  
288 curved, almost perpendicular to stem of CuA. Anal lobe well developed.

289 **Abdomen:** That of female long, slender, tubular, cerci two-segmented (Fig. 6 C); male unknown.

290 **Additional remarks:**

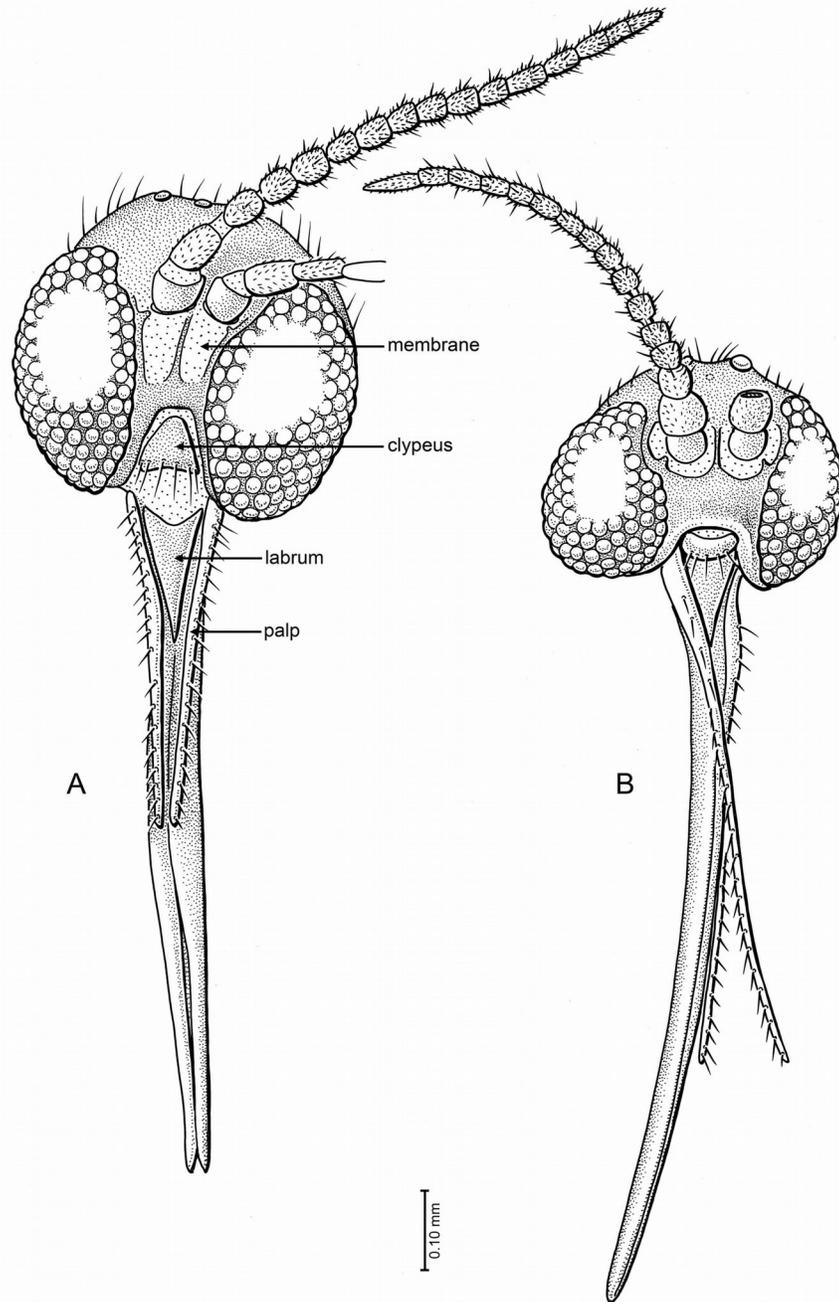
291 **Tad-442** (Fig. 5 B, 6 C, 7 B, 8 A, B): Holotype female; preservation: The specimen is very well  
292 preserved and virtually complete save for the distal tarsomeres of 4 legs (which are lost at the  
293 amber surface). Head and its appendages are very well preserved and fully observable; right  
294 wing is slightly distorted by preservation, but the left wing is well preserved. A fully lateral view  
295 (e.g., thorax) is not observable.

296 **Tad-492** (Fig. 6 D, 8 C, D): Paratype female; preservation: Specimen is largely complete but not  
297 intact; dorsum of the thorax and abdomen are separated from the rest of the body along with the  
298 wings (which are still attached to the thorax); a fracture along the line of separation prevents a  
299 full lateral view of the intact portion of the pleurites. Otherwise, the head and its appendages,  
300 legs, wings, and terminalia are well preserved with many details observable.

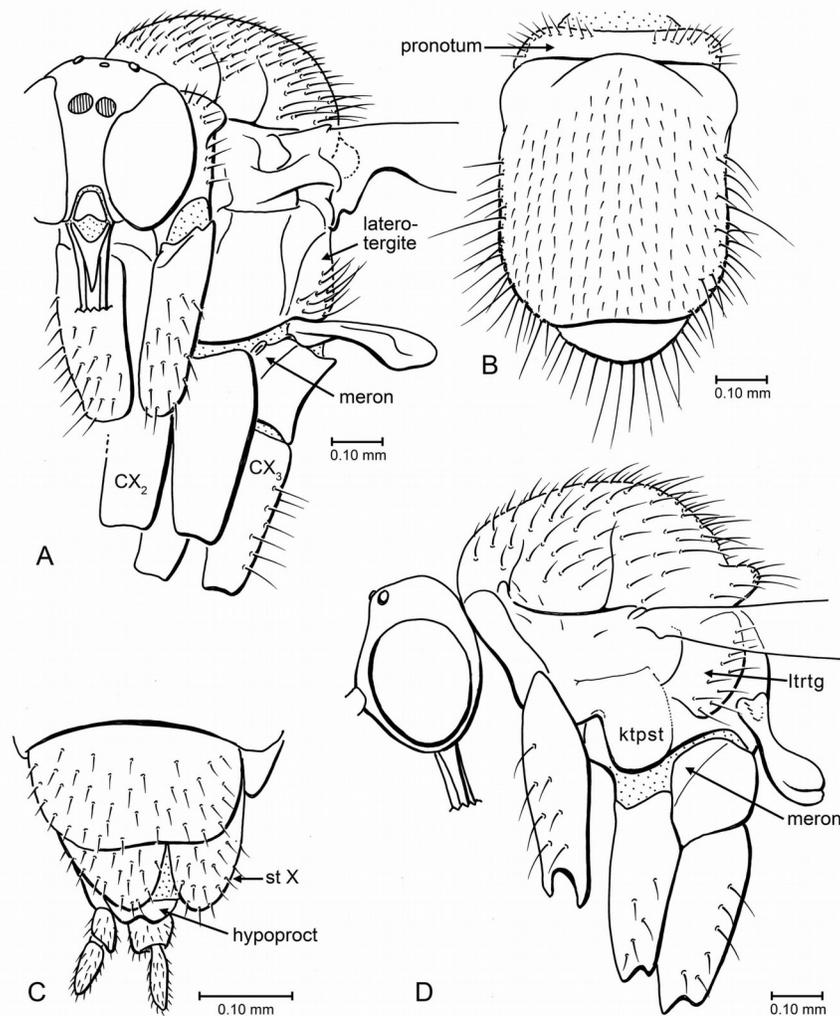
301 Measurements: Head height: 0.38 mm; proboscis length: 0.90 mm; palpus length: 0.45 mm;  
302 antenna length: 0.68 mm; body length without head: 2.64 mm; wing length from humeral vein:  
303 1.83 mm.

304 **Tad-888** (Fig. 9 A, B): Paratype, sex unknown; preservation: Most of abdomen and mid and hind  
305 legs missing; both wings incomplete.

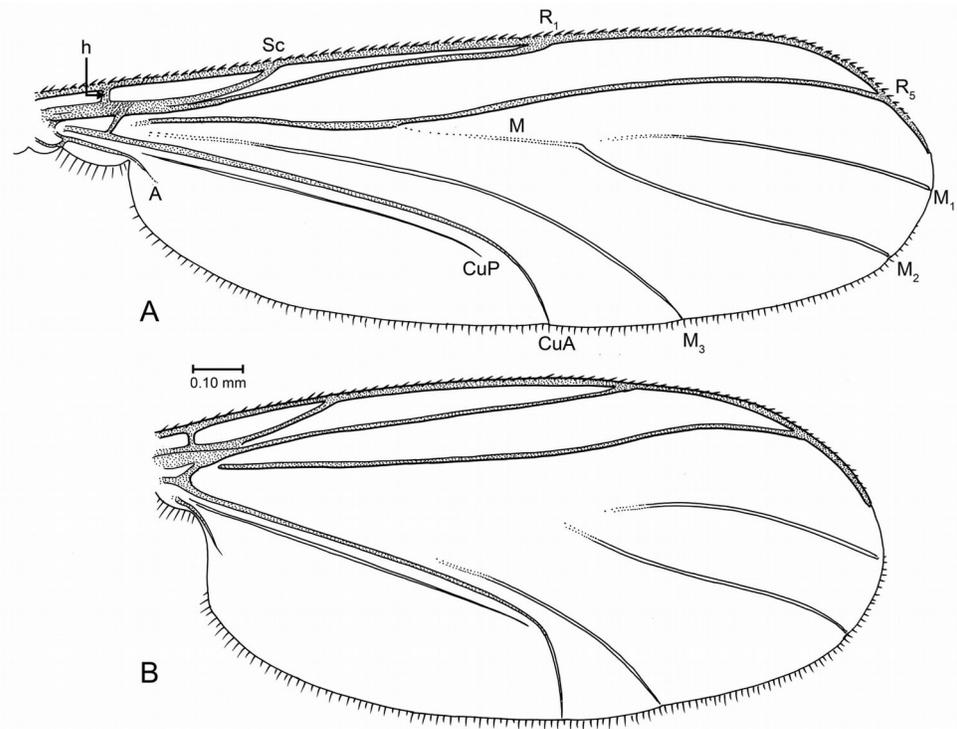
306 Measurements: Head height: 0.22 mm; antenna: 0.5 mm; proboscis: 0.5 mm; palpus: 0.35 mm.



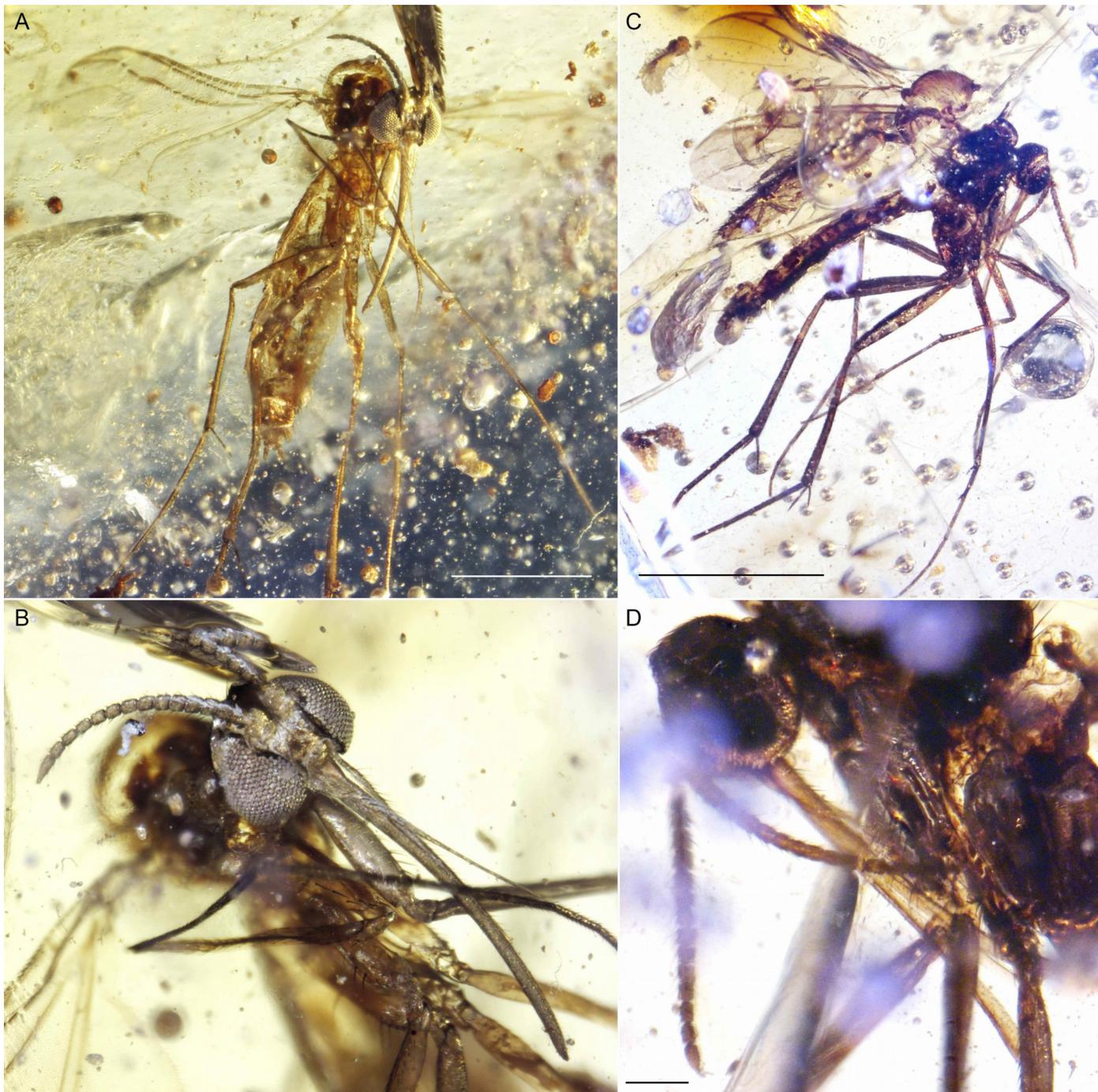
307 Fig. 5. Drawings of frontal view of heads (same scale). A. *Indorrhina sahnii* n. sp., holotype Tad-  
308 418 B. *Lygistorrhina indica* n. sp., holotype Tad-442.



309 Fig. 6. Drawings of head, thorax and terminalia. A. *Indorrhina sahnii* n. sp., holotype Tad-418,  
 310 head and thorax, fronto-lateral view. B. *Indorrhina sahnii* n. sp., holotype Tad-418, thorax,  
 311 dorsal. C. *Lygistorrhina indica* n. sp., holotype Tad-442, female terminalia, ventral. D.  
 312 *Lygistorrhina indica* n. sp., paratype Tad-492, thorax and head, lateral (thorax reconstructed from  
 313 both sides). Only the base of the proboscis is shown in figs. A, D.



314 Fig. 7. Drawings of wings (same scale). A *Indorrhina sahnii* n. sp., holotype Tad-418. B.  
315 *Lygistorrhina indica* n. sp., paratype Tad-492.



316 Fig. 8. Photographs of *Lygistorrhina indica* n. sp. A. *Lygistorrhina indica* n. sp., holotype female  
317 Tad-442, habitus, fronto-lateral view. B. *Lygistorrhina indica* n. sp., holotype female Tad-442,  
318 head, frontal view. C. *Lygistorrhina indica* n. sp., paratype Tad-492, habitus, lateral view. D.  
319 *Lygistorrhina indica* n. sp., paratype Tad-492, head, lateral view. Scale bars: A. 0.5 mm, C. 1 mm,  
320 D. 0.1 mm.



321 Fig. 9. Photographs of *Lygistorrhina indica* n. sp. A. *Lygistorrhina indica* n. sp., paratype Tad-  
 322 888, habitus, lateral view. B. *Lygistorrhina indica* n. sp., paratype Tad-888, thorax and head. Sale  
 323 bars: A. 0.5 mm, B. 0.5 mm.

324

### *Indorrhina* Stebner and Grimaldi, new genus

325

LSID urn:lsid:zoobank.org:act:D8BCCDD4-D601-467A-9478-482E3ADF269C

326

**Figs 5 A, 6 A, B, 7 A, 10 A-D**

327 **Diagnosis:** Proboscis moderately long (ca. 2.17X head length); antenna with 14 flagellomeres,  
 328 articles cylindrical in shape; antenna relatively short (1.8X length of head); median ocellus small,  
 329 in nearly transverse line with lateral ones; laterotergite lobate, setose; wing relatively long and  
 330 narrow, length/width 2.8; Sc complete; stem of M and bases of M<sub>2</sub> branch present but faint to  
 331 spectral; hind coxa without lateral concavity.

332 **Type Species:** *Indorrhina sahnii*, n.sp.

333 **Comments:** The new genus appears to be phylogenetically intermediate between *Asiorrhina* and  
 334 *Lygistorrhina*. The proboscis length is shorter than in *Lygistorrhina*, more similar to that of  
 335 *Asiorrhina* (2.05-1.75X head depth). Unlike *Asiorrhina*, however, the antenna of *Indorrhina* is  
 336 not laterally flattened and is considerably shorter (1.8X head depth, vs. 2.5X in *Asiorrhina*).  
 337 Since the male of *Indorrhina* is unknown, it cannot be checked if the gonostylus is apically  
 338 forked, a unique characteristic of *Asiorrhina*. Conditions of the ocelli and laterotergite in  
 339 *Indorrhina* are shared with *Lygistorrhina*. *Indorrhina* differs from that genus by a hind tibia that

340 is not apically broadened, lack of a concavity on the hind coxa, the shorter proboscis, and by  
341 retaining bases to M veins, a feature that also separates it from the two other Eocene taxa  
342 *Palaeognoriste* and *Parisognoriste*.

343 **Etymology:** Prefix based on India; suffix, -rrhina, from the Greek for nose or proboscis, in  
344 reference to the slender proboscis.

345 ***Indorrhina sahnii* Stebner and Grimaldi, new species**

346 LSID urn:lsid:zoobank.org:act:4380AECC-6418-4EB0-BB1B-FC5E12CCCC8F

347 **Figs 5 A, 6 A, B, 7 A, 10 A-D**

348 **Diagnosis:** As for the genus, by monotypy.

349 **Material:** Holotype, female, Tad-418, in Early Eocene Cambay amber, deposited in the BSIP.

350 **Locality:** Cambay Formation (early Eocene), Tadkeshwar lignite mine, Tadkeshwar, Gujarat,  
351 India, 21°21.400'N, 73°4.532'E.

352 **Etymology:** Patronym for Professor Ashok Sahni, dean of Indian paleontology, who provided  
353 advice and encouragement to the authors for research on Cambay amber.

354 **DESCRIPTION:** Based on unique female, Tad-418 (holotype).

355 **Measurements:** Head height: 0.39 mm; body without head: 2.68 mm; wing length, from humeral  
356 vein: 1.94 mm; antenna length: 0.76 mm; proboscis length: 0.81 mm; palpus length: 0.43 mm.

357 **Head** (Fig 5 A): Slightly flattened antero-posteriad (not subspherical), occipital and postocellar  
358 setae well developed, frontal setae absent. Eyes well separated (frons well developed), with  
359 slight medial emargination near antennal base; no differentiation of facets; interocular setulae  
360 very short, sparse, and fine. All three ocelli present, median ocellus smaller than lateral ones, in  
361 nearly transverse line. Face well developed, with a large membranous area beneath each antennal  
362 base. Oral margin very deeply incised, with clypeus (roughly trapezoidal in shape) closely fitting  
363 into oral margin; clypeus flat, surrounded by membrane, anterior margin with row of 6 setae. Palp  
364 moderately long, length 0.5X that of proboscis; 1-segmented, with longitudinal row of >20 setae  
365 along all of lateral surface; palp slightly tapered apicad. Labrum long triangular, anterior margin  
366 concave, glabrous. Proboscis moderately long, length 2.17X the head depth, relatively stout  
367 (particularly at base), longer than fore femur. Antenna with 14 flagellomeres, total length  
368 relatively short (1.8X depth of head). Scape bare, barrel-shaped; pedicel longer than wide;  
369 flagellomeres longer than wide, lengths greater in apical four articles, cylindrical (not laterally  
370 flattened); each flagellomere with subapical whorl of setae; apical flagellomere tapered.

371 **Thorax** (Figs 6 A, B): Scutum convex but not strongly arched or dome-shaped; entirely covered  
372 with setae. Acrostichals long, arranged into fairly even rows; long setae on lateral margins of  
373 scutum. Scutellum short and broad, with row of 12-14 long setae on posterior margin, no setae on  
374 dorsal surface. Pleura mostly bare. Laterotergite lobate, with posterior and ventral margins raised  
375 above pleural wall; setose, setae not confined to posterior margin.

376 **Legs**: Fore coxa slightly longer than other coxae; fore coxa and hind coxa setose; mid coxa bare;  
377 hind coxa without lateral concavity. Tibiae and tarsi with longitudinal rows of setulae. Fore tibia  
378 slightly longer than fore femur. Tibial spurs 1 : 2 : 2. Hind tibia with short, transverse comb of  
379 thick setae at apex. All pretarsal claws with apices pointed, none blunt.

380 **Wing** (Fig. 7 A): Wing relatively long and narrow, length/width 2.8, apex of wing not broadly  
381 rounded. Vein C extended to approximately 2/3 distance between R<sub>5</sub> and M<sub>1</sub>. Sc complete; R<sub>1</sub>  
382 ending slightly beyond mid-length of wing. Presence/absence of setulae on R veins not  
383 observable. Stem of M and base of M<sub>2</sub> fork present but faint to spectral, base of M<sub>1</sub> lost; M<sub>1</sub> and  
384 M<sub>2</sub> parallel for most their length; M<sub>1</sub> ending at wing apex. M<sub>3+4</sub> largely intact, most of stem  
385 present (though incomplete); CuA long, apically curved but not acutely so; CuP close and parallel  
386 to CuA. Anal lobe present but not highly developed.

387 **Abdomen**: Long, slender, tubular; cerci 2-segmented.

388 **Remarks:**

389 Holotype Tad-418; preservation: Specimen is complete and fully intact, though portions are  
390 obscured: the ventral abdominal region by a bubble, and portions of the mid- and hind tibiae and  
391 tarsi from a fracture through the piece. The head, proboscis, thorax, and wings are particularly  
392 well preserved, with no collapse or crumpling of the cuticle. A full frontal view of the head is  
393 observable, but only an oblique view of the thoracic plura is possible.



394 Fig. 10. Photographs of *Indorrhina sahnii* n. gen et sp., holotype female Tad-418. A. habitus,  
395 lateral view. B. Thorax and head, dorsal view. C. Head, frontal view. D. Wing. Scale bars: A. 1  
396 mm, B. 0.1 mm, D. 0.1 mm.

397 **DISCUSSION**

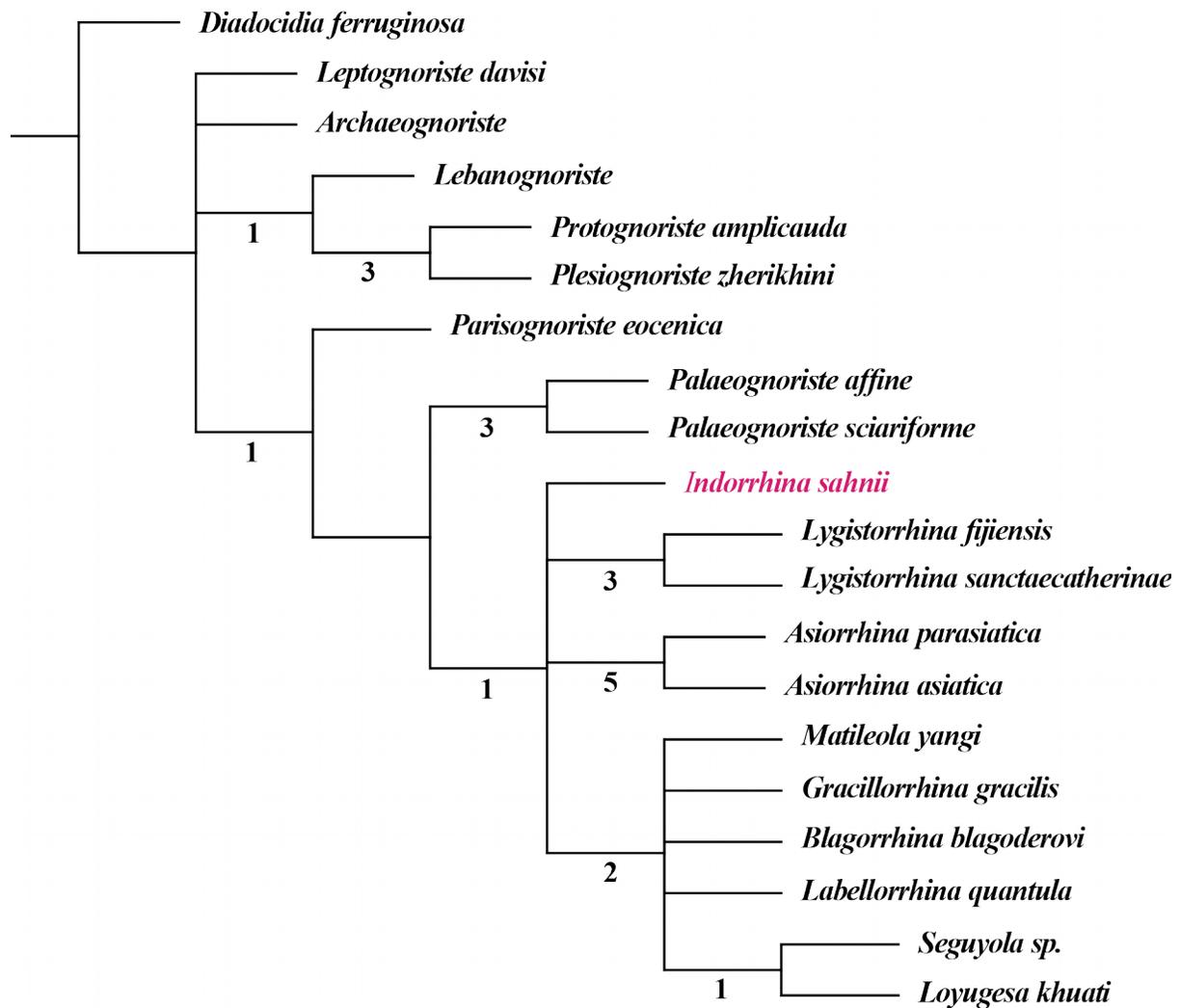
398 With eight fossils in three species and three different genera the diversity of Lygistorrhinidae in  
399 Cambay amber exceeds that in Baltic amber, which has revealed only two species within the  
400 genus *Palaeognoriste* so far (*P. affine* Meunier, 1912 and *P. sciariforme* Meunier, 1904). This is  
401 most surprising considering the profound differences in sampling. Baltic amber is the best studied  
402 amber deposit in the world. Being mined commercially for decades, probably tens-of-thousands  
403 of insect inclusions are sorted out every year. In contrast, Cambay amber, which has been  
404 collected and studied only a few years, has revealed about 2000-3000 insect inclusions so far,  
405 overall based on work in four labs (BSIP, AMNH, Steinmann Institute Bonn, University of  
406 Kansas). A reasonable explanation for the greater diversity of Lygistorrhinidae in Cambay amber  
407 may be found in the climatic conditions prevailing at the time of amber formation. Recent  
408 Lygistorrhinidae are essentially circumtropical, occurring around the world in tropical regions  
409 (even remote islands), their northernmost extensions being into wet, warm temperate areas of  
410 southeast U.S. (*Lygistorrhina sanctacatherinae*) and Japan (*L. pictipennis*). At the time of amber  
411 formation the Indian subcontinent was just entering the equatorial humid-belt (e.g. Kent and  
412 Muttoni, 2008), resulting in an extremely hot and humid tropical climate. Virtually all plants  
413 recorded from Vastan mine are restricted to tropical and subtropical regions today, i.e. they grow  
414 under very warm and very humid conditions. It has therefore been concluded that the palaeoflora  
415 is indicative of a warm and very humid climate, with certain elements such as dipterocarps  
416 suggesting a tropical rainforest growing in the vicinity of Vastan (Singh et al., 2015; Tripathi &  
417 Srivastava, 2012). More precisely, the reconstruction depicts a terrestrial lowland environment  
418 with a mesophytic mixed forest growing under tropical climate and with sufficient humidity  
419 (Singh et al., 2015). This general reconstruction of the Eocene palaeoforest in India fits well with  
420 the ecological requirements of extant representatives of Lygistorrhinidae.

421 The fossil record of Lygistorrhinidae shows a high congruence with the cladistic results, i.e.  
422 earlier fossils represent only older lineages (see phylogenetic analysis in Blagoderov & Grimaldi,  
423 2004; Blagoderov, Hippa & Nel, 2010). The genera only known from Cretaceous ambers seem to  
424 belong to a basal stem group, whereas *Palaeognoriste*, which is only known from the Eocene,  
425 presumably represents a sister group to all the extant genera (Blagoderov & Grimaldi, 2004;  
426 Blagoderov, Hippa & Nel, 2010). The taxa found in Cambay amber clearly support this by the  
427 absence of 'Cretaceous' taxa and by the presence of the 'Eocene' taxon *Palaeognoriste*, as well as  
428 the presence of the phylogenetically younger extant genus *Lygistorrhina*, and the fossil genus

429 *Indorrhina* n. gen., which appears to be within the clade of extant taxa that form the sister group  
430 to *Palaeognoriste* (Figure 11).

431 *Paleognoriste orientale* n. sp. possesses at least 7 features that differ with the two species of the  
432 genus in Baltic amber: broader, shorter wing; stem of M and base of M forks absent; apex of  
433 vein CuA more acutely bent; gonostylus more curved; apex of labellar lobes blunt; clypeus  
434 projecting forward,  $\Omega$ -shaped; antenna much longer than proboscis. However, given the overall  
435 similarity of the three species in proportions of body regions, appendages, and wing venation,  
436 these differences do not warrant erecting a separate genus. The finding adds another record to the  
437 pattern of apparently shared fossil taxa between Cambay and Baltic amber, as already been  
438 reported from the Diptera (Grimaldi & Singh, 2012; Stebner et al., 2017), bees (Engel et al.,  
439 2013), and termites (Engel et al., 2011).

440 The most unexpected finding is *Lygistorrhina* in Cambay amber. This is a clearly defined,  
441 unquestionably monophyletic genus. The only difference between the 21 Recent species and the  
442 Cambay species is that the latter lacks the shallow depression on the lateral surface of the  
443 metacoxa, and the setae on the laterotergite are not in a row on the posterior margin. Otherwise,  
444 *L. indica* n. sp. is clearly closely related to recent *Lygistorrhina*.. This approximately triples the  
445 age of *Lygistorrhina*, the prior oldest record being a species in Miocene Dominican amber  
446 (Grund, 2012; there are at least four other species of *Lygistorrhina* in this amber [D. Grimaldi,  
447 unpubl.]). Biogeographically, this finding is difficult to interpret because of the poor geographical  
448 sampling of the Recent species of *Lygistorrhina*. For example, there are nine New World species  
449 (but with nearly 30 total, based on study of museum specimens by D.G.); five species in central  
450 Africa and the Comoro Islands; three in southeast Asia; and three species in the Australasian  
451 region (including New Caledonia and the Fiji archipelago). There are few or no described  
452 species from large areas: most of Central America, all of the Greater Antilles, Andean South  
453 America, Madagascar, India, southern China, much of southeast Asia, most of Indonesia, and all  
454 of New Guinea. Based on study of extant material by the senior author (D. G.) there are likely to  
455 be well over 100 living species in existence. Unfortunately, living species are morphologically  
456 challenging to separate, and so morphology will probably yield an insufficient number of  
457 characters for an eventual phylogenetic study of the genus.



458 Fig. 11. Phylogeny of Lygistorrhinidae. Strict consensus cladogram of 9 MPT (181 steps), based  
 459 on the matrix of Blagoderov et al., 2010 and including *Indorrhina sahnii* from Cambay amber.  
 460 Numbers below branches refer to Bremer support values.

461 **CONCLUSIONS**

462 Considering the scarcity of Eocene amber deposits, Cambay amber is of great significance  
463 because it fills a gap in the spatial fossil record of the Paleogene and provides information about  
464 phylogenetic relationships, divergence estimations, and biogeographic patterns of certain groups,  
465 and adds information about the palaeoenvironment.  
466 The discovery of a diverse assemblage of Lygistorrhinidae in Cambay amber reinforces the  
467 reconstruction of a tropical palaeoenvironment and, at the same time, indicates climatic  
468 differences between the Cambay amber forest (tropical) and the Baltic amber forest, which was  
469 located distinctly further north and presumably after the peak of Eocene global warming.  
470 The finding of *Palaeognoriste* in Cambay amber adds further evidence that faunal exchange  
471 between India and Europe/Asia occurred before the formation of Cambay amber in the early  
472 Eocene. In this regard the discovery of Lygistorrhinidae in Eocene Fushun amber from northeast  
473 China, Paleocene amber from Sakhalin Island, Russia, Rovno amber from the Ukraine, and any  
474 additional species in the Eocene amber from Oise, France would be very interesting for further  
475 studies.  
476 The oldest finding of *Lygistorrhina* clearly has major implications for estimates of divergence  
477 times in the family as it indicates that this group was in existence since at least the early Eocene,  
478 which may explain its worldwide distribution, including some remote islands.

479 **ACKNOWLEDGEMENTS**

480 The authors thank Ashok Sahni (Centre of Advanced Study in Geology, Panjab University,  
481 Chandigarh, India) and Rajendra. S. Rana (Department of Geology, Hemwati Nandan Bahuguna  
482 Garhwal University, Srinagar, India) for support in field work. The authors are grateful to the  
483 authorities of the Tadkeshwar lignite mine for assistance during fieldwork in Gujarat, India. H.S.  
484 thanks the director of the Birbal Sahni Institute of Palaeosciences (Lucknow, India) for his  
485 support. F. S. thanks Simon Gunkel (Steinmann Institut, University of Bonn, Germany) for  
486 professional support.

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