Revision of the net-winged midge genus Horaia Tonnoir and its phylogenetic relationship to other genera within the tribe Apistomyiini (Diptera: Blephariceridae)

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Revision of the net-winged midge genus *Horaia* Tonnoir and its phylogenetic relationship to other genera within the tribe Apistomyiini (Diptera: Blephariceridae)

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Abstract. Based partly on recent collections from Nepal and northern Thailand, new data are added to the knowledge of *Horaia* Tonnoir. Pupal and larval stages of *H. montana* Tonnoir are re-described, larval descriptions for *H. manaliella* (Kaul) are provided, and two new species, *H. diminutiva* and *H. namtoki*, and a new subspecies, *H. montana piedmonti*, are described. Dichotomous keys to adults, pupae and instar IV larvae of blepharicerid genera from south-east Asia and of all known species of the genus *Horaia* are provided. Phylogenetic analysis of the tribe Apistomyiini suggests that *Horaia* is a monophyletic genus closely related to a clade containing *Apistomyia* Bigot and *Parapistomyia* Zwick. This clade is, in turn, sister to a weakly supported clade comprising *Theischingeria* Zwick + *Austrocurepura* Dumbleton. The New Zealand endemics *Peritheates* Lamb + *Neocurepura* Lamb are proposed as sister group to other apistomyiines, within which *Nothohoraia* Craig + (*Curupirina* Stuckenberg + *Nesocurepura* Stuckenberg) is sister group to the remaining genera. The proposed phylogeny supports Zwick’s Antarctic origin hypothesis for the biogeography of the Apistomyiini in Asia and Australasia.

Introduction

The Blephariceridae is a highly specialized family of aquatic Diptera. Larvae and pupae, which inhabit cascades, waterfalls and torrential streams, display a number of unique adaptations to rheophilic life. All four larval instars have the head, thorax and first abdominal segment fused into a compact cephalic division (*aka* cephalothorax). The following four abdominal segments are separate, but the remaining abdominal segments are fused into a single anal division. This leads to a compact body shape consisting of six major divisions, each equipped with a ventral suctorial disc, a pair of lateral prolegs and a pair of gills. These adaptations allow larvae to resist the constant pressure of water current in torrenticolous habitats (Frutiger, 1998). Larvae persist mainly on a diet of periphytic algae and represent an important primary consumer in torrenticolous habitats (Alverson et al., 2001; Alverson & Courtney, 2002).

Blepharicerid pupae have a streamlined shape and a pair of prominent thoracic respiratory organs. Pupae are attached permanently to rocks in rapidly flowing, highly oxygenated water. The pupal shape creates complex flow patterns over the body and generates negative pressure near the respiratory organs (Pommen & Craig, 1995). This pressure enhances the creation of a plastron, or permanent air bubble, through which gas exchange occurs.

Adults of many blepharicerids are rarely collected and are short-lived. The family’s common name, ‘net-winged midges’, is based on the series of intercalary folds on the wings, which are the result of a complete development of the wings in the pupal stage and a rapid deployment on emergence (Tillyard, 1922). The overall appearance of adults is typical of the ‘nematocerous’ flies, with long antennae and a slender body shape. The ecology and phenology of most blepharicerids is poorly known, partly as a result of the rarity of adult specimens. Adults of most apistomyiines are thought to be nectar feeders, spending most of their life in riparian vegetation (Zwick, 1998; Courtney, 2000a).

Blephariceridae is a monophyletic family that probably originated in the Jurassic (Courtney, 1991). Phylogenetic analyses on nematocerous Diptera (Wood & Borkent, 1989;
Early subfamilial classifications of the Blephariceridae (e.g. Alexander, 1958; Hogue, 1973) recognized four subfamilies: Edwardsininae, Blepharicerinae, Apistomyiinae and Paltostominae. Although some data suggest the family did indeed split into the Blepharicerinae and the Edwardsininae before the Cretaceous (Courtney, 1991), other subfamily designations are questionable. Recent studies (e.g. Zwick, 1977, 1989; Courtney, 2000a) recognize the two subfamilies, with Blepharicerini, Apistomyiini and Paltostomatini considered as tribes within the Blepharicerinae. Monophyly of the Apistomyiini has been well documented (Zwick, 1977), whereas that of the Blepharicerini and Paltostomatini remains contentious. However, a recent investigation of adult mouthparts (Stuckenberg, 2004) provided compelling support for the monophyly of Paltostomatini and the tribe’s phylogenetic affiliation with the Apistomyiini.

The genus *Horaia* has had a significant and historical role in the classification of net-winged midges. In one of the early systematic investigations of the family, Hora (1930) separated the Blephariceridae into two informal groups. One of these included species having larvae with well-marked lateral appendages and constrictions between body divisions. The second group consisted of species with a chiton-like larval form and poorly defined lateral appendages. Hora suspected that the dorsoventrally flattened body of the latter group permitted survival in strong currents. He also suggested that the elongate dorsomedial spines on some specimens reduced further the effects of strong currents. This second group corresponds with the unique larval characteristics of the species *Horaia montana* Tonnoir. The species was formally described soon after publication of Hora’s research.

Tonnoir (1930) described the genus *Horaia* (named after Dr S. L. Hora) and designated *H. montana* as the type species. He based his description on specimens collected in north-eastern India. The original description was based on male and female imagoes dissected from pupae. Detailed descriptions of adult females were published subsequently (Tonnoir, 1932), but descriptions of immature stages were not included. The 1932 paper included the description of a second species, *Horaia longipes*, based on an adult female collected in north-eastern India. No descriptions of adult males, pupae or larvae were provided for *H. longipes*.

Tonnoir (1930, 1932) noted a number of larval and pupal forms of *Horaia*, and suggested that up to three possible species of *Horaia* were present amongst the specimens examined, but were unnamed, lacking adults. Tonnoir mentioned a specimen, described as ‘Larva K’, which he was unable to place within a genus, but which bore similarity to both *Horaia* and the genus *Apistomyia* Bigot.

Much later, Kaul (1976) described the genus *Manaliella* based on specimens from north-western India, and designated *M. manaliella* as the type. Descriptions included imagoes of both sexes dissected from pupae, as well as larvae and pupae. The genus was similar to *Horaia* in the absence of adult mandibles, but differed in wing venation and genitalia. Zwick (1990) synonymized *Manaliella* with *Horaia* based on a lack of significant differences in wing venation and the lack of a detailed description of genitalia. He suggested further that Kaul’s larva was a misidentified member of the genus *Philorus* Kellogg. Pupal descriptions were valid because adult descriptions were based on dissected imagoes.

Global and regional catalogues of Blephariceridae (Alexander, 1958; Hogue, 1973) have described *Horaia* as restricted to the Himalayan regions of India and Nepal. Recent collections indicate a distribution extending to northern Thailand and Vietnam. Examination of recently collected Nepalese and Thai specimens suggests the presence of additional species of *Horaia*, as well as previously undescribed immature stages of known species.

In this paper, we describe two new species and one new subspecies of *Horaia*, and provide, if possible, complete descriptions or re-descriptions of larvae, pupae, adult males and adult females of all known species. We provide keys for larvae, pupae and adults of all south-east Asian blepharicerid genera and all known species of *Horaia*. The results of a phylogenetic analysis of *Horaia* and other apistomyiine genera are placed in a biogeographical framework.

**Materials and methods**

**Material**

All species of the genus *Horaia* Tonnoir, except *H. longipes*, have been examined. Most specimens were collected by the junior author between 1994 and 2004. The association of larvae with pupae and of pupae with adults was chiefly by the ontogenetic method (Hogue & Bedoya-Ortiz, 1989). Pupa–adult associations were also made by individual rearings (Courtney, 1998). Additional specimens were borrowed from or are deposited with the following (acronyms used throughout the text): CNC, The Canadian National Insect Collection, Ottawa, Ontario, Canada; CMUB, Department of Biology, Chiang Mai University, Chiang Mai, Thailand; DATH, National Insect Collection, Department of Agriculture, Bangkok, Thailand; IM, the Indian Museum, Calcutta, India; ISIC, Iowa State University Insect Collection, Ames, Iowa, U.S.A.; QSBG, Queen Sirikit Botanic Garden, Mae Rim, Chiang Mai, Thailand; PZ, the private collection of Dr P. Zwick, Limnologische Fluss-Station Schlitz des Max-Planck-Instituts für Limnologie, Schlitz, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.

**Specimen preparation**

Most field-collected and laboratory-reared specimens were fixed in 70–80% ethanol (EtOH). Morphological studies were based on whole animal preparations, slide mounts and scanning electron microscopy (SEM). Slide-mounted material was cleared in cedarwood oil and mounted in...
Canada Balsam. Genitalia were cleared in dilute potassium hydroxide and slide mounted temporarily in glycerin. After the genitalia had been removed, adults were dried chemically with hexamethyldisilazane (HMDS). Specimens were observed using a dissecting microscope (Olympus SZX-12, Olympus America, Inc., Center Valley, PA) and a compound microscope (Nikon E800, Nikon Corporation Co., Ltd., Kanagawa, Japan), and drawings were rendered with the aid of camera lucida. Light micrographs were recorded with a digital camera (SPOT RT®, Diagnostic Instruments, Sterling Heights, MI), and high-resolution images were constructed using Helicon Focus 3.10® (Helicon Soft Ltd., Kharkov, Ukraine). Material for SEM examination was critical point dried and sputter-coated with gold–palladium. SEM images were captured digitally on a JEOL JSM5800LV microscope (JEOL Ltd., Tokyo, Japan).

**Terms for structures**

Terms for adult structures follow Merz & Haenni (2000), as well as recent papers on Blephariceridae (Zwick, 1977, 1998; Courtney, 2000a, b). Terms for male terminalia are based on Sinclair (2000) and Courtney (2000a, b), and those for the female postabdomen follow Kotrbá (2000) and Courtney (2000a, b). Names for larval structures are based primarily on Courtney et al. (2000) and Courtney (2000a, b). Microsculptural terminology follows that of Harris (1979).

**Descriptive format**

Diagnoses are provided for all species. Complete descriptions of adults, pupae and instar IV larvae are provided for all new species, where possible. Previously unknown life stages for named species are described; otherwise, reference is made to original descriptions. When applicable, sample sizes are provided before each description, with values presented as a mean followed by a range in parentheses. Larval body length is provided, although it is highly variable within a given species and instar (Kitakami, 1950; Craig, 1969). Antennal structure, proleg shape, gill filament number, setal length and cranial width are consistent within an instar (Craig, 1969; Courtney, 2000b). Larval cranial width refers to the distance between the antennal bases. Larval characters, unless otherwise noted, refer to instar IV.

The following abbreviations are used for life stages: L, larva; P, pupa; Pex, pupal exuviae; A, adult. Abbreviations for label and locality information include the following: E, east; Kh, Khola (stream/river); N, north; NP, National Park; Rd, road; S, south; SFR, Shivapuri Forest Reserve; trib, tributary of; W, west; Xing, crossing.

**Phylogenetic analysis**

Phylogenetic relationships were evaluated according to cladistic principles [sensu Hennig (1966)], as modified by Wiley (1981), Schuh (2000) and others], in which common ancestry is determined on the basis of synapomorphies.

Decisions about character polarity were based on outgroup methods (Watrous & Wheeler, 1981; Maddison et al., 1984). Ingroup and outgroup taxa were examined for phylogenetically informative characters. Only for *H. longipes* was the original description (Tonnoir, 1932) used. Outgroup generic characters were determined from exemplars or from recent generic descriptions and re-descriptions. Outgroups [exemplar species] and/or generic description included: *Peritheates* Lamb [harrisi Campbell] (Craig, 1969), *Neocurupira* Lamb [multiple species] (Craig, 1969), *Nothohoraia* [micrognathia] Craig (Craig, 1969), *Austrocurupira* Dumbleton [nicholsoni (Tillyard)] (Stuckenberg, 1969), *Curupirina* Stuckenberg (Stuckenberg, 1969), *Nesocurupira* Stuckenberg (Stuckenberg, 1969), *Theischingeria* [riecki] Zwick (Zwick, 1998), *Apistomyia* Bigot [multiple species] (Tillyard, 1922; Tonnoir, 1923; Zwick, 1977; Zwick, 1998) and *Parapistomyia* Zwick [multiple species] (Zwick, 1977, 1998). *Edwardsina* Alexander [multiple species] (Zwick, 1977), *Paltostoma* Schiner [multiple species] and *Blephariceria* Macquart [multiple species] were included as non-apistomyiine outgroups. Phylogenetically informative characters were identified and given a numeric code. Unclear, continuous and autapomorphic characters were excluded; weights were equal and multistate characters were considered unordered. Cladistic analyses were performed using the branch-and-bound option in PAUP 4.0b10 (Swofford, 2002), and character state transformations were analysed in MACCLADE 4.05 (Maddison & Maddison, 2002). Bootstrap values were calculated in PAUP (500 replicates) and Bremer support values were obtained using TREEROT 2.0 (Sorenson, 1999).

**Keys to Blephariceridae genera of south-east Asia and to species of the genus *Horaia***

**Larvae (instar IV)**

Larvae of *H. longipes* are unknown.

| 1. Dorsal prolegs present (Fig. 1); antennae three- | Philorus Kellogg |
| segmented........................................ | |
| – Dorsal prolegs absent (Figs 3; 5; 20–24; 30–34; 40–44; 55–59); antennae two- or three-segmented .......... 2 |
| 2(1). Antennae two-segmented, segments separated by | Blephariceria Macquart |
| broad, membranous area; prolegs acutely tapered or | |
| pointed (Fig. 3).............................. | |
| – Antennae two- or three-segmented, segments not | |
| separated by membranous area; prolegs blunt, or | |
| slightly tapered (Figs 5; 21; 23; 31; 33; 41; 43) ......... 3 |
| 3(2). Body elongate and narrow, trunk segments narrower | |
| than cephalic division; lateral margins of trunk | |
| segments tapered at insertion of prolegs; antennae | |
| two-segmented; seventh pair of prolegs present as small, | |
| setose protuberances on anal division; posterior | |
| margin of anal division emarginate and setose; dor- | |
| sum of each abdominal segment, including posterior | |
| part of cephalic division, unsclerotized except for two | |
| rows of transverse spinules or papillae (Fig. 5) | |

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Body anteroposteriorly compressed, trunk segments at least as broad as cephalic division; lateral margins of trunk segments blunt at insertion of prolegs; antennae two- or three-segmented; seventh pair of prolegs vestigial, represented by pair of bristles or setal patches on anal division; posterior margin of anal division heavily sclerotized and asetose; abdominal segments without transverse rows of spinules or papillae (Figs 20–24; 30–34; 40–44; 55–59) ............... 4

Pupae

Pupae of *H. longipes* are unknown.

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1. Ventrolateral adhesive organs present on abdominal segments IV–VI .......... Philorae Kellogg

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2(1). Inner lamellae of respiratory organs broad, short, leafy (Fig. 2) ................. Blepharicerina Macquart

2(2). Inner lamellae of respiratory organs elongate, triangular (Fig. 4) ............... Apistomyiini

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3(1). Outer lamellae of respiratory organs short, broad, fused at midline (Fig. 6) ........... Apistomyia Bigot

3(2). Outer lamellae of respiratory organs elongate, triangular, at least anterior pair separated at midline (Figs 16–18; 26–28; 36–38; 45–47; 53) .......... 4

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4(3). All lamellae of respiratory organs closely appressed and parallel, elongate and curving posteriorly (Fig. 53); cephalic sclerite triangular and small, never reaching base of respiratory organs (Fig. 53); tergites with numerous, prominent microsculptured papillae (Fig. 54); anal cleft absent .................. *H. montana* Tonnoir

4(4). Respiratory organ with inner lamellae nearly as wide as outer lamellae, distance between inner margins of anterior and posterior pair of outer lamellae subequal (Figs 26–28; 47); each side of abdominal tergites II, III and IV with a prominent, round muscle scar posterior-medial to primary muscle scars, separated from latter by at least the width of the round scar (Fig. 50) ....... *H. namtoki* sp.n.

4(5). Respiratory organ with inner lamellae less than half as wide as outer lamellae, distance between inner margins of anterior and posterior pair of outer lamellae variable (posterior pair closer than anterior pair) (Figs 16–18; 36–38; 45; 46); abdominal tergites II, III and IV with round muscle scar contiguous with or incorporated into primary muscle scars (Figs 48; 49) ................. 5

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5(6). Posterior outer lamellae of respiratory organ almost meeting at midline (Figs 38; 45); inner lamellae tapering gradually and continuously towards apex (Figs 36–38); dorsal half of cephalic sclerite triangular in female (Fig. 37) ............... *H. diminutiva* sp.n.

5(7). Posterior outer lamellae of respiratory organ separated at midline by at least 0.05 mm (Figs 18; 46); inner lamellae margins subparallel in basal half, tapering only in apical half (Figs 16–18); dorsal half of cephalic sclerite semicircular in female (Fig. 17) ................. *H. manaliella* (Kaul)

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2(1). Cross-vein bm-cu absent; R₄ and R₅ veins separate for entire length (Fig. 8) ................. *Blepharicera* Macquart
– Cross-vein bm-cu present; R₄ and R₅ joined as R₄₊₅ vein for some portion (Fig. 7) ........... *Philorus* Kellogg
3(1). R₄₊₅ vein sinuous, reaching wing margin near distal end of R₁₊₂; R₅ (Fig. 9); antennae with at least eight flagellomeres; mandibles present in females .................................................... *Apistomyia* Bigot
– R₄₊₅ vein variable, never sinuous (Figs 10–14); antennae variable, but always with fewer than eight flagellomeres; mandibles absent ....... *Horaia* Tonnoir
4(3). R₃ vein present as detached vein at wing margin (Fig. 10); hind coxae setose; metakatepisternum setose; female tibial spur formula 0–0–0; female hind tarsal claws narrow and straight; female fore femur without anterodorsal row of setae ............... *Manaliella* (Kaul)
– R₃ vein absent (Figs 11–14); hind coxal variable; metakatepisternum glabrous; female tibial spur formula 0–0–2; female hind tarsal claws stout and curved; female fore femur with distinct anterodorsal row of setae ............... 5
5(4). A₁ vein reduced, barely extending beyond anal angle of wing (Figs 11; 12; 14); labrum glabrous and narrow; male pedicel variable, not expanded apically (Fig. 79); upper division of eyes in females well developed, with at least eight rows of ommatidia (Fig. 77) ............................................................... 6
– A₁ vein longer, almost reaching margin of wing (Fig. 13); labrum setose and broad; male pedicel expanded apically (Figs 69; 74); upper division of female eyes absent or present as five or fewer rows of ommatidia (Figs 67; 72) ............................................. 7
6(5). Stump of R₄ vein sometimes present on R₄₊₅ vein (Fig. 12); hind coxae with sparse, pale hairs; large, females c. 6.5 mm body length, 7.0 mm wing length; male antennae glabrous ....................... *Horaia* Tonnoir (Himalayan populations)
– Stump of R₄ vein never present (Fig. 14); hind coxae glabrous; females smaller, c. 5.0 mm body length, 5.3 mm wing length; male antennae setose ...................................................... *H. montana* piedmonti sp.n.
7(5). Maxillary palpi large, spindle-shaped (Figs 67; 69) .......................................................... *H. namitoki* sp.n.
– Maxillary palpi small, globular (Figs 72; 74) ............ 8
8(7). Female eyes divided, upper division present as two rows of ommatidia .................... *H. diminutiva* sp.n.
Female eyes not divided ............ *H. longipes* Tonnoir

**Horaia Tonnoir, 1930**


**Horaia manaliella** (Kaul, 1976)

(Figs 10; 15–24; 46; 49; 61–63)


**Diagnosis.** Larva: Body broad to oval. Lateral margins of abdominal segments parallel at insertion of prolegs. Body anteroposteriorly compressed, trunk segments at least as wide as cephalic division. Antennae two- or three-segmented. Gill filaments absent in instar I; one in each tuft in instar II; three in instar III; five in instar IV, with three projecting anteriorly, two projecting posteriorly. Abdominal tergites ornamented with ridges and plates, but with few or no setae or papillae. Dorsal prolegs absent. Seventh pair of prolegs reduced to single pair of bristles or setal patches. Posterior margin of anal division without prominent setae. Pupa: Broad, oval. Lamellae of respiratory organs elongate and triangular, not fused at midline. Abdominal tergites either foveolate and rugose or densely papillose, never glabrous. Male: R₄₊₅ vein straight, unforked. Eyes subholoptic, divided, upper division forming hemispherical top half of head. Antennae seven- to nine-segmented; scape and pedicel expanded, twice as broad as flagellomeres; flagellomere shape and number irregular, often fused. Mandibles absent. Maxillary palpi one-segmented. Labella elongate, with pseudotracheae. Female: Wings, antennae and mouthparts similar to males. Eyes dichoptic; divided or undivided.

**Remarks.** The wing venation is similar to that of *Peritheates* and *Nesocurupira*, with straight, unforked R₄₊₅ vein; adults can be distinguished by characters of the mouthparts. Pupae are unremarkable within the tribe. Larvae are identified by the shape of the anal division and the lack of prominent sensilla along the posterior margin of this division. Larvae of *H. montana* superficially resemble those of *Nothohoraia*, but the former can be distinguished by the large size, laterally projecting prolegs, spinulous lateral margin and absence of cephalic ‘antennal’ protruberances.
rugose; anal cleft prominent. Male: A1 vein almost reaching wing margin; R4þ5 vein straight; R5 vein present at wing margin but absent basally; pedicel expanded apically; front femur setose apically; hind coxae and metakatepisternum setose; ventral parameres broad, blunt; dorsal paramere narrow, elongate. Female: Hind legs extremely long; tibial spur formula 0–0–0; hind tarsal claws straight and slender; hypogynial plate broad apically; hypogynial valves with transverse rows of setiforms.

Larva (Figs 20–24). Measurements, instar II (N = 7) body length 1.1 mm (0.9–1.8), cranial width 0.29 mm
(0.28–0.33); instar III \((N = 24)\) body length 2.5 mm (1.7–2.9), cranial width 0.45 mm (0.42–0.47); instar IV \((N = 35)\) body length 3.5 mm (2.6–5.0), cranial width 0.62 mm (0.56–0.66). Antennae two-segmented, glabrous, dark brown to black; segments subequal in length. Cranial sclerites dark brown to black (Fig. 21); posterior margin of frontoclypeal apotome reaches posterior cranial margin forming a broad V-shape (Fig. 21); posterior tentorial pits narrow, dark. Trunk dark brown to black; each abdominal segment with undulate anterior ridge, curved posterior ridge and central triangular sclerotization (Figs 20–22); pair of prominent oval muscle scars lateral to each triangular sclerotization; tergites markedly sclerotized and strigate laterally, with few setiform sensilla. Prolegs with feeler broad basally, narrowing in middle, expanded and circular apically (Figs 23; 24); proleg base ventrally with rectangular patch of spines; first pair of prolegs markedly smaller than other prolegs (Figs 20; 23). Anal division broad posterior to sixth pair of prolegs, lateral margins subparallel, posterolateral corner curved (Figs 20; 22; 24). Chaetotaxy: cephalic division ventrolaterally with numerous elongate setae; circle of setae surrounding mouthparts; stiff comb of setae on anterior margin of genae; thick, broad mass of pale setae on dorsum of each proleg; spiniform setae in transverse row anterior and posterior to dorsal base of each proleg; single stout bristle and mass of pale setae at each posterior corner of anal division (Fig. 24); posterior margin of anal division without prominent sensilla (Fig. 20).

Pupa (Figs 15–19; 46; 49). See Kaul (1976). Other characters, not previously noted, as follows. Body square anteriorly in males, parabolic in females; lateral margins of abdominal segments rounded (Fig. 15). Cephalic sclerite large, semicircular in both sexes but broader in males, latter with two anterior protuberances (Figs 16; 17), height greater than height of respiratory lamellae. Lamellae of respiratory organs triangular in shape (height approximately 0.5 mm); outer lamellae divergent; inner lamellae less than half as wide as outer lamellae, subparallel in basal half, tapering in apical half; anterior and posterior lamellae separated medially, but posterior lamellae closer (Figs 16–18; 46). Abdominal tergites foveolate, rugose towards lateral margins, with sparse microsculptured papillae (Figs 19; 49); tergites II–VI each with pair of crescent-shaped muscle scars on either side of midline (Fig. 49). Anal cleft prominent. Colour uniform light brown, respiratory organs darker.

Adult male. See Kaul (1976). Terminalia (Figs 62; 63): Epandrium simple. Cerci well developed, parallel, densely setose; interlobular depression shallow V-shape; individual lobes broadly rounded and fused medially. Gonostyli elongate, densely setose; gonocoxal lobes short, flattened,
Figs 15–24. Light micrographs of pupae and larvae of *Horaia manaliella* (Kaul). Fig. 15. Male (above) and female (below) pupae, dorsal view. Fig. 16. Male pupa, frontal view. Fig. 17. Female pupa, frontal view. Fig. 18. Pupal respiratory organ, dorsal view (anterior = above). Fig. 19. Pupal abdomen, dorsal view (anterior = left). Fig. 20. Instar IV larva: habitus, ventral (left) and dorsal (right) views. Fig. 21. Instar IV larva: cephalic division and abdominal segments II–III, dorsal view. Fig. 22. Instar IV larva: anal division and abdominal segments IV–V, dorsal view. Fig. 23. Instar IV larva: cephalic division and abdominal segments II–III, ventral view. Fig. 24. Instar IV larva: anal division and abdominal segments IV–V, ventral view. Abbreviations: anal d, anal division; atI–atIV, abdominal tergites I–IV; ceph sc, cephalic sclerite; frcly ap, frontoclypeal apotome; mtt, metatergite; pr VI, sixth proleg. Scale bars: 0.5 mm.
Figs 25–34. Light micrographs of pupae and larvae of *Horaia namtoki* sp.n. Fig. 25. Male (above) and female (below) pupae, dorsal view. Fig. 26. Male pupa, frontal view. Fig. 27. Female pupa, frontal view. Fig. 28. Pupal respiratory organ, dorsal view (anterior = above). Fig. 29. Pupal abdomen, dorsal view (anterior = left). Fig. 30. Instar IV larva: habitus, ventral (left) and dorsal (right) views. Fig. 31. Instar IV larva: cephalic division and abdominal segment II, dorsal view. Fig. 32. Instar IV larva: anal division and abdominal segments IV–V, dorsal view. Fig. 33. Instar IV larva: cephalic division and abdominal segments II–III, ventral view. Fig. 34. Instar IV larva: anal division and abdominal segment V, ventral view. Scale bars: 0.5 mm.
Figs 35–44. Light micrographs of pupae and larvae of *Horaia diminutiva* sp.n. Fig. 35. Male (above) and female (below) pupae, dorsal view. Fig. 36. Male pupa, frontal view. Fig. 37. Female pupa, frontal view. Fig. 38. Pupal respiratory organ, dorsal view (anterior = above). Fig. 39. Pupal abdomen, dorsal view (anterior = left). Fig. 40. Instar IV larva: habitus, ventral (left) and dorsal (right) views. Fig. 41. Instar IV larva: cephalic division and abdominal segments II–III, dorsal view. Fig. 42. Instar IV larva: anal division and abdominal segments IV–V, dorsal view. Fig. 43. Instar IV larva: cephalic division and abdominal segment II, ventral view. Fig. 44. Instar IV larva: anal division and abdominal segments IV–V, ventral view. Scale bars: 0.5 mm.
Figs 45–52. Scanning electron micrographs of pupae of *Horaia*. Fig. 45. *H. diminutiva* sp.n.: respiratory organs, dorsal view. Fig. 46. *H. manaliella* (Kaul): respiratory organs, dorsal view. Fig. 47. *H. namtoki* sp.n.: respiratory organs, dorsal view. Fig. 48. *H. diminutiva* sp.n.: muscle scars on abdominal segment III, dorsal view (anterior = above). Fig. 49. *H. manaliella* (Kaul): muscle scars on abdominal segment III, dorsal view (anterior = above), arrow indicating isolated, round muscle scar. Figs 51; 52. *H. diminutiva* sp.n., microsculpture on abdominal segment III. Scale bars: 5 μm (Fig. 52), 50 μm (Fig. 51), 200 μm (Figs 46–50), 0.5 mm (Fig. 45).
Figs 53–60. Scanning electron micrographs of pupae and larvae of *Horaia montana* Tonnoir. Fig. 53. Pupa: respiratory organs and cephalic sclerite, frontal view. Fig. 54. Pupa: microsculpture on branchial sclerite. Fig. 55. Instar IV: habitus, lateral view. Fig. 56. Instar IV: habitus, ventral view. Fig. 57. Instar IV: abdominal segment IV, ventral view (anterior = above). Fig. 58. Instar IV: abdominal segment IV, dorsal view (anterior = above). Fig. 59. Instar IV: anal division, ventral view. Fig. 60. Instar IV: maxillary palpus, indicating ‘F’ sensilla. Scale bars: 10 μm (Fig. 60), 20 μm (Fig. 54), 200 μm (Figs 53; 57–59), 1 mm (Figs 55; 56).

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Glabrous. Genital capsule large, more than twice as long as wide. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme short and broad. Ventral parameres elongate, slightly longer than aedeagus, broad and blunt at apex; gonocoxal apodemes elongate, half as long as ventral parameres; dorsal paramere elongate, narrow, uniform; lateral parameral lobes absent.

Adult female. See Kaul (1976). Terminalia (Fig. 61): Posterior margin of sternite VIII broadly bilobate, medial depression narrow, U-shaped. Genital fork V-shaped, narrow in anterior two-thirds, broadening in posterior third. Hypogynial plate parallel; individual valves elongate, rounded; inner margins of valves parallel. Accessory glands not seen. Spermathecae three in number, corpora not seen; ducts long, simple. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate setose, each valve with eleven prominent setiforms in a transverse row on dorsal surface.


Figs 61–66. Adults of Horaia manaliella (Kaul) and H. montana Tonnoir. Fig. 61. H. manaliella: female terminalia, ventral view. Fig. 62. H. manaliella: male terminalia, dorsal view. Fig. 63. H. manaliella: male terminalia (phallic structures), dorsal view. Fig. 64. H. montana: female terminalia, ventral view. Fig. 65. H. montana: male terminalia, dorsal view. Fig. 66. H. montana: male terminalia (phallic structures), dorsal view. Abbreviations: ae, aedeagus; ag, accessory gland; c, cercus; dp, dorsal paramere; ea, ejaculatory apodeme; ep, epandrium; ga, gonocoxal apodeme; gc, gonocoxite; gf, genital fork; gl, gonocoxal lobe; gs, gonostylus; hv, hypogynial valves; sVIII, sternite VIII; sp, spermathecal ducts; vp, ventral parameres. Scale bars: 100 µm.
Specimen mounted on slide. *Allotype female*, same data as holotype. Specimen mounted on slide with pupal exuviae. Holotype and allotype possibly deposited IM [neither available for examination].

**Material examined.** See Supplementary material.

**Distribution.** Found in Himalayan India and throughout Nepal (Fig. 82). Often found in the same locations as *H. montana*. Collections suggest a relatively asynchronous phenology, with larval to adult records at some localities extending from April to October.

**Remarks.** Adults differ in many ways from other *Horaia*, but larval and pupal form confirms the placement of *H. manaliella* within the genus. The shape of the cephalic sclerite (round) and position of the posterior lamellae (separated at midline) permit the separation of pupae from those of *H. diminutiva*. Tonnoir’s (1930) original description of ‘Larva K’ probably corresponds to the immature stages of *H. manaliella*, whereas Kaul’s (1976) description of larval *H. manaliella* represents a misidentification of the genus *Philorus* (Zwick, 1990). Larvae of *H. manaliella* are distinguished from those of *H. namtoki* by the colour of the lateral genae (dark), shape of the proleg feelers (expanded apically) and patch of ventral spines at the proleg base (rectangular), and from *H. diminutiva* by the shape of the anal division and the presence of a dorsal sclerotized triangular plate on each abdominal segment.

**Horaia namtoki* sp.n.**

(Figs 25–34; 47; 50; 67–71; 83)

**Diagnosis.** Larva: Antennae two-segmented; lateral surface of genae pale; ventral cephalic division with sparse

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setae; proleg feeler broad basally, tapering gradually to blunt apex, proleg base ventrally with ovoid spine patch; tergites with triangular sclerotizations between transverse ridges; abdominal tergites glabrous or with few setae laterally; lateral margin of anal division subparallel, posterolateral corner rounded. Pupa: Body square anteriorly in males, parabolic in females; cephalic sclerite large, dorsal half circular in females; outer lamellae of respiratory organ divergent; inner lamellae nearly as wide as outer lamellae, tapering gradually towards apex; anterior and posterior lamellae separated medially by approximately the same distance; abdominal tergites foveolate and rugose, segments II–IV with round muscle scar posteromedial to primary scars; anal eleft prominent. Male: Maxillary palpi spindle-shaped; pedicel expanded apically; cerci widely separate; dorsal paramere with bilobed opacity in basal half. Female: Eyes not divided; maxillary palpi spindle-shaped; hypopygial valves short and stout.

Larva (Figs 30–34). Measurements, instar II \((N = 3)\) body length 1.9 mm (1.7–2.0), cranial width 0.28 mm (0.27–0.29); instar III \((N = 25)\) body length 2.8 mm (2.4–3.2), cranial width 0.43 mm (0.40–0.46); instar IV \((N = 33)\) body length 4.2 mm (2.7–5.1), cranial width 0.62 mm (0.55–0.66). Antennae two-segmented; glabrous, dark brown to black; segments subequal in length. Cranial sclerites dark brown, lateral genae pale posterior to antennal sockets (Fig. 31); posterior margin of frontoclypeal apotome extends to posterior cranial margin forming narrow V-shape (Fig. 31); posterior tentorial pits narrow, dark. Trunk pale to dark brown; each abdominal segment with undulate anterior ridge, curved posterior ridge and central triangular sclerotization (Figs 30–32); pair of prominent oval muscle scars lateral to each triangular sclerotization; tergites markedly sclerotized and striigate laterally, with few setiform sensilla. Prolegs with feeler broad basally, tapering gradually to blunt apex (Figs 33; 34); proleg base ventrally with

Figs 72–76. Adults of *Horaia diminutiva* sp.n. Fig. 72. Female head, frontal view. Fig. 73. Female terminalia, ventral view. Fig. 74. Male head, frontal view. Fig. 75. Male terminalia (phallic structures), dorsal view. Fig. 76. Male terminalia, dorsal view. Scale bars: 100 μm.
large, circular patch of spines (Figs 33; 34); first pair of prolegs markedly smaller than other prolegs (Figs 30; 33). Anal division broad posterior to sixth pair of prolegs, lateral margins subparallel, posterolateral corner curved (Figs 30; 32). Chaetotaxy: cephalic division ventrolaterally with sparse setae; circle of setae surrounding mouthparts; stiff comb of setae on anterior margin of genae; sparse pale setae on dorsum of each proleg; spiniform setae in transverse row anterior and posterior to dorsal base of each proleg; two to three stout bristles and mass of pale setae at each posterior corner of anal division (Fig. 30); posterior margin of anal division without prominent sensilla.

Pupa (Figs 25–29; 47; 50). Measurements, male ($N = 16$) length 3.8 mm (3.3–4.3), width 1.7 mm (1.4–2.0); female ($N = 18$) length 4.0 mm (3.4–4.5), width 1.9 mm (1.6–2.2). Body square anteriorly in males, parabolic in females, lateral margins of abdominal segments rounded (Fig. 25). Cephalic sclerite large, semicircular in both sexes but broader in males (Figs 26; 27), height greater than or subequal to height of respiratory lamellae. Lamellae of respiratory organs triangular in shape (height approximately 0.5 mm); outer lamellae divergent; inner lamellae nearly as wide as outer lamellae, tapering gradually to pointed apex; anterior and posterior lamellae widely separated medially, with distance between inner margins subequal (Figs 26–28; 47). Abdominal tergites foveolate, rugose towards lateral margins, with sparse microsculptured papillae (Figs 29; 50); tergites II–VI each with a single, circular muscle scar medial to pair of crescent-shaped muscle scars on either side of midline (Fig. 50). Anal cleft prominent. Colour uniform light brown, respiratory organs darker.

Adult male. Head and terminalia only, dissected from pupa. Head (Fig. 69): Normal type, subholoptic. Clypeus rounded and bulbous, longer than wide. Eyes meet dorsally; eyes divided, upper division large, forming hemispherical top half of head; lower division smaller, about as wide as upper division at callis oculi; callis oculi bare and narrow; upper ommatidia diameter $1.5 \times$ as large as lower. Proboscis

Figs 77–81. Adults of *Horaia montana piedmonti* ssp.n. Fig. 77. Female head, frontal view. Fig. 78. Female terminalia, ventral view. Fig. 79. Male head, frontal view. Fig. 80. Male terminalia (phallic structures), dorsal view. Fig. 81. Male terminalia, dorsal view. Scale bars: 100 µm.
long, free portion 1.5 × head height, sparsely setose on basal half; mandibles absent; palpi one-segmented, elongate, spindle-shaped; labrum elongate, one-third length of proboscis, densely setose. Antennae seven-segmented, any or all of flagellomeres II–V partially or fully subdivided into two segments; scape broad and quadrate; pedicel broad, elongate, expanded apically; flagellomeres slender; all segments setose. Terminalia (Figs 70; 71): Epandrium simple, emarginate posteriorly, with anterior row of setiform sensilla. Cerci well developed, parallel, sparsely setose; interlobular depression deep, V-shape; individual lobes rounded. Gonostylus large, densely setose; gonocoxal lobes elongate, flattened and glabrous. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme broad and oval-shaped. Ventral parameres elongate, straight, longer than aedeagus; gonocoxal apodemes narrow, half as long as ventral parameres; basal half of dorsal paramere with bilobed opacity; lateral parameral lobes absent.

Adult female. Head and terminalia only, dissected from pupa. Head (Fig. 67): Normal type, dichoptic. Clypeus rounded and bulbous, longer than wide. Eyes separate, not divided. Proboscis long, free portion 2.5 × head height, sparsely setose on basal half; mandibles absent; palpi one-segmented, elongate, spindle-shaped; labrum elongate, one-third length of proboscis, densely setose. Antennae seven-segmented, pedicel broad, but not expanded apically, otherwise identical to male. Colour uniform light brown. Terminalia (Fig. 68): Posterior margin of sternite VIII broadly bilobate, medial depression broad, U-shaped. Genital fork V-shaped, narrow in anterior third, broadening in posterior two-thirds. Hypogynial plate parallel sided; individual valves short, stout, rounded; inner margin of valves parallel. Accessory glands large, oval. Spermathecae three in number, corpora ovoid, small with long, simple ducts. Chaetotaxy: sternite VIII without prominent setae; hypogynial plate glabrous, valves with ten prominent setiforms each on dorsal surface.

Type material. Holotype male, THAILAND: Chiang Mai Province, Doi Suthep-Pui NP, Namtok Monthatarn, 18°49′N 98°55′E, 3.xi.1994 (GW Courtney) (USNM). Specimen dissected from pupa and mounted on slide in Canada Balsam with pupal exuviae. Allotype female, same locality and date as male (USNM), slide-mounted in Canada Balsam with pupal exuviae. Paratypes, same data as holotype and allotype [1 male A (slide); 1 male A (slide); 1 female A (slide); 1 female A (slide); 5 Pex (slide); 4 Pex (slide); 1 instar II L, 1 instar III L, 1 instar IV L (slide); 2 instar II L, 2 instar III L, 2 instar IV L (slide); 2 instar IV L, 1 male P (EtOH); 3 instar II L, 25 instar III L, 107 instar IV L (EtOH)]. Paratypes deposited in CMUC, ISIC, QSBG and USNM.

Other material examined. THAILAND: Chiang Mai Province, Doi Inthanon NP, Nam Mae Aep above Rd Fig. 82. Distribution of Horaia species in Nepal.

**Etymology.** From the Thai word ‘namtok’ meaning waterfall.

**Distribution** (Fig. 83). The species is currently known only from the Chiang Mai and Mae Hong Son provinces of northern Thailand. Often found in the same localities as *H. montana piedmonti* and unidentified species of *Apistomyia* and *Philorus*. Collection records from every month at some localities suggest a relatively asynchronous phenology.

**Remarks.** Adults and pupae are typical of *Horaia*. Adults can be distinguished from *H. diminutiva* by the shape of the...
maxillary palpi and the undivided female eye. Pupae are separated from other members of the genus by the shape of the respiratory lamellae and the presence of round muscle scars on abdominal tergites II, III and IV. Larvae have the following unique characters: the lateral surface of the genae is pale, the ventral surface of the cephalic division has sparse setae, the base of the prolegs bears large, ovoid spine patches, and the proleg feelers taper gradually to an apex that is not expanded.

**Horaia diminutiva** sp. n.
(Figs 13; 35–45; 48; 72–76; 82)

**Diagnosis.** Larva: Antennae two-segmented; lateral surface of genae dark; ventral cephalic division with numerous setae; proleg feeler broad basally, narrowing in middle, with expanded, circular apex, proleg base ventrally with rectangular spine patch; tergites without sclerotizations between transverse ridges; abdominal tergites mostly glabrous laterally; lateral margin of anal division divergent posteriorly, posterolateral corner angulate. Pupa: Body square anteriorly in males, parabolic in females; cephalic sclerite large, dorsal half triangular in females; outer lamellae of respiratory organ divergent; inner lamellae less than half as wide as outer lamellae, tapering gradually towards apex; anterior lamellae separated medially, posterior lamellae closer than anterior lamellae; abdominal tergites foveolate and rugose; anal cleft prominent. Male: Pedicel expanded apically; flagellomere I elongate; lower eye division triangular; cercal lobes almost completely fused; gonocoxal lobes expanded apically; ventral parameres cross at apices; dorsal paramere with bilobate opacity on basal half. Female: Pedicel broad; flagellomere I elongate; eyes not divided; sternite VIII fused; hypogynial plate broad apically; hypogynial valves fused; necks of spermathecae with characteristic bulge.

**Larva** (Figs 35–44). Measurements, instar I (N = 1) body length 0.86 mm, cranial width 0.12 mm; instar II (N = 5) body length 1.4 mm (1.1–1.7), cranial width 0.24 mm (0.22–0.25); instar III (N = 19) body length 2.3 mm (2.0–2.6), cranial width 0.40 mm (0.33–0.43); instar IV (N = 21) body length 3.1 mm (2.6–3.7), cranial width 0.53 mm (0.50–0.56). Antennae two-segmented, glabrous, dark brown to black; segments subequal in length. Cranial sclerites dark brown to black (Fig. 41); posterior margin of frontoclypeal apotome reaches posterior cranial margin forming a narrow V-shape (Fig. 41); posterior tentorial pits narrow, dark, prominent. Trunk medium to dark brown; each abdominal segment with transverse to [posterior segments] undulate anterior ridge, curved posterior ridge, without central triangular sclerotization (Figs 40–42); two pairs of oval muscle scars lateral to midline of each trunk segment, tergites strigate between ridges, with few setiform sensilla. Prolegs with feeler broad basally, narrowing in middle, expanded and circular apically (Figs 43; 44); proleg base ventrally with rectangular patch of spines; first pair of prolegs markedly smaller than other prolegs (Fig. 43). Anal division broad posterior to sixth pair of prolegs, divergent posteriorly, posterolateral corner angulate (Figs 42; 44). Chaetotaxy: cephalic division ventrolaterally with numerous elongate setae; circle of setae surrounding mouthparts; stiff comb of setae on anterior margin of genae; elongate, pale setae along dorsum of each proleg; prominent, stout seta extending from each posterior corner of anal division; small, spiniform setae in transverse row anterior and posterior to dorsal base of each proleg; one to two stout bristles and few pale setae at each posterior corner of anal division (Figs 42; 44); posterior margin of anal division without prominent sensilla (Fig. 42).

**Pupa** (Figs 35–39; 45; 48; 51; 52). Measurements, male (N = 28) length 2.8 mm (2.7–3.2), width 1.4 mm (1.2–1.7); female (N = 9) length 3.1 mm (2.8–3.5), width 1.5 mm (1.3–1.7). Body square anteriorly in males, parabolic in females; lateral margins of abdominal segments rounded (Fig. 35). Cephalic sclerite large, semicircular in male (Fig. 36), triangular in female (Fig. 37), height greater than height of respiratory lamellae. Lamellae of respiratory organs triangular in shape (height approximately 0.4 mm); outer lamellae divergent and 0.3 mm wide at base; posterior outer lamellae almost meeting at midline; inner lamellae close set and one-third as wide at base as outer lamellae. Lamellae of respiratory organs triangular to broadly rounded (anterior pair) in shape (height approximately 0.4 mm); anterior lamellae divergent; inner lamellae less than half as wide as outer lamellae, tapering gradually to broadly pointed apex; anterior lamellae separated medially, posterior lamellae contiguous (Figs 36–38). Abdominal tergites foveolate, rugose towards lateral margins, with sparse microsculptured
papillae (Figs 39; 48; 51; 52); tergites II–VI each with pair of crescent-shaped muscle scars on either side of midline (Fig. 48). Anal cleft prominent. Colour uniform light brown, respiratory organs darker.

**Adult male.** Body ($N = 3$ pharate specimens) length 3.3 mm (3.0–3.7). **Head** (Fig. 74): Normal type, subholoptic; uniform light brown colour. Clypeus rounded, bulbous, about as long as wide. Eyes meet dorsally; divided, upper division large, forming hemispherical top half of head; lower division triangular, 0.75× as wide as upper division at callis oculi; callis oculi bare, not as wide as one upper ommatidium; upper ommatidium twice as large as lower. Proboscis long; free portion twice height of head; mandibles absent; palpi small, one-segmented, globular; labrum elongate, densely setose, one-quarter of length of proboscis. Antennae seven-segmented, penultimate flagellomere elongate or divided into two subequal flagellomeres; scape short and quadrate; pedicle expanded apically; flagellomere I elongate, as long as scape and pedicle together; remaining flagellomeres cylindrical with varying length; scape with long setae, remaining segments sparsely setose; all antennal segments concolorous, light brown. **Thorax:** Medium brown colour; dorsum dark brown, almost black; mesothorax with distinct triangular marking on posterior margin; all thoracic sclerites glabrous. **Wing** (Fig. 13): Length 3.5 mm (3.3–3.7) $A_1$ almost reaching wing margin; $R_{4+5}$ straight, reaching margin near wing tip. **Legs:** Not fully sclerotized, characters unclear. **Terminalia** (Figs 75; 76): Epandrium simple, sparsely setose in lateral regions. Cerci well developed, parallel, densely setose; interlobular depression slightly concave; individual lobes rounded, fused medially. Gonostyli elongate, narrow, densely setose; gonocoxal lobes elongate, flattened, glabrous, expanded apically. Genital capsule large, twice as long as wide. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme small, round; ejaculatory apodeme short, broad. Ventral parameres elongate, narrow, longer than aedeagus, apices cross beyond apex of aedeagus; gonocoxal apodemes elongate, broad, half as long as ventral parameres; dorsal paramere with bilobate opacity in basal half; lateral parameral lobes absent.

**Adult female.** Body ($N = 1$ pharate specimen) length 3.2 mm. **Head** (Fig. 72): Normal type, dichoptic; uniform light brown colour. Clypeus bulbous and rounded, as long as wide. Eyes separate, divided, upper division present as two
rows of small ommatidia, callis oculi narrow. Proboscis elongate, free portion 2.3 x height of head; mandibles absent; palpi small, one-segmented, globular; labrum elongate, one-fifth the length of the proboscis, setose. Antennae seven-segmented, pedicel broad, not expanded apically, otherwise antennae identical to male. Thorax and wing identical to male. Legs: Not fully sclerotized, most characters unclear; anterodorsal row of hairs present on fore femur, hind tarsal claws broad, curved. Terminalia (Fig. 73): Posterior margin of sternite VIII slightly bilobate, medial depression slight concave. Genital fork shallow U-shaped. Hypogynial plate narrow basally, broadening apically; individual valves rounded, fused; medial depression shallow V-shape. Accessory glands not seen. Spermathecae three in number; corpora not seen; necks with characteristic bulge; ducts simple, long. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate setose, each valve with eleven prominent setiforms in transverse row on dorsal surface.

**Type material.** Holotype male, NEPAL: Dolkha District, Rojenaagee Kh above Jiri Rd, 27°41’N 85°59’E, 19.iv.2000, emerged 21.iv.2000 (GW Courtney) (USNM). Specimen pinned with pupal exuviae, genitalia in glycerin microvial. Allotype female, same locality and date as male, emerged 19.iv.2000 (USNM). Specimen pinned with pupal exuviae, genitalia in glycerin microvial. Paratypes, same date and location as holotype and allotype [1 male A, reared (pinned); 1 male A, reared (EtOH); 121 instar III L (EtOH); 115 instar IV L (EtOH); 14 male P, 1 female P, Pex (EtOH)]. Paratypes deposited in USNM and ISIC.


**Etymology.** The name is derived from the Latin adjective 'diminutivus', meaning tiny, in reference to the species’ small size.

**Distribution** (Fig. 82). Known only from the Dolkha and Sindhupalchok districts of central Nepal. Some locations contain both *H. diminutiva* and *H. montana*.

**Remarks.** Adults and pupae are typical of *Horaia*. Adults can be distinguished from *H. namtoki* by the shape of the maxillary palpi and the presence of a small upper eye division in the females. Pupae are similar to those of *H. manaliella*, but can be distinguished by the proximity of the posterior respiratory lamellae (nearly contiguous at midline) and the shape of the female cephalic sclerite (triangular). Mature larvae are distinct from *H. namtoki* by the following characters: lateral surface of genae is dark, ventral surface of cephalic division has numerous setae, base of prolegs with rectangular spine patches, and proleg feelers expanded apically. It is difficult to distinguish *H. diminutiva* from *H. manaliella*, especially in early instar larvae; however, mature larvae can be recognized by the lack of triangular sclerotizations on the abdominal tergites and the shape of the anal division (divergent behind sixth proleg and with angulate posterolateral margins).

**Horaia longipes** Tonnoir, 1932

**Horaia longipes** Tonnoir, 1932: 273 [original description].

**Diagnosis.** Female: A1 vein almost reaching wing margin; R4+5 vein straight; front femur with anterodorsal row of setae; hind legs long, femora thin; tibial spur formula 0–0–2.

**Larva, pupa and male.** Unknown.

**Female.** See Tonnoir (1932).

**Type material.** Holotype female, INDIA: Sikkim, Pashoke Jhora near Tista bridge, date unknown (S. L. Hora). Possibly deposited IM [not available for examination].

**Remarks.** Known only from type location in northeastern India: the type specimen is unavailable for study, and the status and relationships of *H. longipes* remain unclear.

**Horaia montana** Tonnoir, 1930

(Figs 11; 12; 53–60; 64–66; 82; 83)


**Horaia sp.** Tonnoir, 1932: 274.

**Diagnosis.** Larva: Chiton-shaped; antennae three-segmented; lateral surface of genae dark; ventral cephalic division with sparse setae; proleg feeler broad basally and of more or less uniform diameter to blunt apex, proleg base ventrally with ovoid spine patch, feeler base with anterior and posterior protuberances; tergites with crescent-shaped sclerotizations anteriorly, most specimens with two elongate, submedian dorsal spines on cephalic division and a single elongate, median dorsal spine on each subsequent division; lateral and posterior margins of anal division curved continuously, semicircular. Pupa: Body anteriorly parabolic in both sexes; cephalic sclerite broadly (male) to acutely (female) triangular; height much less than height of respiratory lamellae; respiratory organs elongate, close-set and curved towards posterior; outer lamellae of respiratory organ divergent; inner lamellae convergent, nearly as wide.

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as outer lamellae, tapering gradually towards apex; anterior and posterior lamellae separated medially by approximately the same distance; abdominal tergites densely covered with papillae. Male: A1 vein reduced, barely extending beyond anal angle of wing; stump of R4 sometimes present; labrum short, narrow and glabrous; hind coxae setose; dorsal paramere with bilobed opacity in basal half. Female: Front and mid tibiae tapered apically; spermathecae large, spherical; accessory gland elongate, tapered.

** Larva (Figs 55–60).** Instar I (N = 14) body length 1.0 mm (0.8–1.3), cranial width 0.20 mm (0.17–0.21); antennae one-segmented, black; prolegs small, conical, weakly sclerotized; no gill filaments; cranial sclerite dark brown almost black; egg burster pale, nearly as long as frontoclypeal apotome; trunk pale, with a pair of dark, transverse sclerotized ridges on each abdominal segment. Instar II (N = 16) body length 2.0 mm (1.4–2.3), cranial width 0.38 mm (0.34–0.42); antennae three-segmented; prolegs pale, weakly sclerotized, sparsely setose; one gill filament; trunk pale, each abdominal segment with three dark, transverse ridges. Instar III (N = 25) body length 3.2 mm (2.5–4.0), cranial width 0.63 mm (0.59–0.66); antennae three-segmented; three gill filaments, two directed anteriorly, one directed posteriorly; trunk pale to medium brown; cranial sclerites light reddish to dark brown; dorsal spines sometimes present; prolegs abruptly broadened at base; lateral margin of tergites with ridge of spinules anterior and posterior to base of each proleg. Instar IV (N = 44) body length 5.3 mm (3.6–7.1), cranial width 1.10 mm (0.90–1.22). Antennae three-segmented; all segments black, glabrous, cylindrical; first segment short, broad; third segment elongate, as long as first two segments combined. Cranial sclerites pale to reddish to almost black, darker in larger specimens; posterior margin of frontoclypeal apotome extends to posterior cranial margin forming U-shape. Trunk pale to dark brown; each segment with prominent, crescentic, dark ridges; a pair of oval muscle scars on each side of each segment directly behind the ridges (Figs 55; 58). Dorsal spines present in some specimens (Fig. 55); spines arising from midline at posterior transverse ridge on abdominal segments II–VI; spines long (approximately 0.8 mm, regardless of size of specimen), dark and undulate; two spines also arise from submedian dorsal region of cephalic division. Prolegs with feeler broad basally and of more or less uniform diameter to blunt apex (Figs 56–59); proleg base ventrally with ovoid patch of spines, feeler base with anterior and posterior protuberances (Figs 57; 58); first pair of prolegs somewhat smaller than other prolegs (Fig. 56). Anal division curved continuously, semicircular, with heavily sclerotized posterior margin. Chaetotaxy: cephalic division ventrolaterally with sparse setae; few setae surrounding mouthparts; stiff comb of setae on anterior margin of gennae; elongate, pale setae along dorsum of each proleg; comb of spiniform sensilla at lateral margin of tergites anterior and posterior to each proleg (Figs 57; 58); single stout bristle on each posterolateral margin of anal division, posterior margin of anal division few to many prominent sensilla (Fig. 59).

** Pupa (Figs 53; 54).** Measurements, male (N = 10) length 5.2 mm (4.8–5.6), width 2.6 mm (2.2–2.8); female (N = 1) length 5.1 mm, width 2.5 mm. Body broadly parabolic anteriorly in both sexes; lateral margins of abdominal segments rounded. Cephalic sclerite broadly (male) to acutely (female) triangular (Fig. 53); height much less than height of respiratory lamellae; respiratory organs elongate (length 1.7 mm, width at base 0.8 mm), close-set and curved posteriorly; outer lamellae of respiratory organ divergent; inner lamellae convergent, nearly as wide as outer lamellae, tapering gradually towards apex; all lamellae separated medially by at least 0.18 mm (Fig. 53). Branchial sclerite and abdominal tergites densely covered with papillae (Fig. 54). Anal cleft absent. Colour uniform dark brown, respiratory organs darker, almost black.

** Adult male.** See Tonnoir (1930). **Terminalia (Figs 65; 66):** Epandrium simple. Cerci well developed, large, parallel, densely setose at apices; interlobular depression broad, U-shaped; individual lobes rounded laterally and fused medially. Gonostyli elongate, sparsely setose; gonocoxal lobes elongate, flattened, glabrous. Genital capsule large, 1.5× longer than wide. Aedeagal rods of phallos comprising three simple, elongate rods. Base of ejaculatory apodeme round. Ventral parameres elongate, slightly longer than aedeagus, parallel; gonocoxal apomeres elongate, broad, half as long as ventral parameres; dorsal paramere with bilobed opacity in basal half; lateral parameral lobes absent.

** Adult female.** See Tonnoir (1930); (1932). **Terminalia (Fig. 64):** Posterior margin of sternite VIII broadly bilobate, median depression broad, U-shaped. Genital fork V-shaped; narrow in anterior quarter, broadening widely in posterior three-quarters. Lateral margins of hypogynial plate parallel; individual valves elongate, rounded; inner margins of valves parallel. Accessory gland large, elongate, tapering to a point anteriorly. Spermathecae three in number, corpora large, spherical, irregular; ducts long and simple. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate densely setose, valves with ten prominent setiforms each on dorsal surface.

** Type material.** **Holotype male, INDIA:** Meghalaya, Khasi Hills, Lashdat stream, 10.x.1929 (S. L. Hora). **Allotype female,** same data as holotype. Holotype and allotype both possibly deposited at IM [neither available for examination].

** Material examined.** See Supplementary material.

** Distribution.** (Figs 82; 83). Found throughout the Himalayan region of Nepal and northern India. Often found in the same location as other members of Horaia, as well as other genera. Collections suggest a relatively asynchronous phenology, with larval to adult records at some localities extending from April to October.

** Remarks.** Adults are distinctive from most other Horaia in their large size and reduced A1 vein. Adults can be distinguished...
from *Horaia montana piedmonti* by the larger size, setose hind coxae and glabrous male antennae. In some specimens, both male and female, a segment of the R<sub>4,5</sub> vein is seen on the R<sub>4,5</sub> vein (Tonnoir, 1930). Pupae of *Horaia montana* are unique in a number of features, including the shape of the respiratory organs and the presence of abundant papillae on the branchial sclerites and abdominal tergites. Larvae of *Horaia montana* are unique amongst *Horaia* because of the chiton-like shape and spinulous lateral margin. A number of different larval forms of *Horaia montana* are known, but differences between these forms are inconsistent, with intermediate morphotypes plentiful, and some differences possibly due to changes associated with growth and molting. Coloration and relative body size can change in the course of a single instar, but sclerotized structures (i.e. suctoriel discs, cephalic sclerites, antennae, mouthparts) are invariant (Craig, 1969). The presence or absence of dorsal spines does not appear to be a species-defining character (Tonnoir, 1930).

### *Horaia montana piedmonti* ssp.n.

*(Figs 14; 77–81; 83)*

**Diagnosis.** Larvae and pupae indistinguishable from Himalayan *H. montana*, including variation in the presence of dorsal spines. Male: A<sub>1</sub> vein reduced, barely extending beyond anal angle of wing; labrum short, narrow and glabrous; antennae nine-segmented and setose; dorsal paramere with bilobed opacity in basal half. Female: Dorsal eye division with five rows of ommatidia; accessory gland elongate, tapered.

**Larva.** Indistinguishable from Himalayan *H. montana*.

**Pupa.** Indistinguishable from Himalayan *H. montana*.

**Adult male.** Body (*N* = 2) length 4.4 mm (4.1–4.7). **Head** *(Fig. 79):* Normal type, subholoptic; uniformly light brown. Clypeus rounded, bulbous, about as long as wide. Eyes meet dorsally; eyes divided, upper division large, forming hemispherical top half of head; lower division triangular, nearly as wide as upper division at callis oculi; callis oculi narrow and bare; upper ommatidia twice as large as lower; upper division pale, lower division darker. Proboscis long, setose, free portion 1.8× head height; mandibles absent; palpi small, one-segmented, globular; labrum short, narrow, glabrous, one-quarter the length of the proboscis; setae present on basal half of proboscis. Antennae nine-segmented; any or all of flagellomeres V–VII fully or partially subdivided into two segments; scape and pedicel broad; flagellomeres slender. **Thorax:** Identical to male. Front and mid leg with prominent anterodorsal row of setae on femur; joints of hind tarsal segments oblique; tibial spur formula 0–0–2, tarsal spurs short, stout and black, anterior spur half as long as posterior; claws simple, elongate, curved. Leg segment measurements are given in Table 1. **Wing:** Length 5.3 mm (5.0–5.5); identical to male. **Terminalia** *(Figs 80; 81):* Epandrium simple, sparsely setose. Hypogynial plate parallel sided; individual valves elongate, rounded; inner margin of valves parallel. Accessory gland elongate, tapering to a point at anterior end. Spermathecae not seen. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate densely setose; valves with eleven prominent setiforms each on dorsal surface.

Other material examined. See Supplementary material.

Etymology. From the French 'piedmont' meaning foot-hill, in reference to the species being similar to Himalayan *H. montana*, except for the much smaller size.

Distribution (Fig. 83). Found in the northern provinces of Thailand and presumably in mountainous regions to the north (Myanmar) and east (Laos), perhaps as far as northern Vietnam (D. Currie, 2000, personal communication, Royal Ontario Museum, Toronto, Canada). It seems likely that the distribution of *H. montana* includes much of the area between northern Thailand and the Himalayas. Collection records from every month at some localities indicate a relatively asynchronous phenology.

Remarks. The present taxon is considered an allopatric subspecies of Himalayan *H. montana*. Adults are similar to the latter in body shape and wing venation, but much smaller in body and wing size. Adults can be distinguished from Himalayan specimens by the absence of setae on the hind coxae and the setose male antennae. Larvae and pupae are indistinguishable from those of Nepalese *H. montana*. Adult males have been collected frequently at mercury vapour lights and black lights, making *H. montana* piedmonti one of the few species of net-winged midge that can be collected by this method.

Phylogenetic relationships

Results

The characters used in the phylogenetic analysis are summarized in the Appendix. The analysis included twenty-four characters and eighteen taxa. Of these, fourteen were adult characters, three were pupal characters and seven were larval characters. Parsimony analysis produced four trees with a length of thirty-three steps. A strict consensus of these (Fig. 85) had a consistency index (CI) of 0.82, retention index (RI) of 0.91 and a rescaled consistency index (RC) of 0.75. Bootstrap analyses showed strong to moderate support for several clades, e.g. Apistomyiini, *Peritheates* + *Neocruripira*, *Nothohoraria* + (*Neocruripira* + *Cururipina*), *Horaia* + (*Apistomyia* + *Parapistomyia*) and *Apistomyia* + *Parapistomyia*. However, Bremer support was generally low for most clades. Although the genus *Horaia* was supported as monophyletic, the bootstrap values and Bremer support were relatively weak.

Discussion

Within the Blepharicerinae, Apistomyiini is a monophyletic group. Although supported by relatively few synapomorphies, the following character provides compelling evidence of monophyly: elongate labella with pseudotrachea (in taxa in which the labellum is reduced, an elongate pupal sheath usually reveals its past presence) (Alexander, 1958; Zwick, 1998; Stuckenberg, 2004). Several other shared characters, including maxillary palpi reduced to two or fewer segments, basal segment of labial palpi joined longitudinally and forming dorsal channel, presence of four pairs of adhesive organs in pupae and presence of a clypeal shield in larvae, are considered to provide support for the monophyly of Paltostomatini + Apistomyiini.

Genus-level classification of the Apistomyiini has been hampered by a lack of specimens of all life stages from all genera (Tonnoir, 1932). Thus, phylogenetic analyses have been based exclusively on incomplete descriptions of species. An overwhelming factor in any attempt to analyse the Apistomyiini is the frequency of convergence amongst the genera (Stuckenberg, 1958; Zwick, 1977).

Early phylogenetic analyses of the Apistomyiini relied heavily on characters of wing venation. The guiding principle of these studies has been a progression from ancestral states with a full complement of veins (e.g. as in *Edwardsina*) to a derived reduction in venation (e.g. as in *Hammatorrhina* Loew) (e.g. Kitakami, 1950; Alexander, 1958; Dumbleton, 1963). Within the Apistomyiini, the presence of a forked R₄+₅ vein, with R₄ and R₅ separate at the tip (e.g. *Neocruripira*), is considered to be ancestral (Craig, 1969). An unforked R₄+₅ vein is common to *Horaia*, *Apistomyia*,

Table 1. Leg segment measurements (mm) of adult male of *Horaia montana piedmonti* ssp.n.

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<th>t5</th>
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<tr>
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Table 2. Leg segment measurements (mm) of adult female of *Horaia montana piedmonti* ssp.n.

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<tr>
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</table>

© 2007 The Authors
Parapistomyia, Nesocurupira, Theischingeria and Peritheates. This change in venation is likely to have arisen independently many times. The exact nature of the change (i.e. whether the R₄ or R₅ vein was lost) is impossible to determine. Even amongst genera with the ancestral, forked condition, it is likely that the presence of a forked R₄₋₅ vein is convergent (Zwick, 1977). For this reason, the use of the radial veins for phylogenetic analysis is discouraged. At most, the only character useful for analysis is the sinuous shape of the R₄₋₅ vein, synapomorphic to Apistomyia and Parapistomyia. An extra vein fragment in the radial sector of H. manaliella is of an uncertain origin. The condition of the A₁ vein is another ambiguous character. The ancestral condition, seen in Peritheates and Nesocurupira, is a complete or nearly complete A₁ vein. The degree of vein reduction from the ancestral state varies inter- and intragenerically. One extreme reduction indicates relationships within Horaia. Both H. montana and H. montana piedmonti have the A₁ vein greatly reduced.

Adult mouthparts usually are consistent within a genus (Kitakami, 1950). Mandible presence in adult females is plesiomorphic for the Blephariceridae (Zwick, 1977): their absence is common to nearly all Apistomyiini, yet is susceptible to convergence (Stuckenberg, 1958, 2004; Zwick, 1977). Mandibles have been regained in the Apistomyia as a result of character reversal (Zwick, 1998), and the presence of weak mandibles in members of the Parapistomyia may represent a transitional state. The reduction of other mouthparts, notably the labella, has arisen independently several times in the family (Stuckenberg, 1969, 2004). A characteristic reduction of the labrum, producing a slender, asetose condition, is an autapomorphy of H. montana. The plesiomorphic condition of the maxillary palpi in Apistomyiini is two segments, a quadrate palpiger and an elongate distal segment (Zwick, 1977). The two-segmented condition is seen in Nesocurupira, Peritheates, Curupirina and Austrocurupira, although the general reduction of mouthparts in Nesocurupira, Theischingeria and Nothohoraia obscures this character. The presence of Lauterborn’s organ on the second palpal segment is a synapomorphy of Apistomyia and Horaia. Further reduction of the maxillary palpi to a small, globular shape has taken place in all species of Horaia, except H. manaliella and H. namtoki.

The eyes in adult Apistomyiini vary, including dichoptism, holoptism and sexual dimorphism. Although useful key characters, the variability, even within genera, makes this suite of characters of questionable phylogenetic use (Stuckenberg, 1958, 2004; Craig, 1969).

Informative antennal characters in the Apistomyiini include the reduction of flagellomere number (Kitakami, 1950). From an ancestral condition of as many as twelve flagellomeres (e.g. as in Nothohoraia), there is reduction to as few as five (e.g. as in H. diminutiva). However, genera, species, and even individual specimens can display a range of flagellomere number. Because reduction in flagellomere number is a result of fusion, the determination of definite character states is impossible. When flagellomere number can be accurately determined, similar character states between species are likely to be a result of convergence (Zwick, 1977). Features of the scape and pedicel are easier to determine. The plesiomorphic state, present in Neocurupira, Nothohoraia, Curupirina, Nesocurupira and Peritheates, is a scape and pedicel subequal in width to the flagellomeres. The remaining genera of the Apistomyiini are synapomorphic in having a scape and pedicel greatly expanded to at least twice the width of the flagellomeres (Zwick, 1977).

Phylogenetically informative characters of the leg are few. The tibial spur formula, often useful in other groups, proves convergent in the Apistomyiini (Kitakami, 1950). Tarsal claw shape and size also vary greatly amongst genera and species. The only leg character used in the present analysis is an anterodorsal row of dark setae on the front femora of females (Tonnor, 1930). This character is synapomorphic to all Horaia except H. manaliella. A number of features characterize the hind legs of female H. manaliella, including the absence of tibial spurs, straight joints between the tarsal segments and slender tarsal claws. These characters are autapomorphies of the species and are perhaps associated with extreme lengthening of the hind legs.

Until recently, detailed genital characters have not been included in species descriptions. Many early descriptions neglected to mention the terminalia or provided only crude drawings. For this reason, only the genital characters of examined species can be analysed for evolutionary relationships. Within Horaia, a few conclusions can be drawn from genital characters. In the females, an elongate, tapered accessory gland is an autapomorphy of H. montana. In the males, the presence of a notched or completely bilobate opacity on the basal half of the dorsal paramere is a synapomorphy of the Horaia, excluding H. manaliella.

The immature stages provide useful characters in blepharicerid systematics, as the biology of these stages makes it likely that phylogenetically informative adaptations will be more evident than in adult stages (Hora, 1930).

The Apistomyiini share an oval pupal shape common to most blepharicerids, and variations in gross morphology are few. Curupirina and Nesocurupira share a synapomorphic medial fusion of abdominal tergites VII and VIII (Zwick, 1977). Finely microsculptured papillae are present in H. montana and may have some hydrodynamic function (Hora, 1930). Within Horaia, this feature may be an autapomorphy of the species, although it could be homologous to the foveolate microsculpture of other Horaia.

Analyses of flow patterns indicate that vortices and areas of negative pressure are created around the respiratory organs, regardless of lamellae shape. This would eliminate any evolutionary pressure towards a more efficient lamellar shape (Pommen & Craig, 1995). The ancestral form for Apistomyiine respiratory organs is probably that of Neocurupira (Craig, 1969), which would thus include elongate, triangular outer gill lamellae, all lamellae well removed from the midline, outer lamellae divergent and the tracheal opening present as a U-shaped slit. Parapistomyia, Apistomyia, Nothohoraia and H. diminutiva all show a likely
convergent shift in the positioning of the respiratory organs towards the midline. Only the extreme displacement and fusion of the outer lamellae at the midline, as seen in *Apistomyia*, is useful as a defining autapomorphy of that genus (Zwick, 1998). *Apistomyia* shows an extreme reduction in the outer lamellae resulting in low, blunt ridges, an autapomorphy that may be linked to the fusion of the outer lamellae along the midline. Within *Horaia*, little divergence is apparent from the apistomyiine groundplan. In *H. montana*, the outer lamellae are not divergent, but closely set and heavily sclerotized. A similar condition is present, presumably by convergence, in *Austrocurupira*.

Respiratory organs characterized by a straight tracheal opening without an operculum are considered to be plesiomorphic for Blephariceridae (Zwick, 1977). The plesiomorphic condition for the Apistomyiinyi, seen in *Neocurupira, Peritheates, Austrocurupira* and *Theischingeria*, is the presence of an operculum and a U-shaped tracheal opening. In *Nothohoraia, Curupirina* and *Neocurupira*, the tracheal opening is modified into a Y-shape (Zwick, 1998; B. R. Stuckenberg, personal communication, Natal Museum, Pietermaritzburg, South Africa). In *Parapistomyia, Apistomyia* and *Horaia*, character reversal has resulted in a loss of the operculum and a straight tracheal opening (B. R. Stuckenberg, personal communication). The closely set lamellae of *H. montana* make the tracheal opening appear to have an irregular pattern, yet this is only a slight variation on the simple slit seen in other *Horaia*.

The groundplan for the larvae of Blephariceridae includes prolegs on abdominal segment VII and eversible, crochettipped prolegs in the first instar (Courtney, 1990, 1991). This groundplan is seen in the more primitive apistomyiine genera *Neocurupira* and *Peritheates* (Zwick, 1981). Other plesiomorphic larval conditions for the Apistomyiinyi (as seen in *Neocurupira* and *Peritheates*) include an anal division lacking demarcation between the lateral and posterior margins, bearing numerous setiform sensilla along the posterior margin. An increased number of gill filaments represents a convergent character (Zwick, 1977).

Modification of the crochet-tipped prolegs of the first instar larva into seta-tipped prolegs is a synapomorphy of all Apistomyiinyi, excluding *Neocurupira* and *Peritheates*. In *Austrocurupira* and *Theischingeria*, the modification is carried further and the prolegs terminate in aseose, sclerotized plates (Zwick, 1998). In all instars, reduction of the seventh pair of prolegs to a pair of small protuberances or setae is synapomorphic of apistomyiine genera, excluding *Neocurupira* and *Peritheates*. Although many *Apistomyia* and *Parapistomyia* demonstrate the presumed plesiomorphic condition, the absence of setiform sensilla along the posterior margin of the anal division is considered to be synapomorphic of the Apistomyiinyi exclusive of *Neocurupira* and *Peritheates*. Other modifications of the anal division include a square- to paddle-shaped and marked demarcation between the lateral and posterior margins, a shape considered to be synapomorphic of most *Horaia*. The anal division is modified further in *H. montana*, which may reflect the trend towards the larva’s distinct chiton shape. *Nothohoraia* has a similar larval form, albeit presumably via convergence (Zwick, 1977).

Larval mouthparts, particularly the maxillary palpi, indicate a close relationship between *Apistomyia* and *Horaia* (Courtney, 2000a). The plesiomorphic condition for Blephariceridae is a maxillary palpus with nine to ten distinct sensilla, the ‘F’ sensillum comprising one or two broad plates. In *Theischingeria, Apistomyia, Parapistomyia* and *Horaia*, the ‘F’ sensillum is subdivided into a series of sensilla (Fig. 60).

Zwick (1977), in proposing the only previous phylogeny for Apistomyiinea genera (Fig. 84), stated that, although *Apistomyia* and *Horaia* share morphological characters, the closest sister group to *Horaia* is most likely *Austrocurupira* on the basis of the condition of the adult labium, the base of which is split for over half its length. This must be convergence, as our proposed phylogeny (Figs 85; 86) indicates that *Horaia* is a monophyletic genus with *Apistomyia + Parapistomyia* as its sister group (in accordance with Zwick, 1998, we consider the genus *Hamatorrhina* as part of *Apistomyia*). Other differences from Zwick’s (1977) phylogeny include the establishment of *Nothohoraia* as sister group to *Neocurupira + Curupirina* on the basis of the shape of the tracheal opening in the pupal respiratory organs. Although bootstrap support was weak, our analysis suggested *Theischingeria* as the sister group to *Austrocurupira*, based primarily on the modification of the first-instar prolegs. Furthermore, the *Theischingeria + Austrocurupira* clade is proposed as sister group to the (*Apistomyia + Parapistomyia + Horaia*) clade, with the five genera defined primarily by the enlarged antennal scape and pedicel.

Within the genus *Horaia*, relationships are not fully resolved because of a lack of all life stages for some species. Synapomorphic reduction of the adult maxillary palp is defined *Horaia* exclusive of *H. namtoki* and *H. manaliella*. The placement of *H. longipes* is uncertain because of a lack of knowledge about genitalia, larvae and pupae.

**Biogeography**

The distribution and life history of Blephariceridae have presented a challenge to systematists seeking to draw biogeographical conclusions. Blephariceridae are limited to specific habitats and do not survive for long when removed from riparian corridors. Consequently, local distribution can be explained primarily by past movement along land routes, and the family could have persisted only in and around mountain streams (Tillyard, 1922). A single example exists of a species present on non-continental islands: *Paltostoma schineri* Williston, present on Caribbean islands (Scott, 1915; Stuckenberg, 1969). Their poor capacity for dispersal makes Blephariceridae particularly useful in biogeographical studies (Zwick, 1981).

Blephariceridae probably originated in the Southern Hemisphere and moved north (Tillyard, 1922). The Edwardsininae are limited to Australia, southern South America and Madagascar, a relicual Gondwanan distribution.
(Zwick, 1977). The Blepharicerinae are more widespread, with each tribe endemic to specific zoogeographical zones. The Blepharicerini are Holarctic and Oriental, the Paltostomatini are found in South Africa and the Neotropics, and the Apistomyiini are restricted to the Palearctic, Oriental and Australasian regions.

The presence of plesiomorphic endemics in New Zealand is not uncommon amongst the Diptera (Brundin, 1967). The most basal members of the Apistomyiini (Neocurupira, Peritheates, Curupirina, Nesocurupira and Nothohoraria) are confined to New Zealand and New Caledonia (Zwick, 1977, 1981), whereas derived genera are found in Asia, Europe, New Guinea and Australia. Stuckenberg (1969) and Craig (1969) suggested that the Apistomyiini originated in Asia. According to this hypothesis, the present distribution of the Apistomyiini is the product of radiation in Asia and subsequent waves of colonization into the Australasian region via land bridges. The Asian origin hypothesis matches Ross’s (1956, 1967) conclusions about the radiation of Trichoptera into Australia.

Our results are in accord with Zwick’s (1977, 1981) Antarctic origin hypothesis: the Apistomyiini are a subgroup of a Neotropical branch of Paltostomatini. This branch split with Paltostomatini whilst South America and New Zealand remained connected via Antarctica. Apistomyiines then spread into Asia via New Caledonia. As this continuous landmass was split, ancestral genera were isolated (Zwick, 1977). The new placement of Nothohoraria as sister group to Curupira + Nesocurupira adds strength to this argument. Within Asia, a radiation into the present genera Apistomyia, Parapistomyia and Horia occurred. Whether Theischingeria + Austocurupira represent isolated ancestral genera or a product of radiation in Asia is unclear. Subsequent to these radiations, Horia remained within Asia, whereas Apistomyia spread west to Europe, east to Japan and south to New Guinea and Australia. Parapistomyia is present only in New Guinea and Australia, making it likely that the split with Apistomyia took place after departure from Asia.

The biogeography of the Horia is difficult to ascertain. The most widespread species is H. montana, but it is also the most derived, and its present distribution may be a product of extreme range expansion. The basal species, H. manaliella and H. namtoki, are limited to Nepal and Thailand, respectively, but these may be relict populations. Certainly, a lack of specimens of all species and genera, particularly from the mountainous regions of south and south-east Asia, hampers any attempts to draw conclusions about species range.

Supplementary material

The following material is available online at www.blackwell-synergy.com under DOI reference doi:10.1111/j.1365-3113.2006.00360.x

S1. Supplementary material-additional distributional data.

Acknowledgements

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References


Courtney, G.W. (2000b) Revision of the net-winged midges of the genus Blepharicera Macquart (Diptera: Blephariceridae) of


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Appendix: phylogenetic characters and matrix

See text for full descriptions of characters and states.

**Adult**

1. R₄₋₅ vein: straight basally (0); sinuous throughout length (1).

2. A₁ vein: extending well beyond anal angle (0); ending at anal angle (1).
3. Female mandibles: present (0); absent (1).
4. Labrum: normal, broad (0); reduced, slender (1).
5. Maxillary palpi: normal (0); with sense organs (1).
6. Maxillary palpi: three or more segments (0); two segments (1); one segment (2).
7. Maxillary palpi: elongate, cylindrical (0); short, globular (1).
8. Scape and pedicel: slender, subequal in width to flagellomeres (0); expanded, twice as broad as flagellomeres (1).
9. Female front femora: normal (0); with anterodorsal row of dark setae (1).
10. Female accessory glands: globular, indistinct (0); distinct, elongate, tapered (1).
11. Male dorsal paramere: uniform plate (0); basal half with bilobate opacity (1).
12. Prementum: short, with distinct median carina (0); enlarged, with reduced median carina (1).
13. Basal segment of labial palpi: separate, unmodified (0); joined longitudinally and forming a dorsal channel in which the syntrophium resides (1).
14. Apical segment of labial palpi: short, without pseudotracheae (0); elongate, with pseudotracheae (1).

**Pupa**

15. Abdominal tergites VII and VIII: separate (0); fused medially (1).

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**Character matrix**

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