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The monophyly of the Glaurocarini (Diptera: Tachinidae: Tachininae) with the description of a new species of *Semisuturia* from Australia

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Abstract

The Glaurocarini are a small Old World tribe of tachinids belonging to the subfamily Tachininae. Two genera are currently recognized, *Glaurocara* Thomson with 16 species and *Semisuturia* Malloch with eight species. In this study we describe *Semisuturia moffattensis* Inclán, O'Hara, Stireman & Cerretti sp. n. from Queensland and New South Wales and compare it with congeners as well as other glaurocarines. The new species is readily identifiable among world glaurocarines by having a row of setae on lower 2/3 of facial ridge. We further evaluate the monophyly of the Glaurocarini on the basis of morphological characters of both adult and larval stages. A molecular phylogenetic analysis also supports monophyly of the tribe but does not support a close relationship between Glaurocarini and Ormiini as has been suggested previously. Finally, we provide new morphological evidence from both adults and first instar larvae to support the monophyly of both *Semisuturia* and *Glaurocara*.

Keywords

CAD gene; morphology; phylogenetics; first instar larva; Ormiini; parasitoid; systematics

Introduction

The Glaurocarini are a small Old World tribe of mostly pale-coloured tachinids belonging to the subfamily Tachininae. Two genera are recognized, *Glaurocara* Thomson, 1869 and *Semisuturia* Malloch, 1927. *Glaurocara* is known from 16 species, 10 in

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the Afrotropical Region (where the genus is widespread; O'Hara & Cerretti 2016), four in the Oriental Region (Singapore and Malaysia; Crosskey 1976, 1977), and two in the Palaearctic Region (southern Russian Far East and Korean Peninsula; Richter 1988, 2004). *Semisuturia* is known from eight species, three in the Oriental Region (Malaysia and maritime Southeast Asia; Crosskey 1976, 1977) and five in the Australasian Region (eastern Australia; Cantrell & Crosskey 1989). *Semisuturia* was treated as a junior and invalid synonym of *Doddiana* Curran, 1927 in the Oriental works of Crosskey (1976, 1977), but became the valid name for the genus when *Doddiana* Curran was discovered to be a junior homonym of *Doddiana* Turner, 1902 (Lepidoptera: Pyralidae) (Cantrell 1988; Cantrell & Crosskey 1989). Özdikmen (2007) proposed *Currana* as a replacement name for the preoccupied *Doddiana* Curran, presumably unaware that *Semisuturia* has priority as a well-established synonym of *Doddiana*. Crosskey (1962) published a key to the Oriental species of *Semisuturia* (as *Doddiana*) and *Glaurocara*.

Glaurocarines are generally rarely collected and poorly represented in collections and this may be due in part to the nocturnal and/or elusive behavior observed for some of them (cf. Crosskey 1973, 1976; authors observations). It is thus not surprising that very little is known about the natural history of glaurocarines. *Glaurocara flava* Thomson has been reared from the katydid *Ruspolia differens* (Serville) (Orthoptera: Tettigoniidae: Conocephalinae) and its ovipositional behavior and larval instars have been carefully described (Crosskey 1965, 1984). More recently, a specimen of an unidentified *Glaurocara* species (cf. *flava*) (Fig. 1) emerged from the penultimate male nymph of *Acilacris incisus* Naskrecki (Tettigoniidae: Meconematinae), collected in Mozambique (Sofala, Gorongosa N.P., Mt. Gorongosa, southern slope (–18.462417, 34.053139) 18–20.vi.2012, adult parasitoid emerged 26.vii.2012); interestingly the katydid remained alive for a few hours after the emergence of a mature larva of *Glaurocara* (P. Naskrecki pers. comm. 2016). Only a single host is known for *Semisuturia*, that being the spotted stem borer *Chilo sacchariphagus* (Bojer) (Lepidoptera: Crambidae) that is parasitized by *S. mellea* (Wiedemann) in Java (Crosskey 1976). There was an unsuccessful attempt to introduce this fly into Mauritius to control this same pest (Ghani 1962; Ghani & Williams 1963; Crosskey 1976). It is intriguing to wonder how such closely related tachinids have shifted hosts from katydids to moths (or vice versa); yet this plasticity characterizes the developmental strategy of several lineages of Tachinidae, especially among the Exoristinae and Tachininae (cf. Cerretti et al. 2014).

Tachinids are generally understudied in most regions despite their high diversity worldwide (Stireman et al. 2006; O'Hara 2008). Australia in particular has a tachinid fauna that is estimated to be many times larger (3500–4000 species, O'Hara et al. 2004) than the approximately 520 currently recognized species (Ginn 2012). This paper describes a new Australian species of *Semisuturia* that is noteworthy because its bristled facial ridge is unusual among Glaurocarini (see Cantrell 1988:102) and Tachininae in general, and has posed the issue of re-circumscribing the tribal and generic limits. The concept of *Semisuturia* is discussed in relation to that of its sister taxon *Glaurocara* and the monophyly of the Glaurocarini is reanalysed.

Fig. 1. Live specimen of *Glaurocara* sp. (cf. *flava* Thomson) from Gorongosa National Park, Mozambique (image courtesy of P. Naskrecki).

Material and Methods

Specimens

Male terminalia were dissected and prepared for examination following the methods described by Cerretti & Pape (2012). Composite focus-stacking images were produced from multiple images captured using a Nikon DS-L1 digital camera (Nikon, Tokyo, Japan) mounted on a Leica MZ12.5 stereomicroscope (abdomen, habitus, head and wing) or on a Leica DMLS compound microscope (terminalia) (both microscopes: Leica, Wetzlar, Germany), and processed with CombineZM (http://combinezm.software.informer.com/). First instar larvae were extracted from the female abdomen after having been treated with 10% KOH, dehydrated with Xylene following treatment with Ethyl Cellosolve on a slide, and then mounted with Euparal, except those of Fig. 5F–H which were preserved in glycerin. Images of the larvae in Figs. 6, 8F–G and 9 were taken with a Nikon 1 J2 digital Camera (Nikon) attached to a Nikon Optiphot microscope; other larval images were taken using the same equipment as for the male terminalia. Uncoated first instars of *S. moffattensis* sp. n. were examined with a Hitachi TM1000 environmental scanning electron microscope (ESEM).

Information for each specimen label is given verbatim. Data from each line is separated by a diagonal slash and a space (/#) and data from each label is enclosed in quotation marks.

Repositories of specimens are given in square brackets using the following acronyms:

ANIC	Australian National Insect Collection, CSIRO, Canberra, ACT, Australia
CNC	Canadian National Collection of Insects, Ottawa, ON, Canada
JOSC	J.O. Stireman collection at Wright State University, Dayton, OH, USA
KUM	Kyushu University Museum, Kyushu University, Fukuoka, Japan
MZUR	Zoological Museum, 'Sapienza' University of Rome, Rome, Italy
TAU	Department of Zoology, Tel Aviv University, Tel Aviv, Israel

Terminology

Morphological terminology follows Cumming & Wood (in press).

Genetic data and phylogenetics

Sequences of the 5' end of the CAD gene (regions 1 and 2; Moulton & Wiegmann 2004) were obtained for ten tachinid taxa, including three Glaurocarini (Table 1). The remaining "outgroup" taxa were chosen from among other Tachininae based on a preliminary phylogenetic analysis of more than 300 tachinid taxa from an ongoing project to reconstruct the phylogeny of the Tachinidae (e.g., see Winkler et al. 2014). Sequences were obtained using the primers, DNA extraction/amplification protocols, and sequencing facility described in Winkler et al. (2015). Sequences were edited using CodonCode Aligner 3.5 (CodonCode Corporation, Dedham. MA, USA) and aligned using ClustalW (Larkin et al. 2007) implemented in MEGA 6.0 (Tamura et al. 2013). An intron of length ca. 50–80 bp was omitted from the final data set due to difficulty in inferring homology. Final aligned sequence lengths ranged from approximately 750 bp (region 1) to 1500 bp (regions 1 and 2; see Table 1). Maximum Likelihood (ML) phylogenetic analyses were conducted in RAxML (Stamatakis 2014) implemented via the CIPRES Science Gateway (Miller et al. 2010; https://www.phylo.org). ML analyses used a GTR+I+G model of nucleotide substitution with sites partitioned by codon position. We also performed a ML analysis of the translated amino acid alignment using a JTT matrix model of amino acid substitution. Trees were evaluated with 1000 bootstrap replicates. *Nemoraea* sp. (nr. *pellucida* (Meigen)) was used as an outgroup. Parallel phylogenetic analyses were conducted in MEGA 6.0 using Neighbor Joining and Maximum Parsimony (SPR, 10 initial random addition replicates, 1000 bootstraps) to confirm results of ML analyses.

Taxonomic account

Semisuturia moffattensis Inclán, O'Hara, Stireman & Cerretti sp. n.

Type material. Holotype male: "Australia Queensland/ Carnarvon N.P. 1060 m/ Mount Moffatt, summit/ 25°03.47′S 148°02.66′E/ 13 December 2013 P. Cerretti" (ANIC). Paratypes: 6 males, same data as holotype (1 CNC, 5 MZUR); 10 additional males from the same locality but labelled as: "AUSTRALIA, QLD. (Queensland)/

Table 1. Tachinid taxa of the subfamily Tachininae for which the CAD gene was sequenced for phylogenetic analyses.

Tribe	Species	ID	Locality	GenBank accession No.
Ernestiini	*Brachelia westermanni* (Robineau-Desvoidy)	T682	South Africa: Western Cape, Swartberg Pass, 897 m (33°17.546′ S, 22°03.022′ E), 16 October 2012	KX833254
Ernestiini	*Chlorotachina flaviceps* (Macquart)	T801	Australia: Queensland, Conondale N.P., Mt. Allan (26°38.39′ S, 152°38.07′ E) 19 December 2013	KX833256
Ernestiini	*Chlorotachina* nr. *froggattii* (Townsend)	T819	Australia: Queensland, Mt. Moffat Rd. NW of Injune (25°17.5′ S, 148°0.3′ E), 10 December 2013	KX833260
Ernestiini	*Triarthria setipennis* (Fallén)	T037/T052	USA: California, Santa Cruz Co. UC Santa Cruz (36°59.5′ N, 122°03.5′ W), 13 July 2005 USA: California, Santa Cruz Co. Meder St. (36°58.5′ N, 122°03.6′ W), 13 July 2005	KX833263
Ernestiini?	New genus, n. sp.	T811	Australia: Queensland, Carnarvon NP, Mt. Moffat Section, Fly Hill (24°58.35′ S, 147°59.63′ E), 11 December 2013	KX833255
Glaurocarini	*Glaurocara flava* Thomson		Uganda: Kabanyoro, University Farm (00°27.52′ N, 32°36.13′ E), ex. *Ruspolia differens*, host collected December 2015	KX833257
Glaurocarini	*Semisuturia* nr. *pallens* (Curran)	T797	Australia: Queensland, Conondale N.P., Mt. Allan (26°38.39′ S, 152°38.07′ E), 19 December 2013	KX833259
Glaurocarini	*Semisuturia moffattensis* Inclán et al.	T806	Australia: Queensland, Carnarvon NP, Mt. Moffat Section, Mt. Moffat (25°3.47′ S, 148°2.65′ E), 13 December 2013	KX833258
Nemoraeini	*Nemoraea* cf. *pellucida* (Meigen)	T559	South Korea: Gyeongsangbuk-do, Taegu, Palgongsan Mtn. Park (36°03.2′ N, 128°37.8′ E), 22 August 2012	KX833261
Ormiini	*Ormia* n. sp.	T250	USA: Arizona, Pima Co. Santa Rita Mts., Box Cyn (31°48.1′ N, 110°45.6′ W), 12 August 2007, 1550 m	KX833262

For *Triarthria*, two specimens were sequenced to obtain the full gene fragment.

Carnarvon NP, Mt Moffat/ sec. (Section) Mt Moffat 25°3.47′S/ 148°2.65′E 13 December 2013./ Stireman & Winkler" (JOSC); 1 female: "Australia QLD/ Brisbane Forest Park/ 27°25′05″S 152°50′13″E/ 13–19.vi.1998 N. Power/ MT #4 across creek" (CNC); 1 male: "Australia Queensland/ Great Sandy N.P. (National Park)/ nr. (near) Freshwater Lake/ campgrd. (campground), hilltop/ 26°00.3′S 153°09.0′E/ 7.x.2002 J.E. O'Hara" (CNC); 1 female: "Australia Qld/ Great Sandy Nat. Pk/ Freshwater Camp/ 7/10.x.02 G.&M. Wood" (CNC); "Australia QLD/ Mt. Glorious 27°19′54″S/ 152°45′29″E 3–9.i.1998/ T. Hiller, MT" (CNC).

Etymology. The specific epithet derives from the type locality Mount Moffatt and should be treated as a Latin adjective.

Recognition. *Semisuturia moffattensis* is readily distinguished from congeners by having (i) facial ridge straight, 1.25–1.30 times as long as length of frons, with a row of robust setae on lower 2/3 (Fig. 2C), (ii) antenna entirely yellow (Fig. 2C), (iii) abdomen yellow with a small black posteromedian spot on tergite 5 (Fig. 2L), and (iv) bend of M_1 at a right angle (a very short M_2 appendix may be present in some specimens) (Fig. 2G, H).

Description. Body length: 4.2–5.8 (5.4) mm.

Male (measurements in parentheses refer to the holotype)

Coloration (Fig. 2A). Head light yellow, except ocellar triangle which is brownish. Fronto-orbital plate and parafacial covered with a thin layer of whitish microtomentum. Upper part of occiput brown, covered with light microtomentum. Antenna yellow with a brownish arista that is paler in the thickened portion of third aristomere (Fig. 2C). Thorax (including legs and scutellum) yellow, without microtomentum. Tegula and basicosta yellow. Wing membrane hyaline, veins basally yellowish, shading into light brown apically (Fig. 2G). Haltere yellow. Abdomen yellow with a small black posteromedian spot on tergite 5 (Fig. 2L).

Head (Fig. 2C, E). Head distinctly higher than long, height of facial ridge (measured in lateral view from base of vibrissa to ventral margin of antennal scape) 1.25–1.30 times as long as length of frons (measured in lateral view from dorsal base of antennal scape to base of inner vertical seta). Compound eye covered with short, scattered ommatrichia (barely visible under high magnification), as long as three eye facets or slightly longer. Ocelli present; ocellar setae well-developed, proclinate. Frons at its narrowest point 0.6–0.7 (0.66) times as wide as compound eye in dorsal view. Outer vertical seta not differentiated from postocular setae. Six or 7 frontal setae descending to upper or lower margin of antennal pedicel. Frontal setae medioclinate, rarely crossed medially. Fronto-orbital plate with sparse short hair-like setae (Fig. 2E). Upper reclinate and proclinate orbital setae absent. Parafacial bare below lower frontal seta. Parafacial at its narrowest point 0.50–0.61 (0.54) times as wide as width of postpedicel at mid-length. Facial

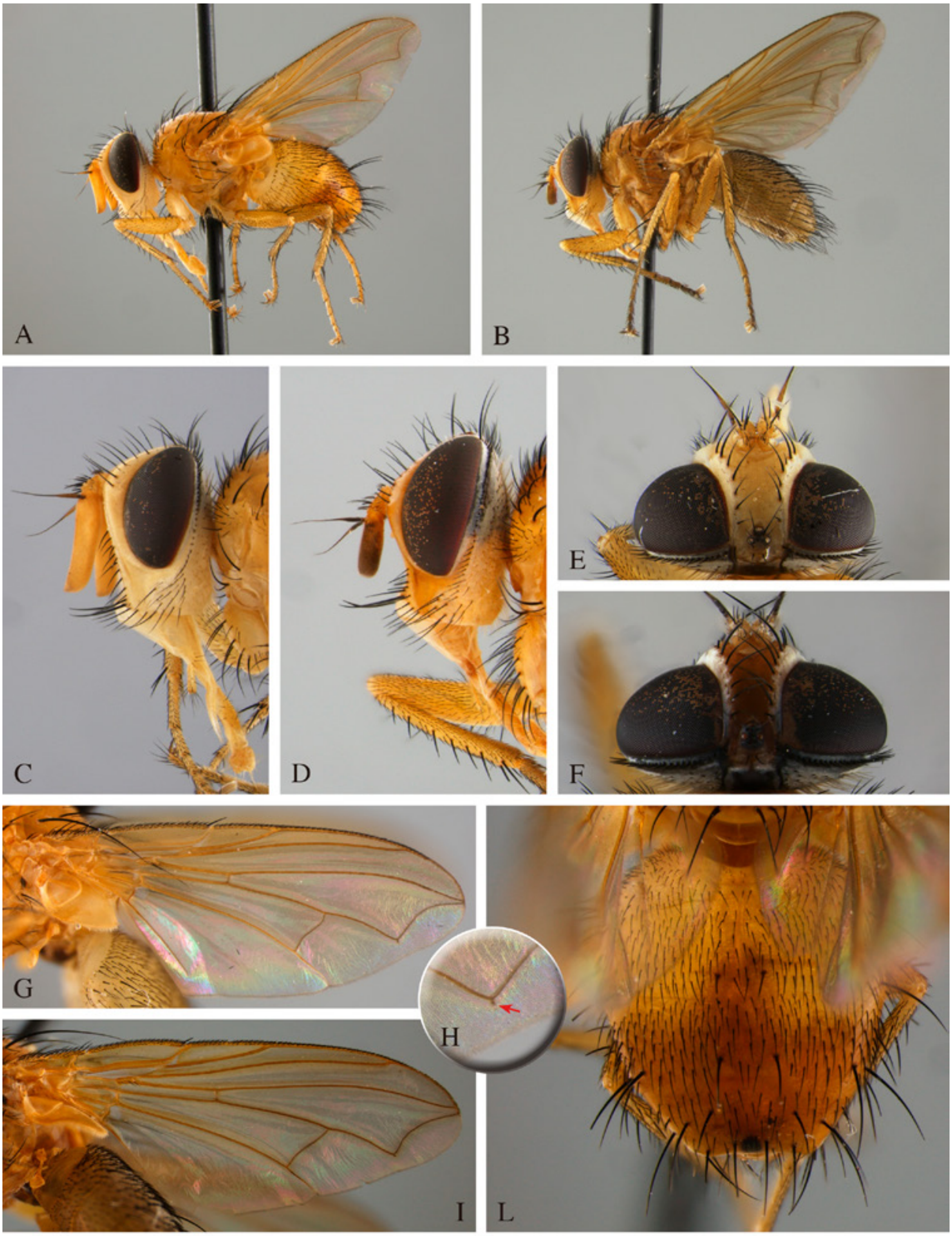

Fig. 2. Males of *Semisuturia* spp. (A) *S. moffattensis* sp. n., habitus (holotype, ANIC); (B) *S. parviseta* (Malloch) (Australia, Queensland, MZUR), habitus; (C) *S. moffattensis* sp. n., head in lateral view (paratype, MZUR); (D) *S. parviseta*, head in lateral view; (E) *S. moffattensis* sp. n., head in dorsal view (paratype, MZUR); (F) *S. parviseta*, head in dorsal view; (G) *S. moffattensis* sp. n., wing (holotype), H. Detail of bend of M_1 of Fig. G (red arrow indicates M_2 appendix); (I) *S. parviseta*, wing; (L) *S. moffattensis* sp. n., abdomen (holotype).

ridge straight with a row of robust, decumbent setae on lower 2/3. Vibrissa arising at about level of lower facial margin. Lower facial margin clearly visible in lateral view. Genal dilation well-developed and covered with black setae, often with one or more setae that are distinctly larger than the rest. Postgena and lower occiput with pale setae only. Upper half of occiput with or without black setae behind postocular row. Gena 0.39–0.47 (0.40) times as high as compound eye in lateral view. Postpedicel 4.30–5.01 (4.55) times as long as pedicel; postpedicel more or less sharply pointed dorsoapically. Arista short pubescent (i.e., microtrichia at most as long as maximum basal diameter of arista), thickened approximately on basal 1/3–1/4. First aristomere distinctly shorter than wide; second aristomere about as long as wide (or slightly shorter). Prementum 3–4 times as long as wide. Palpus very short, less than 1/2 the length of the prementum, subcylindrical or very slightly clavate, with long setae on distal third.

Thorax. Prosternum and proepisternum bare. Postpronotum with 3 (rarely 2) setae arranged in a shallow triangle (ca. 120–160°). Scutum with 1 posthumeral seta; 2 presutural and 3 postsutural acrostichal setae (first postsutural seta shorter); 2 presutural and 3 postsutural dorsocentral setae; 1 presutural and 3 postsutural intra-alar setae (first postsutural sometimes hair-like); 2 strong postsutural supra-alar setae (i.e., first postsutural supra-alar seta absent); second postsutural supra-alar seta 2–3 times as long as posterior notopleural seta; two notopleural setae and 1–2 postalar setae. Two katepisternal setae. Katepimeron bare. One strong anepimeral seta. Scutellum with 4–6 pairs of (often asymmetrical) marginal setae: 1 basal; 1–4 (1 only in holotype) laterals, 1 subapical, apical absent. One pair of discal scutellar setae. Central part of dorsal surface of scutellum covered with short, black hair-like setae. Anatergite bare below lower calypter. Upper and lower calypters well-developed. Second costal sector ventrally setose. Costal spine about as long as crossvein r-m. Vein R_{4+5} with only a few setae at base. Bend of vein M_1 at a right angle (Fig. 2G), in some specimens with a very short M_2 appendix (Fig. 2H) about 1/3–1/4 times as long as crossvein r-m. Sector of M_1 between crossveins r-m and dm-m 1.00–1.64 (1.47) times as long as sector between dm-m and bend of M_1. Cell r_{4+5} narrowly open at wing margin. Preapical anterodorsal seta of fore tibia distinctly longer than preapical dorsal seta. Mid tibia with 1 strong anterodorsal seta. Hind tibia with 2 dorsal preapical setae. Preapical posteroventral seta of hind tibia shorter than preapical anteroventral seta. Anterodorsal setae on hind tibia of irregular size (i.e., not arranged in a comb-like row). Posterodorsal margin of hind coxa bare.

Abdomen (Fig. 2L). Mid-dorsal depression of syntergite 1+2 extending to within 1/8 of posterior margin of syntergite. Tergites fused along dorsal midline (a characteristic of glaurocarines). Tergites 3 and 4 each with 1 pair of median marginal setae, without median discal setae. Tergite 5 with a row each of marginal and discal setae; tergite 5 0.90–1.00 (0.97) times as long as tergite 4 measured at mid-length. General setae on tergite 5 more or less erect. Sternite 4 only barely visible.

Male terminalia (Fig. 3A–B, 4A–C). Epandrium broad, short and convex with the anterior epandrial process narrowly developed and lateral epandrial lobe well-developed.

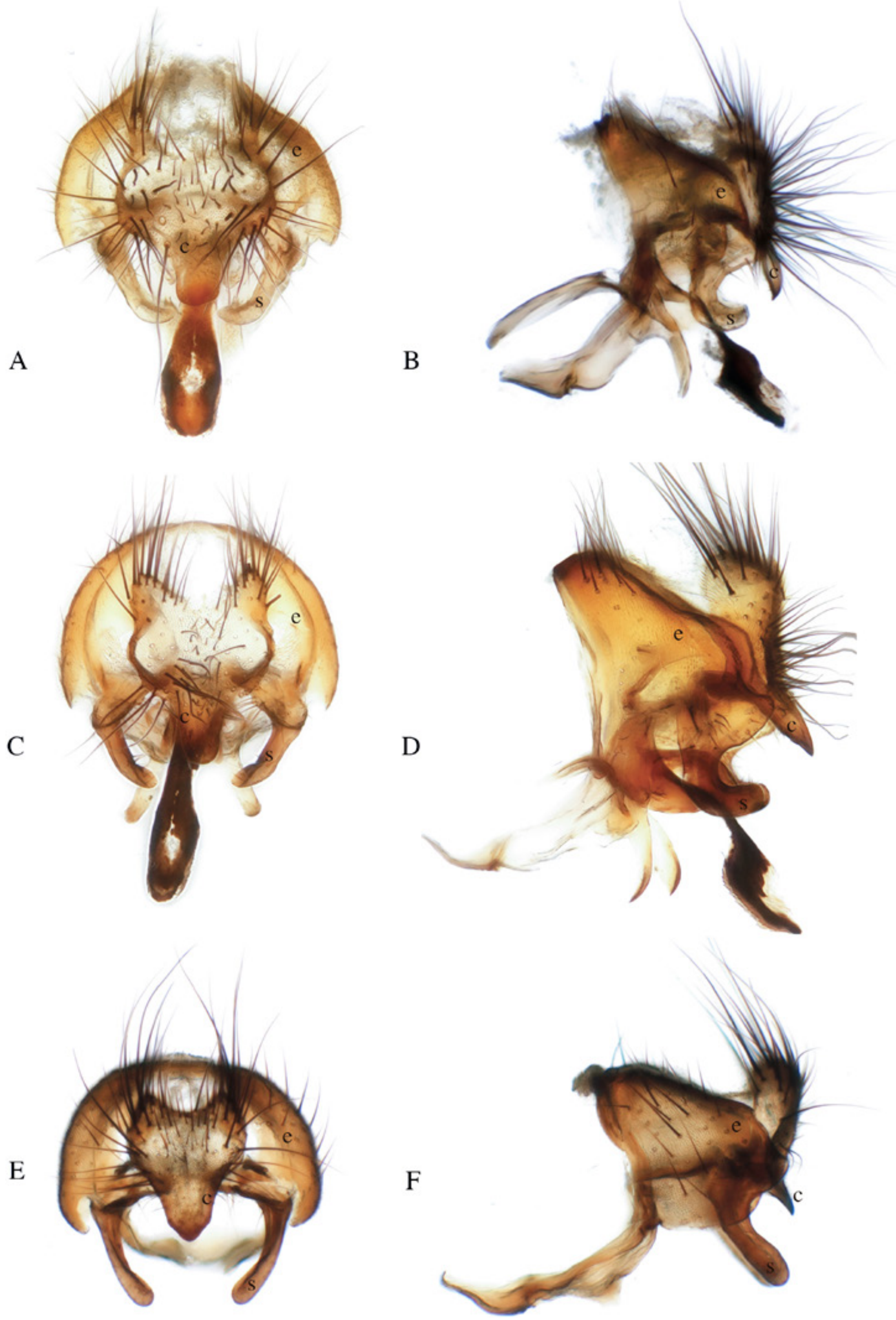

Fig. 3. (A–B) *Semisuturia moffattensis* sp. n., male terminalia (paratype, MZUR): (A) Posterior view; (B) Lateral view. (C–D). *S. parviseta* (Malloch), male terminalia (Australia, Queensland, MZUR); (C) Posterior view; (D) Lateral view. (E–F) *Glaurocara flava* Thomson (South Africa, MZUR), male terminalia: (E) Posterior view; (F) Lateral view. Abbreviations: c, cerci, e, epandrium, s, surstylus.

Cerci medially fused into a syncercus; with a medial patch of rather long setae; basal 2/3 of cerci broad then narrowing towards apex; apical portion of cerci in posterior view lobe-like (Fig. 3A). Cerci, in lateral view, slightly concave with apex slightly hooked ventrally (Fig. 3B). Surstylus, in lateral view, strongly enlarged basally and curved posteriorly, making a "C" shape (Fig. 3B); fused with epandrium on its anterodorsal margin. Hypandrial arms not fused posteromedially. Pregonite well-developed, narrow and tubular in shape. Postgonite well-developed, somewhat hooked in shape. Intermedium present, normally developed. Epiphallus not differentiated. Basiphallus tubular, normally developed, with a well-developed though short dorsobasal extension. Distiphallus slightly longer than basiphallus. Lateroventral region of distiphallus well-developed, strongly sclerotized with robust spines. Medioventral ridge of distiphallus well-developed.

Female

The female differs from the male as follows.

Colouration. Abdomen yellow without black spot on tergite 5.

Head. Height of facial ridge 1.1–1.2 times as long as length of frons. Parafacial at its narrowest point 0.50–0.75 times as wide as width of postpedicel at midlength. Gena 0.30–0.35 times as high as compound eye in lateral view. Postpedicel 3.0–3.6 times as long as pedicel.

Female terminalia. Hemitergite 6 robust with raised posterior ridges, tergites 7 and 8 absent, and syntergite 9+10 reduced and located between the cerci. Hemitergites 6 with strong setae directed medially covering the cerci and sternite 10. Sternites 6 and 7 broad and well-developed, sternite 8 about half as wide as sternite 6, and sternite 10 well-developed. Sternites 8 and 10 covered with several small setae.

First instar (Fig. 5A–H)

Larva with nine sclerotized tergal plates of a dark brown colour (i.e., planidium type), these plates of almost uniform size and covering the entire dorsal and lateral surfaces of segments 3 to 11 (Fig. 5A–B, G). The first and second segments (i.e., head and prothorax) are membranous, very reduced and covered by the sclerotized plate of the third segment (i.e., shield-like plate) (Fig. 5C). Segments 3 to 11 are each covered with a large plate, while segment 12 is covered with two weakly sclerotized hemiplates (i.e., interrupted medioventrally and mediodorsally) before the posterior spiracles (Fig. 5D–F, H). The major segmental plates are distinctly sculptured in a net-like pattern (Fig. 5G). Segment 12 is followed by a pair of small caudal plates (Fig. 5E, F, H). Each hemiplate of segment 12 has a pair of short and fine marginal, whip-like sensillae, one sensilla in a mediodorsal position (barely visible above posterior spiracle in Fig. 5F), and the other in a lateroventral position (Fig. 5E, red arrow). Caudal plates with two pairs of whip-like terminal sensillae, in dorsal and lateroventral positions (Fig. 5D–F). The ventral portion of larva (i.e., the space not covered by plates) is membranous and armed with anterior transverse bands of minute blunt spinules (Fig. 5B).

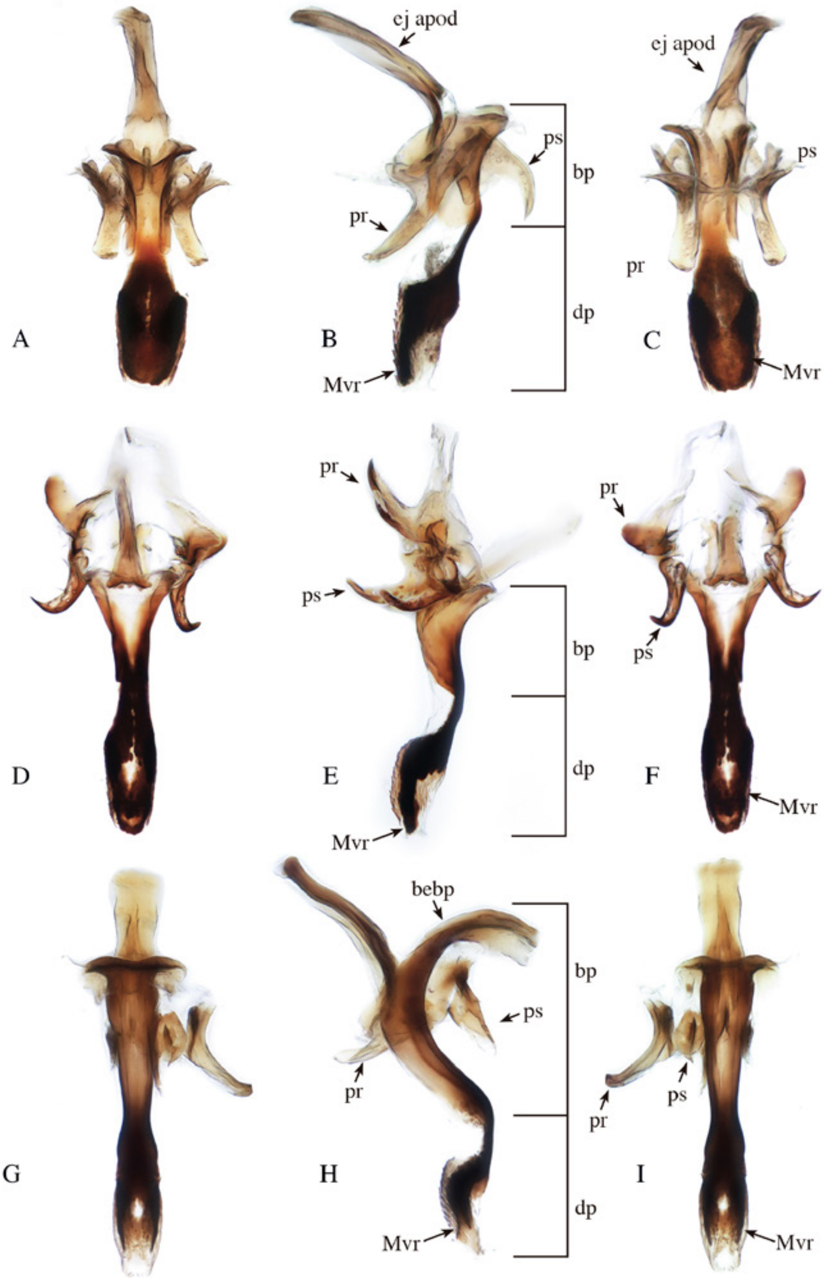

Fig. 4. (A–C) *Semisuturia moffattensis* sp. n., phallus and associated parts (paratype, MZUR): (A) Dorsal view; (B) Lateral view; (C) Ventral view. (D–F) *S. parviseta* (Malloch), phallus and associated parts: (D) Dorsal view; (E) Lateral view; (F) Ventral view. (G–I) *G. flava* Thomson (South Africa, MZUR), phallus and associated parts: (G) Dorsal view; (H) Lateral view; (I) Ventral view. Abbreviations: bp, basiphallus; bebp, basal extension of basiphallus; dp, distiphallus; ej apod, ejaculatory apodeme; Mvr, medioventral ridge; pr, pregonite; ps, postgonite.

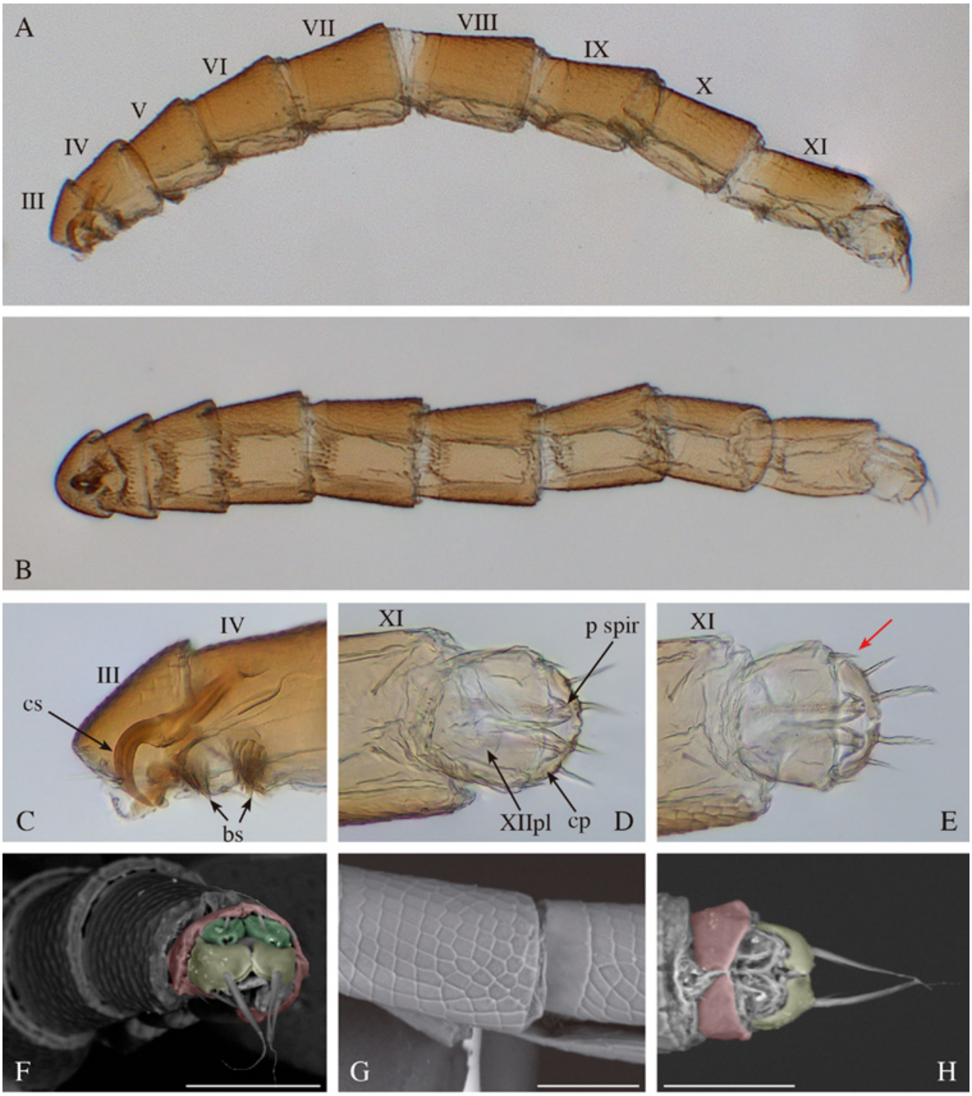

Fig. 5. (A–H) *Semisuturia moffattensis* sp. n., first instar larva (paratype, CNC): (A) Lateral view; (B) Ventral view; (C) Anterior segments and cephaloskeleton in lateral view; (D) Terminal segments in dorsal view; (E) Terminal segments in ventral view (red arrow indicates lateroventral, marginal sensillum of segment 12); (F) Postero-lateral view; (G) Tegumental sculpture in lateral view; (H) Terminal segments in ventral view. Scale bar = 50 µm. Abbreviations: III–XI, Segments 3–11, each covered with a sclerotized plate; XIIpl, hemiplate of segment 12; bs, blunt spinules; cp, caudal plate; cs, cephaloskeleton; p spir, posterior spiracle. Colour coding: green, posterior spiracle; red, hemiplates of segment 12; yellow, caudal plates.

Cephaloskeleton very heavily sclerotized and conspicuous; mouth-hook (labrum) apically pointed and strongly curved into a claw-like shape. Dorsal cornu weakly sclerotized, moderately long and posteriorly pointed; ventral cornu short. Parastomal bars reduced. Cephaloskeleton almost completely enclosed by third segmental plate leaving visible only the mouth-hook (Fig. 5C).

Remarks

Cantrell (1988) gave partial descriptions of two undescribed Australian *Semisuturia* species with a setose facial ridge, as in *S. moffattensis*. The first instar larva of one of them, *Semisuturia* sp. 2, was described and illustrated and resembles the first instar of *S. moffattensis*. It is possible that Cantrell's *Semisuturia* sp. 2 is the same species as *S. moffattensis*.

All specimens from Carnarvon National Park were collected by sweeping a busy swarm of mixed tachinids at the top of a 4.5 m high bush on the peak of Mt. Moffatt.

Identification key to distinguish *Semisuturia* Malloch and *Glaurocara* Thomson

1. Bend of M strongly abrupt. Apical scutellar setae usually present (absent in some specimens of *G. flava* of South Africa). Male: dorsobasal extension of basiphallus very large and well-developed (Fig. 4H). First instar with segments 3 to 11 each covered with a sclerotized dorsal plate and segments 4 to 11 each additionally with 2 lateral plates on each side (Figs. 7, 8) .... *Glaurocara*

– Bend of M moderately abrupt (Fig. 2G–I). Apical scutellar setae absent. Male: dorsobasal extension of basiphallus small (Fig. 4B, E). First instar with segments 3 to 11 each covered with a single large sclerotized plate (Figs. 5, 6) .... *Semisuturia*

Phylogenetic results

Overall, molecular phylogenetic analyses using Maximum Likelihood (ML) resulted in relatively short internodes and low bootstrap support for clades (Fig. 10A, B). The reconstruction using amino acids resulted in somewhat better resolution than the one using nucleotides, but still with low bootstrap support. However, in both trees, the species newly described here groups with *Semisuturia* nr. *pallens* (Curran) with 100% support, rather than with *Glaurocara flava*. In addition, the three members of the Glaurocarini form a well-supported monophyletic group. Note that in neither tree is *Ormia* reconstructed as sister to the glaurocarines, but rather joins the ernestiine *Brachelia* or *Brachelia* + *Triarthria* with low support. Neighbor Joining analysis reconstructed the same tree topology as the more thorough ML analysis of nucleotide data with similar branch support, as did bootstrap consensus trees from the parsimony analysis. In summary, *Semisuturia moffattensis* was always placed sister to the other *Semisuturia* species, the tribe Glaurocarini was always monophyletic, and *Ormia* was never sister to the Glaurocarini.

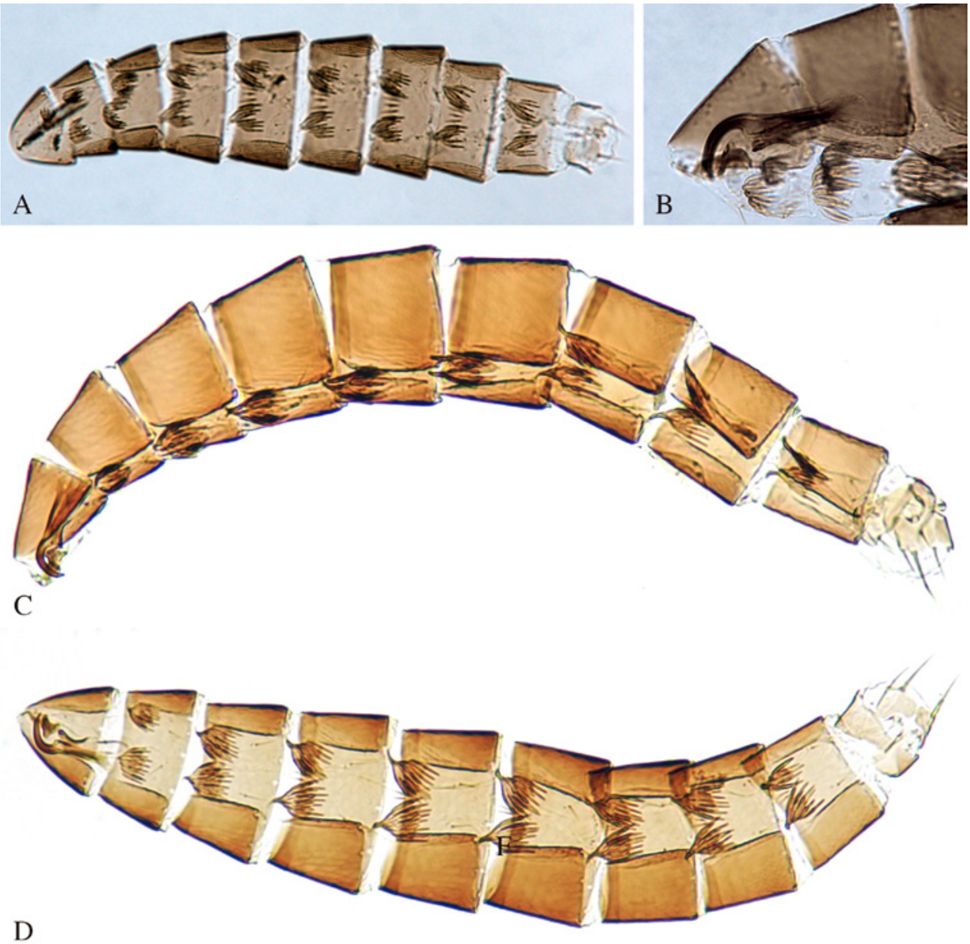

Fig. 6. *Semisuturia* spp., first instar larva. (A–B) *Semisuturia* sp. (Sabah, Malaysia, KUM): (A) Ventral view. (A) Anterior segments and cephaloskeleton in lateral view. (C–D) *Semisuturia* sp. (Viti Levu, Fiji, KUM): (C) Lateral view; (D) Ventral view.

Discussion

The monophyly of the Glaurocarini

The Glaurocarini are thought to be closely related to the Ormiini, with which they share a similar habitus, pale colouration (except for a few dark brown or metallic-coloured *Glaurocara* in the Afrotropics), and other interesting characteristics like a planidial first instar and a dorsobasal extension on the basiphallus. In particular, this last trait has been suggested as a possible synapomorphy supporting monophyly of this group (Tschorsnig 1985). Tschorsnig (1985) and Ziegler (1998) included the glaurocarines in the Ormiini, but O'Hara & Cerretti (2016) kept both the Glaurocarini

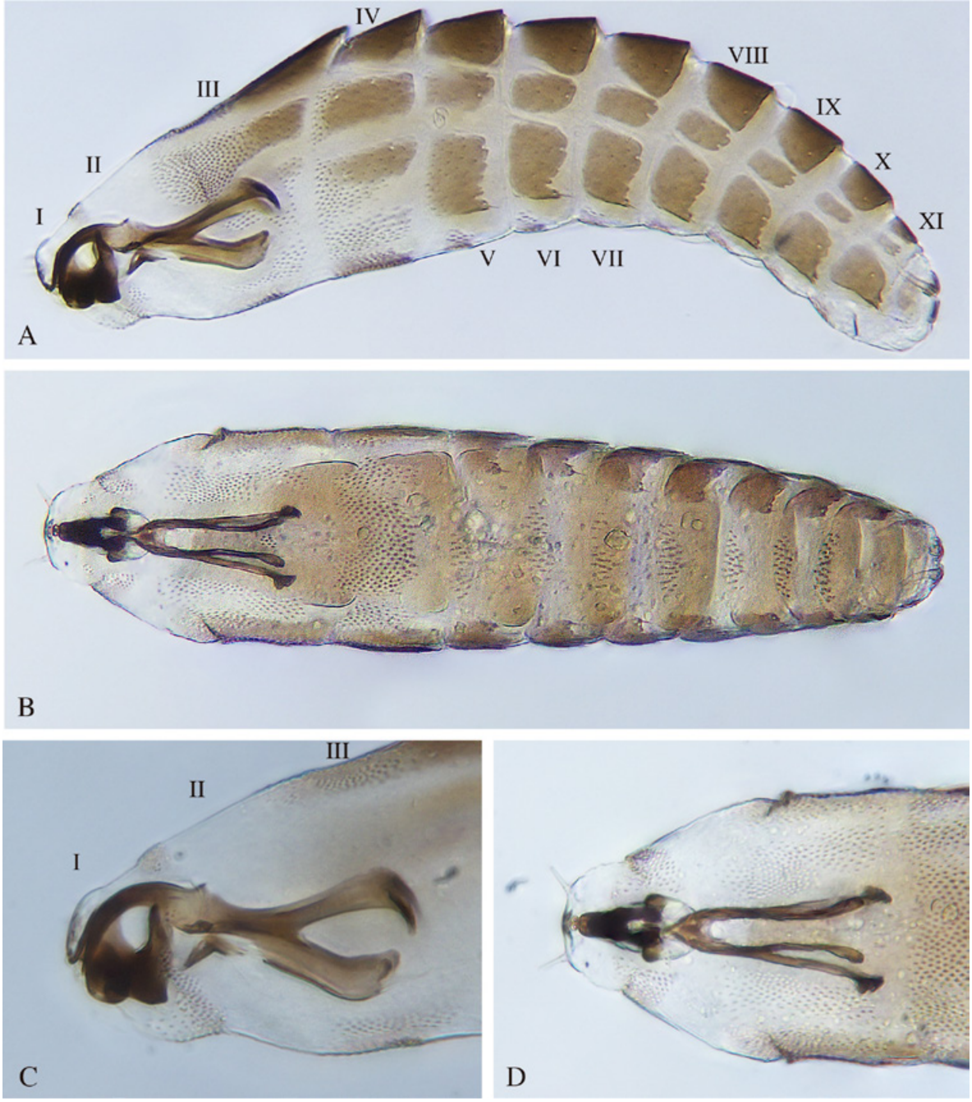

Fig. 7. (A–D) *Glaurocara* cf. *flava* Thomson, first instar larva (South Africa, MZUR): (A) Lateral view; (B) Ventral view; (C) Anterior segments and cephaloskeleton in lateral view; (D) Anterior segments and cephaloskeleton in ventral view.

and Ormiini as separate tribes. Here, we support keeping these tribes based on the following evidence:

1. External characters: The Ormiini are particularly well-supported as a monophyletic group due to the highly derived condition of the prosternum, which is inflated and has evolved into an auditory receptor capable of detecting the mating calls of hosts. In contrast, a remarkable and probably derived feature

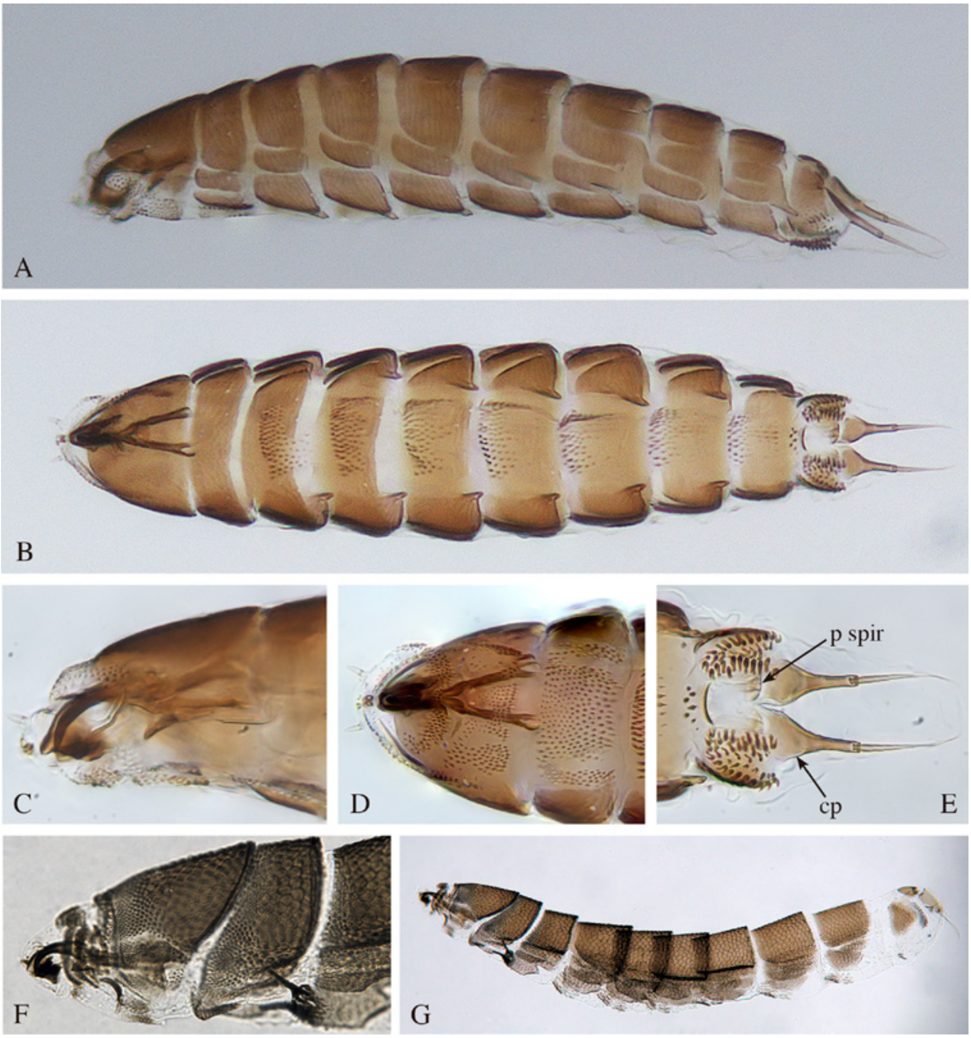

Fig. 8. *Glaurocara* spp., first instar larva. (A–E) *Glaurocara nigrescens* Mesnil (Madagascar, TAU): (A) lateral view; (B) ventral view; (C) anterior segments and cephaloskeleton in lateral view; (D) anterior segments and cephaloskeleton in ventral view; (E) posterior segments in ventral view. (F–G) *Glaurocara* sp. (?*lucidula* Richter) (Tochigi, Japan, KUM): (F) anterior segments and cephaloskeleton in lateral view; (G) lateral view. Abbreviations: cp, caudal plate; p spir, posterior spicacle.

shared by all glaurocarines is the dorsally fused abdominal tergites resulting in the obliteration of the sutures in this area (Fig. 2L). This character state, although independently evolved in distantly related groups (a few Phasiinae and Dexiinae as well as scattered members of the tachinine tribes Ernestiini (including the former Linnaemyini and Loewiini), Bigonichetini, Germariochaetini, Megaprosopini, and possibly others; cf. Crosskey 1973, 1976, 1984;

Tschorsnig & Richter 1998; Cerretti et al. 2012; Cerretti et al. 2014), may represent a homoplasious apomorphy supporting glaurocarine monophyly.

2. Male terminalia: Although Tschorsnig (1985) included *Semisuturia* (as *Doddiana*) and *Glaurocara* in the Ormiini (based on information from the literature), his description of male terminalia appears to be mostly based on ormiine features (p. 97); e.g., (i) hypandrial arms narrow, fused, (ii) pregonite platiform, (iii) and ventral side of distiphallus membranous. These, probably derived, character states are not shared by *Glaurocara* and *Semisuturia* in which the hypandrial arms are separated, the pregonite is lobe- or hook-like, and the distiphallus is sclerotized ventrally (Fig. 4). In particular, the platiform pregonite is a quite rare condition in non-dexiine Tachinidae, having evolved independently in the Acemyini (see Tschorsnig 1985; Cerretti et al. 2014: character 103; Shima & Tachi 2016) and in (at least) some Palpostomatini (cf., Cantrell 1988: 179, Fig. 67; Shima pers. obser). Moreover, the likely synapomorphic epandrial complex of the Glaurocarini is highly divergent from that of the Ormiini. Both *Semisuturia* and *Glaurocara* have the surstylus thickened basally, strongly bent posteriorly (i.e., C-shaped in lateral view) and firmly fused to epandrium (Fig. 3).
3. First instar: The cephaloskeleton of the first instar of glaurocarines and ormiines is quite different. In the Ormiini the apical portion (i.e., the labrum) is broad and rounded in lateral view (as in Tachinini, Ernestiini, and many other Tachininae) and parastomal bars are moderately elongated (Fig. 9A–C), whereas in the Glaurocarini the labrum is sharply pointed and strongly curved downward (claw-like) and the parastomal bars are strongly reduced (Figs. 5–8). In particular, the reduced parastomal bars may represent a strong autapomorphic support for the monophyly of Glaurocarini.

Further support for monophyly of the Glaurocarini is revealed by analyses of nucleotide and amino acid sequence data from the CAD gene. Although Glaurocarini were recovered as a monophyletic group not far from the ormiine genus *Ormia*, the latter never clustered as sister to the former, regardless of inference method (Fig. 10). Similar results have been found in preliminary molecular analyses of several nuclear genes from more than 300 tachinid taxa (Stireman et al., unpublished data). However, we should note that only a small sampling of taxa were included in these analyses and bootstrap support for basal branches in the tree are low. More taxa and data are needed to fully understand the relationships of taxa near the Glaurocarini tribe.

Monophyly of the glaurocarine genera

Within the Glaurocarini, the generic limits of *Semisuturia* and *Glaurocara* have been based on weak morphological characters, namely: the shape and sharpness of bend of M_1 and the chaetotaxy of the scutellum (Crosskey 1962, 1973, 1976, 1984). Crosskey (1962) noted that *Semisuturia* can be distinguished from *Glaurocara* by having the

Fig. 9. (A–C) First instar larvae of other Tachininae, in lateral view: (A) *Aulacephala hervei* Bequaert (Ormiini) (Ryukyus, Japan, KUM); (B) *Therobia* sp. (Ormiini) (Tsusima Is., Japan, KUM); (C) *Tachina luteola* (Coquillett) (Tachinini) (Niigata, Japan, KUM).

bend of M_1 rounded and no M_2 appendix. Although the sharpness of the bend of M_1 may be helpful to identify a glaurocarine specimen to genus level, the presence/absence of a M_2 appendix is clearly variable among specimens of the same genus if not the same species. The second character used by Crosskey (1962) is the presence of apical scutellar setae: absent in *Semisuturia* and present though small in *Glaurocara*. Even

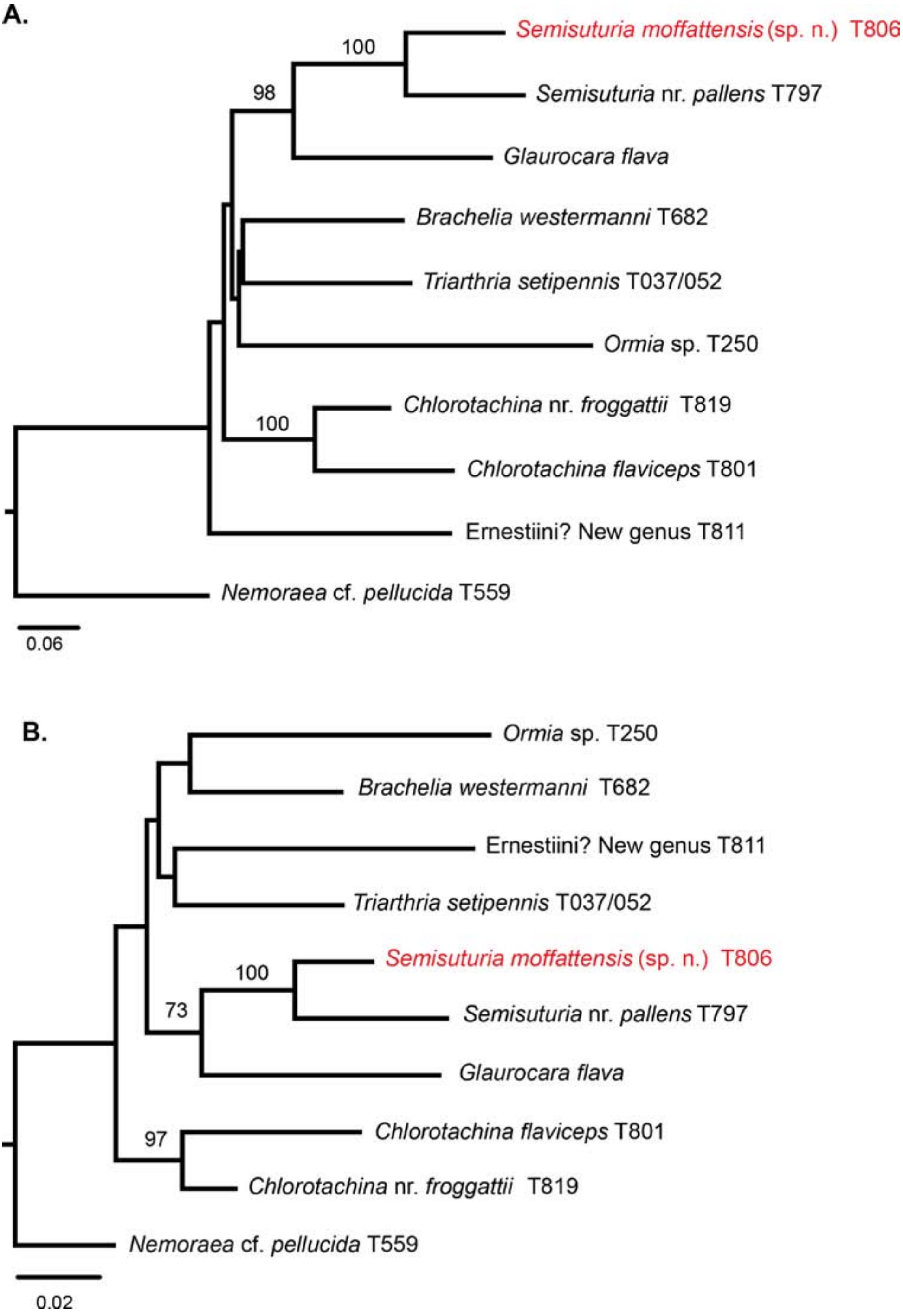

Fig. 10. Maximum Likelihood reconstructions of the Glaurocarini and other Tachininae based on nucleotide (A) and amino acid (B) sequences for the nuclear gene CAD. Numbers above or beside branches indicate percent bootstrap support for branches with >70%.

in this case some specimens of *Glaurocara* (e.g., *G. flava*) lack these setae making the character unreliable.

In this work we found new evidence of both adults (male terminalia) and first instar larvae to define and separate *Semisuturia* and *Glaurocara*. We found that *Glaurocara* species have a very large and well-developed dorsobasal extension of the basiphallus (Fig. 4H), which is probably a derived condition that readily contrasts with the smaller extension in *Semisuturia* (Fig. 4B, E). The first instar of *Glaurocara* has segments 3–11 each covered with a sclerotized dorsal plate and segments 4–11 each additionally with 2 lateral plates on each side. A similar condition is shared by the ormiine genera *Aulacephala* Macquart and *Therobia* Brauer (Fig. 9A, B). In contrast, *Semisuturia* is characterized by having a single large, sclerotized plate on each of segments 3 to 11 (Figs. 5, 6). Plates 4–11 are semicircular, in transversal section, and cover most of the dorsolateral surface of each segment, whereas the plate on segment 3 (i.e., the first apparent segment of the larva) is large, shield-like and covers the first two segments and the cephaloskeleton. We think that this condition is derived and supports monophyly of the genus *Semisuturia*. Cantrell (1988) noted this as well for his "*Semisuturia* sp. 2" (possibly *S. moffattensis*), but numbered the segments as 2–10 instead of 3–11. Cantrell (1988) also treated the last pair of sclerotized plates (i.e., the caudal plates, segment 12 in his terminology) as a "true" additional segment. We disagree and follow Crosskey (1965) in treating these plates, arising posterior to the posterior spiracles, as appendages of the last segment (segment 12; Cantrell's segment 11). The recognition of the caudal plates is important as a *Glaurocara* species from Madagascar has the caudal plates developed into cone-like processes from which a pair of sensillae arise posteriorly (Fig. 8E), whereas *Glaurocara* species from mainland Africa and *Semisuturia* species have the caudal plates not cone-like and provided with a pair of small whip-like sensillae (Fig. 5E, F).

Semisuturia moffattensis and the generic limits of Semisuturia

Semisuturia species are united in having the first instar with one large, semicircular, sclerotized plate on segments 4–11 and a large sclerotized, shield-like plate on segment 3. *Semisuturia moffattensis* shares these characteristics but also possesses some distinctive features that make it readily identifiable within the genus. Among the most evident are the higher than long head and the facial ridge straight with a row of robust, decumbent setae on lower 2/3. This last character state is unique among Glaurocarini and very rare among Tachininae in general: by way of example, only three of 128 Palaearctic tachinine genera have species with robust setae on the facial ridge (see Cerretti et al. 2012: character 18 states 5 and 6, character 19 state 2). Also, *S. moffattensis* has almost no sexual dimorphism in the width of the frons and its long postpedicel almost reaches the lower facial margin.

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