



# The prickly blade mapped: establishing homologies and a chaetotaxy for macrosetae of penis ventral plate in Gonyleptoidea (Arachnida, Opiliones, Laniatores)

ADRIANO B. KURY\* and OSVALDO VILLARREAL M.

*Departamento de Invertebrados, Museu Nacional/UFRJ, Quinta da Boa Vista, São Cristóvão, 20.940-040, Rio de Janeiro, RJ, Brazil*

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For the first time a hypothesis of homology is proposed for the macrosetae which compose the armature of the distal truncus penis of the Gonyleptoidea. Previous attempts to name them in the literature have not been continued because they started by referring to macrosetae based on their position, which may change widely, and all of them were very narrow in scope. The present project instead names groups of macrosetae that do not mandatorily refer to their position, thus compensating for their hypothesized secondary position shifts. Using criteria of topology, shape and exclusion, six groups of setae are recognized, A–E, and their topological and phylogenetic distribution is studied and described in all families of Gonyleptoidea and two other related families of Grassatores. A cladistic analysis is performed, providing the following results: (1) the Microsetata are recovered including Metasarcidae/Cosmetidae sister to an expanded Gonyleptidae; (2) the genera *Quindina* (Cranaidae) and *Zygopachylus* (Manaosbiidae) are transferred to **Nomoclastidae** rank nov., hitherto regarded as a subfamily of Stygnidae, now a sister group of the Microsetata; (3) Zamorinae, currently placed in Cranaidae, is the sister group to Nomoclastidae, and it is therefore transferred to this family; (4) an expanded Gonyleptidae is recovered, including Manaosbiidae and Cranaidae, but the independence of these families is also recovered because the Gonyleptidae *stricto sensu* form a clade; (5) the Ampycinae, in spite of many particularities, are recovered inside Gonyleptidae; (6) the zamorine-less Cranaidae are recovered as a monophyletic sister group to Gonyleptidae, but not nested inside it. ***Jabbastygnus* gen. nov.** is described in Stygnidae along with its type species *J. huttonum*, from Colombia.

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## INTRODUCTION

Genital morphological characters of harvestmen are widely recognized for their great potential to establish homologies for phylogenetic reconstruction in systematics. Nevertheless, homology has scarcely been proposed in the literature and negligible use has been made of this massive source of information.

Analyses of component structures of male genitalia of Opiliones have been conducted by Martens (1976, 1986, 1988) with great success, recognizing constituent parts, conductors, titillators, movements and ex-

pansion. More recently, there have been further attempts to identify, to name and/or to relate some elements, for example the wide variation of the groundplan in Sandokanidae (Schwendinger & Martens, 2002), the naming of pergula, rutrum and stragulum in Zalmoxoidea (Kury & Pérez-G. 2002; Kury, 2003a), detailed study of component parts in Samooidea (Pérez-G. 2006), the recognition of hammer + lamina parva in ‘Tricommatinae’ [= Cryptogeobiidae] (Kury, 1992a, 2014), and the shape, accessories and attachment of glans in Cosmetidae and Gonyleptidae (Kury, 1994; Kury & Barros, 2014). A general review of penis structure is presented by Macías-Ordóñez *et al.* (2010).

Notably, the macrosetae of distal truncus penis are almost always neglected in descriptions and

\*Corresponding author. E-mail: adrianok@gmail.com

character surveys, and only superficially referred to (usually comparisons are limited to simple counts), perhaps owing to the lack of homology hypotheses. Here, for the first time, an attempt is made to relate them, to name them and to follow their changes in place and shape along the evolution of a group of Opiliones, although this is complicated owing to the great plasticity of these phaneres.

A set of characters is unveiled, which are useful for phylogenetic analyses. In the descriptions of the patterns we were able to detect a large number of potential synapomorphies for many groups of Gonyleptoidea. Likewise, a hitherto unknown group is detected, which is deemed basal to Microsetata, forcing a redefinition of this clade, and with the creation of a broader clade here called Laminata.

## HISTORICAL BACKGROUND

Šilhavý (1938) proposed the use of the penis as a valuable feature for systematics of Opiliones, but for decades authors mostly limited themselves to illustrate the penis without describing it or to understand the parts. Martens (1976, 1986) undertook a huge step forward by establishing groundplans for several families of Opiliones, but he did not attempt to study homology among macrosetae. A few authors (e.g. Kury, 1989; Pinto-da-Rocha, 1997; DaSilva & Gnaspini, 2010; Cruz-López & Francke, 2012; 2013a, b; Zhang & Zhang, 2012; Zhang, Kury & Zhang, 2013) forwarded names for setae or groups of setae of the ventral plate in Laniatores, but these were based on purely circumstantial evidence, bound to small circumscriptions, not used for homology comparisons, and limited to ‘dorsal–ventral–distal–apical–basal–intermediate’ and the like (see Table 1 for a synopsis).

Cruz-López & Francke (2013b) recognized what they called a ‘*Paramitraceras* pattern’ with five characters, three of which relate to the distribution of setae on VP, which they call ‘pars distalis’ following Pérez-G. (2006, in the text, but this reference is missing in their list), although Pérez-G. usage is different. Using their own terminology, they referred to the multiplication of macrosetae A, to the disjoint location of macrosetae C versus B + A and to the much reduced central pair of macrosetae E.

## MATERIAL AND METHODS

### STUDY OF SETATION

Homology between groups of setae and individual setae was sought to start with relative position and place of insertion, accounting for secondary multiplication and losses, but without postulating unparsimonious changes. In the descriptions and illustrations of the

**Table 1.** Previous nomenclature for macrosetae of penis ventral plate

Groups used here	Cruz-López & Francke (2012–2013) (Stygnopsidae)	Kury (1989) (Gonyleptidae)	Pinto-da-Rocha (1997) (Stygnidae)	DaSilva & Gnaspini (2010) (Gonyleptidae)	Zhang & Zhang (2012) (Epedanidae)	Zhang <i>et al.</i> (2013) (Podoctidae)
A	SI (sedas laterales)/LS (lateral setae)	basal group	BS (basal setae)	basal group	DS (part), VS (part)	LS
B	SI (sedas laterales)/LS (lateral setae)	basal group	none	basal group	VS	VS (part)
C	SI (sedas laterales)/LS (lateral setae)	apical group	DS (distal setae)	apical group	VS	DS (part)
D	none/DMS (dorsal microsetae)	apical group	none	more basal seta of apical group	DS	DS (part)
E	Ms (microsedas)/VMS (ventroapical microsetae + ventroapical macrosetae)	none	IS (intermediary seta)	none	VS	VS (part)

chaetotaxy, a sample of species of all gonyleptoid families is used, targeting the highest morphological diversity within each one. Throughout the text, taxonomic units are referred to only by genus for brevity. Some morphotypes were left identified only down to genus and we did not attempt to describe the respective species. The only exception is a new stygnid described below because it constitutes a new genus with a unique pattern of chaetotaxy, and which we did not want to leave unnamed.

To study exoskeleton surface sculpture and armature, scanning electron microscopy (SEM) was used to obtain initial images in diverse positions. These were studied, interpreted and thus served as a base for schematic drawings, presented here for clarity. Vouchers are listed in Table 2. A few schematic illustrations have been adapted from literature sources (also listed in Table 2). Published sources of macrosetae patterns, used for comparison but not illustrated here, are listed on Table 3.

#### ABBREVIATIONS

SEM was carried out with a JEOL JSM-6390LV at the Center for Scanning Electron Microscopy of Museu Nacional/UFRJ. All measurements are in millimetres. Abbreviations of the repositories cited are: MNRJ-HS, Private Collection Helia Soares, presently in MNRJ; MNRJ, Museu Nacional, Rio de Janeiro. Other abbreviations used: MaLP, Gonyleptoidea with ventral plate tagmatized into malleus + lamina parva (i.e. Agoristenidae, Cryptogeobiidae, Gerdesiidae, Stygnidae); MS, macrosetae; VP, ventral plate.

#### DELIMITATION OF TAXA

In the descriptions we follow a phylogenetic order, derived from our analysis and the recent literature, based on the following rationale:

- 1 Metasarcinae is no longer considered a basal Gonyleptidae, but as a separate family Metasarcidae closest to Cosmetidae in a recent molecular study (Pinto-da-Rocha *et al.*, 2014), to which we concur (see cladistic analysis below). Sharma & Giribet (2011) did not treat Metasarcinae in their analysis.
- 2 Nomoclastinae is traditionally a basal group in Stygnidae (Pinto-da-Rocha, 1997), but our current analysis recovered it as the sister group of Microsetata, prompting us to elevate this taxon to family rank. Likewise, *Quindina* (hitherto in Cranaiidae) and *Zygopachylus* (hitherto in Manaosbiidae) are here listed under Nomoclastidae, being further below formally transferred to this family. Likewise, Pinto-da-Rocha (pers. comm., 2012), working independently on Manaosbiidae, concluded that *Zygopachylus* and related genera do not form a clade

with the true Manaosbiidae. Sharma & Giribet (2011) used one terminal of our Nomoclastidae (*Zygopachylus*, there called 'Manaosbiidae') and it was placed outside the assemblage Gonyleptidae/Cranaiidae. They have not used any 'true' Manaosbiidae as a terminal.

- 3 The 'true' Manaosbiidae is the inverse case of Nomoclastidae, as some species appeared among the terminals of Pinto-da-Rocha but not in Sharma & Giribet (2011).
- 4 Following Kury (2014) *contra* Pinto-da-Rocha *et al.* (2014) the Tricommatinae are here considered as part of Gonyleptidae, while most species until then included in this taxon belong to Cryptogeobiidae (the 'Tricommatinae' of Pinto-da-Rocha) and are treated separately under this family. Sharma & Giribet (2011) treated neither Tricommatinae nor Cryptogeobiidae.
- 5 There is a small group of Amazonian species that have genitalia remarkably similar to the Cryptogeobiidae, as already noted by Kury (1995: 318–319). This assemblage is sister group to the Cryptogeobiidae (according to Pinto-da-Rocha *et al.*, 2014) and has therein been described as family Gerdesiidae. This family is also featured here in the macrosetae descriptions.
- 6 Owing to the huge diversity of Gonyleptidae, we have treated independently two subgroups, separating the K92 from the basalmost group of Pinto-da-Rocha (here called Pachylinae group and including *Junicus* because of the immediate similarity). We use here the term 'K92' denoting a group of five nominal subfamilies in Gonyleptidae, as proposed by Caetano & Machado (2013).
- 7 Recent molecular work (Sharma & Giribet, 2011; Pinto-da-Rocha *et al.*, 2014) joins Ampycinae with Cranaiidae, both inside and outside Gonyleptidae, and in both cases its official status stands as a subfamily of Gonyleptidae. However, Cranaiidae has been formally moved into Gonyleptidae (Pinto-da-Rocha *et al.*, 2014) as Cranainae. Here, Ampycinae is treated separately, but formally still within Gonyleptidae, while Cranaiidae is kept apart.
- 8 Zamorinae is an aberrant group of 'Cranaiidae' (Kury, 2012b), which has not so far been treated in any analyses. Our current analysis recovers it as the sister group of Nomoclastidae, but because of the large morphological gap it is here treated separately.

#### CLADISTIC ANALYSIS OF THE LAMINATA

The unranked clades Greater Gonyleptidae (GG: Gonyleptidae + Cranaiidae + Manaosbiidae) and Microsetata (Cosmetidae + Metasarcidae + GG) are used here as proposed by Kury (2014). Both are tested using a cladistic analysis, conducted herein.

**Table 2.** List of sources (vouchers or literature) used for the schematic illustrations of macrosetae

## Agoristenidae:

1. *Agoristenus* sp. – 1 ♂ (MNRJ 2195) Dominican Republic, Monseñor Nouel, 1 km after cross of Blanco and Bonaó, 28.viii.1987 Abud & L Armas leg.
2. *Globibunus rubrofemoratus* Roewer, 1912–22 ♂ 21 ♀ (MNRJ 19308) Ecuador, Loja, Zamora huayco, Reserva Privada El Madrigal, S 04.03977°, W 079.17515°, alt. 2200 m, 27.iii.2011 A Chagas, A Giupponi & A Kury leg.

## Ampycinae:

3. *Hernandarioides plana* Pickard-Cambridge, 1905 – Adapted from Kury & Quintero 2014, figs 10–12, based on 1 ♂ (MIUP AK 004) from Panama, Prov. Chiriquí: Jurutungo, Parque Internacional La Amistad (PILA), Distrito Renacimiento, 1800–2110 m, 13–16.iii.2006, R. Miranda leg.
4. *Hexabunus armillatus* (Butler, 1873) – 2 ♂ 1 ♀ (CAS AK 096) Ecuador, Napo 20 km E Puerto Napo, Alinahui (1°0'S, 77°25'W) 450 m, xi.1994, V. Roth leg.
5. *Hutamaia caramaschii* Soares & Soares, 1977–2 ♂ 1 ♀ (MNRJ 4459) Brazil, AM, Humaitá, Igarapé Banheiro, 10–11.iii.1976 U Caramaschi leg.

## Assamiidae:

6. *Pungoica simoni* Roewer, 1914–1 ♂ (USNM AK 030) Liberia, Mt. Coffee, iii.1895 RP Currie leg.
7. *Sermouaius* sp. – (AMNH AK 187) Papua New Guinea, D'Entrecasteaux Is., Normandy Island, Mt. Pabinama, about 3 Mi. ENE of Cape Prevost, 820 m, 1956 JL Brass leg.

## Cosmetidae:

8. *Metalibitia paraguayensis* (Sørensen, 1884) – 5 ♂ 8 ♀ (MNRJ 4496) Brazil, Rio Grande do Sul, Canoas, 2001 DR Pedroso leg.
  9. *Metarhaucus* sp – 4 ma 12 ♀ (FMNH AK 14b) Ecuador, Morona-Santiago, Cusuimi on Rio Cusuimi, 150 km SE Puyo, 300 m, 18–23.vii.1971, B. Malkin leg.
  10. *Sibambea* sp. – 1 ma 1 ♀ (FMNH AK 121g) Ecuador, Morona-Santiago, Cusuimi on Rio Cusuimi, 150 km SE Puyo, 300 m, 18–23.vii.1971, B. Malkin leg.
- Cranaiidae:
11. *Chiriboga albituber* Roewer, 1959 (MCZ AK 004) Ecuador, Pichincha, Quito to Sto. Domingo, 1300–2400 m, 23–25.ii.1965, L. E. Peña leg.
  12. *Phalangodus* sp. – 5 ♂ 6 ♀ (MNRJ 2163) Colombia, Santander, Zapatoca, Cueva Alsacia, 27.i.1997, S Garcia leg.
  13. *Phareicranaus circumlineatus* – 1 ♂ 1 ♀ (MNRJ 7917) Venezuela, Monagas, Estrada entre Cueva del Guácharo and Caripe, 1000 m, 3.xii.2002, A Pérez & A Giupponi.
  14. *Zamora granulata* Roewer, 1928–1 ♂ 1 ♀ (MNRJ 19266) Ecuador, Pastaza, Rio Alpayacu, between Shell and Mera, along the river banks, 01.46715°S, 078.10314°W, 1065 m, 22.iii.2011, A Chagas, A Giupponi, A Kury & M Vega leg.

## Cryptogobiidae:

15. *Taquara bicoloripes* (H. Soares, 1974) – 2 ex. (MNRJ 2218) Brazil, Rio de Janeiro, Serra dos Órgãos National Park, 5–6.xi.2009 C Sampaio & A Giupponi leg.

## Epedanidae:

16. *Dibunus similis* Roewer, 1912 – Adapted from Weber 1988, fig. 24, based on ♂ holotype (SMF 191) Philippines, Bohol.
17. *Epedanus pictus* Thorell, 1876 – Adapted from Weber 1988, fig. 22, based on ♂ holotype (MCSNG) Malaysia, Borneo, Sarawak, 1865, G. Doria & O. Beccari leg.
18. *Pseudobiantes japonicus* Hirst, 1911–1 ♂ ♀ (AMNH AK 065) Japan, Shikoku, Mt. Takanawa, 5.ix.1956, T Kunita leg.

## Gerdesiidae:

19. *Gerdesius* sp. – 1 ♂ 2 ♀ (MNRJ 2411) Brazil, Amazonas, Manaus, Reserva Km 41, Rio Preto da Eva, 02°28'S, 59°43'W, vii.2003, G. Machado leg.

## Gonyleptidae:

20. *Acanthopachylus aculeatus* (Kirby, 1819) – 15 ♂ 12 ♀ (MNRJ 18918) Uruguay, Lavalleja, Ciudad de Minas, Parque de Vacaciones, xii.2005 E Wienskosi leg.
21. *Gonyleptes horridus* Kirby, 1819 – Adapted from figs 7A–C in Pinto-da-Rocha *et al.* 2012.
22. *Mitobates triangulus* Sundevall, 1833–3 ♂ 2 ♀ (MNRJ 5743) Brazil, Rio de Janeiro, Rio de Janeiro, Tijuca, 400 m, 20.iv.1997 A Giupponi leg.

## Manaosbiidae:

23. *Barrona williamsi* Goodnight & Goodnight, 1942 – Adapted from Townsend *et al.* 2011, figs 16–19, based on material from Panama.
24. *Syncranaus cribrum* Roewer, 1913–1 ma 2 ♀ (MNRJ-HS 692) Brazil, Pará, Belém, Instituto Agronômico, 20.viii.1971, A Peracchi leg.

## Metasarcidae:

25. *Chacoikeontus clavifemur* Roewer, 1929–1 ♂ (USNM AK 122) and 1 ♂ 1 ♀ (USNM AK 123) Bolivia, La Paz, Cerro Uchumachi, 7 Km SW Coroico ca 1900 m, 16°15'S, 67°21'W, 24–25.xi.1989, J Coddington, C Griswold, D Silva, S Larcher, E Peñaranda leg.

## Nomoclastidae:

26. *Nomoclastes quasimodo* Pinto-da-Rocha, 1997–4 ♂ 4 ♀ (MNRJ 7762) Colombia, Valle del Cauca, Vereda Los Limones, Cali, 3°28'35.6"N, 76°33'52.9"W, 1214 m, 20.vii.2012 JA Moreno leg.
27. *Quindina bella* Roewer, 1915–7 ♂ 7 ♀ (MNRJ 17946) Colombia, Tolima, Ibagué, viii.2006 A Giupponi leg.
28. *Zygopachylus albomarginis* Chamberlin, 1925–2 ♂ 3 ♀ (CAS AK 049) Panama, Canal Zone, Summit Park, 18–19.i.1987 ES Ross leg.

## Pyramidopidae:

29. *Pyramidops pygmaeus* Loman, 1902–1 ♂ (USNM AK 032) Nigeria, Oyo Ibaden, IITA, pitfall traps, 20–21.v.1974, B Critchley leg.

## Stygnidae:

30. *Auranus hehu* Pinto-da-Rocha & Tourinho, 2012 (adapted from figs 13D–F in Pinto-da-Rocha & Tourinho, 2012).
31. *Eutimesius* sp. – 2 ♂ 1 ♀ (IAvH 3000054) Colombia, Norte de Santander, Toledo, Parque Nacional Natural Tamá, Vda. El Diamante, Alto de Herrera, 1000 m 26.ix.1999, V Rodríguez.
32. *Jabbastygnum huttonum* sp. nov. – 1 ♂ paratype (IAvH 3000042) Colombia, Boyacá, Villa de Leyva, Santuario de Fauna y Flora Iguaque, Sitio Laguna Iguaque 3450 m, 5°38'N, 73°29'W, 16.x.1998, D. Forero leg.
33. *Ricistygnum quineti* Kury, 2009 – ♂ holotypus 1 ♀ paratype (MNRJ 02112) Brazil, Ceará, Serra de Baturité, Guaramiranga (Parque das Trilhas) 860 m, 04°16'S, 038°56'W, mata úmida de altitude, winkler, 23.vii.2002, Yves Quinet leg.

## Stygnopsidae:

34. *Hoplobunus boneti* (Goodnight & Goodnight, 1942) – 2 ♂ (AMNH AK 311) Mexico, SL Potosí, Cueva de los Sabinos, near Valles, underground waterway to Devil's Hole, 26.iii.1946, EJ Dontzin & E Ruda leg.
35. *Karos* sp. – 1 ♂ (AMNH AK 310) Mexico, SL Potosí, 20 km SW Tamanzunchale, forest log litter, berlese, coffee plantation, 300 m, 11.vi.1983, S&J Peck leg.

**Table 3.** Published sources of macrosetae patterns not illustrated here but cited in the descriptions

Supraspecific taxa	Species	Source
Agoristenidae	<i>Avima</i> , as <i>Trinella</i>	Villarreal M. & Rodríguez 2004
Agoristenidae	<i>Nemastynus</i>	Pinto-da-Rocha <i>et al.</i> 2012
Agoristenidae	<i>Rivetinus</i>	Pinto-da-Rocha & Hara 2009
Ampycinae	<i>Licornus tama</i> Villarreal & Kury, 2012	Villarreal M. & Kury 2012, figs 16–17
Ampycinae	<i>Pirunipygus paradoxus</i> Roewer, 1936	Pinto-da-Rocha <i>et al.</i> 2012, fig. 5B, C
Assamiidae	diverse genera	Santos & Prieto 2010
Cosmetidae	<i>Cynorta</i>	Kury <i>et al.</i> , 2007
Cosmetidae	<i>Gryne</i> and <i>Roquettea</i>	Ferreira & Kury 2010.
Cosmetidae	<i>Spinopilar</i>	Kury & Pérez-González 2008, figs 4–7
Cranaidae	<i>Aguaytiella</i> , <i>IQUITOSA</i> and <i>Phalangodus</i>	Hara <i>et al.</i> 2014, figs 10–23
Cranaidae	<i>Heterocranaus</i> , <i>Metacranaus</i> and <i>Ventrisudis</i>	Pinto-da-Rocha & Bonaldo 2011, figs 2a, b, 3a–d
Cranaidae	<i>Agathocranaus</i> , <i>Stygnicranaus</i>	Orrico & Kury 2009, figs 4, 5, 10, 11, 18, 19
Cranaidae	<i>Zannicranaus</i>	Kury 2012a
Epedanidae	<i>Epedanellus tuberculatus</i> Roewer, 1911	Suzuki 1973, figs 56–58
Epedanidae	<i>Pasohnus bispinosus</i> Suzuki, 1976	Suzuki 1976, fig. 8F–H
Epedanidae	<i>Plistobunus columnarius</i> Lian <i>et al.</i> , 2011	Lian <i>et al.</i> 2011, figs 26–31
Epedanidae	<i>Takaoia sauteri</i> Roewer, 1911	Suzuki 1977, figs 3A–C
Epedanidae	<i>Toccolus javanensis</i> Kury, 2008	Kury 2008, figs 6–8
Gonyleptidae	<i>Acrographinotus</i>	Acosta 2001, figs 11, 13
Gonyleptidae	Bourguyiinae <i>Asarcus</i>	Yamaguti & Pinto-da-Rocha 2009 figs 96, 98
Gonyleptidae	Bourguyiinae <i>Bourguyia</i>	Yamaguti & Pinto-da-Rocha 2009 figs 83, 85, 92, 94
Gonyleptidae	Caelopyginae	Pinto-da-Rocha 2002, figs 110, 111, 117, 119, 154–155 and 99, 107, also Mendes & Barros 2013, figs 15, 18
Gonyleptidae	<i>Fonckia</i>	Silva <i>et al.</i> 2013, fig. 28
Gonyleptidae	Goniosomatinae ( <i>Acutisoma</i> , <i>Heteromitobates</i> and <i>Serracutisoma</i> ,	DaSilva & Gnaspini 2010, figs 134, 135, 146, 148, 150, 152, 154, 156, 165, 167, 169, 171
Gonyleptidae	Gonyleptinae	Pinto-da-Rocha <i>et al.</i> 2012, figs 8, 10, 11, 13, 14
Gonyleptidae	Hernandariinae	DaSilva & Pinto-da-Rocha 2010, figs 139, 150, 147, 171
Gonyleptidae	<i>Junicus</i>	Acosta 2001, figs 14, 16
Gonyleptidae	<i>Marayniocus</i>	Acosta 2006, figs 8, 10
Gonyleptidae	<i>Nanophareus</i>	Hara <i>et al.</i> 2012
Gonyleptidae	Sodreaninae	Pinto-da-Rocha & Bragagnolo 2010, figs 9, 11
Gonyleptidae	<i>Tricommatas</i> as <i>Pherania</i>	Kury 2003b, figs 12–13
Manaosbiidae	<i>Narcellus</i> as <i>Cranellus montgomeryi</i> Roewer 1932	Townsend <i>et al.</i> 2011, figs 26–29
Manaosbiidae	<i>Rhopalocranaus albilineatus</i> Roewer, 1932	Townsend <i>et al.</i> 2011, figs 30–33
Metasarcidae	<i>Ayacucho</i> , <i>Cajamarca</i> , <i>Metasarcus</i>	Benedetti 2012
Metasarcidae	<i>Incasarcus</i>	Kury & Maury 1998
Stygnidae	<i>Imeri</i> and <i>Yapacana</i>	Pinto-da-Rocha 1997, figs 457–458 and Pinto-da-Rocha & Tourinho 2012, figs 12A–C
Stygnidae	<i>Jime</i>	Pinto-da-Rocha & Tourinho 2012, figs 13G–I
Stygnidae	<i>Pickeliana</i>	Hara & Pinto-da-Rocha 2008, figs 9–10
Stygnidae	<i>Protimesius</i>	Kury & Pinto-da-Rocha 2008, figs 7–9; Pinto-da-Rocha 1997, figs 576–577 Villarreal M. & Pinto-da-Rocha 2006 figs 42–43
Stygnidae	<i>Sickesia</i>	Pinto-da-Rocha 1997, figs 574–575
Stygnidae	<i>Stygnoplus</i>	Pinto-da-Rocha 1997, figs 580–581; Villarreal M. & Rodríguez 2004, figs 4A–C, 6A–C
Stygnidae	<i>Stygnus</i>	Pinto-da-Rocha 1997, figs 566–573
Stygnopsidae	<i>Paramitraceras</i>	Cruz-López & Francke 2012; Cruz-López & Francke 2013a, fig. 33
Stygnopsidae	<i>Philora tuxtlae</i> Goodnight & Goodnight 1954	Cruz-López & Francke, 2013b, figs 12–14 and 51
Stygnopsidae	<i>Troglostygnopsis</i>	Cruz-López & Francke 2013b, fig. 52

*Outgroup terminals:* An extensive array of outgroup terminals have been chosen from among other superfamilies of Grassatores (Assamioidea, Epedanoidea, Samooidea), with a triaenonychid chosen as prime outgroup.

*Ingroup terminals:* To avoid overloading the matrix with redundantly detailed information on each twig in the meandering tree of Gonyleptoidea, we have chosen just one terminal for many families (such as Agoristenidae, Cryptogeobiidae, Gerdesiidae and Stygnopsidae), so that some of the macrosetation patterns illustrated here do not have exact counterparts in the analysis. Within Laminata the representation is much wider, focusing on the Nomoclastidae and the bizarre Ampycinae (to test its inclusion in Gonyleptidae).

*Settings of parsimony analysis:* The character states have been tabulated in a matrix using Mesquite version 2.5 (Maddison & Maddison, 2008). The annotated list of characters is given in Table 4. The matrix of characters states and terminals is given in Table 5. Trees were searched using TNT (Goloboff, Farris & Nixon, 2008) using parsimony under implied weights (Goloboff, 1993) with traditional search algorithm and SPR branch-swapping. Four searches were conducted with TNT using interactive weighting with K concavity values of 1, 3 and 6 as well as a non-weighted analysis (based on prior equal weights). Space was allocated for 10 000 trees in memory and 10 replicates with 10 000 trees each were carried out. A summary of the results of the five analyses is presented in Table 6. Absolute Bremer support (decay analysis) and Bootstrap resampling values (1000 replicates) were calculated using TNT. Values are shown in Figures 14–16.

## RESULTS – DESCRIPTION OF MACROSETAE

As a result of the reduction of the extroverting and unfoldable structures typical of other Laniatores, the glans penis in Gonyleptoidea is poorly movable, attached more or less freely to the dorso-subdistal part of the truncus. The macrosetae (MS) do not encircle the glans, nor are distributed across the distal part of truncus as in other subfamilies, but rather are mainly grouped along the lateral border of a flattened ventral plate (VP).

We recognize five MS groups in Gonyleptoidea, A–E, and each group is detailed as follows.

### GROUPS A AND B

MS A occur typically as two or three pairs while MS B, when present, comprise only one pair. Because MS A and B are mostly associated with each other, they are discussed together. Sometimes it is difficult to tell

which one is B owing to their similar conformation, but often MS B are smaller, out of the main row and inserted slightly more ventrally. MS A and B are typically proximal or basal on the laterals of VP, sometimes latero-dorsal or latero-ventral, following swelling of the malleus (e.g. Agoristenidae, Cryptogeobiidae).

MS A setae may undergo further reduction in number and more rarely multiplication. In general they are robust, often elongate, rarely spatulate or bifid. MS B1 are highly variable in location, isolated or adjacent to the A group. It may take part in a longitudinal row A–B–C or in a transverse/oblique A–B belt.

*Stygnopsidae:* MS A are extremely variable, located in the laterals of distal truncus, sometimes slightly shifted dorsally. In the taxa studied here, MS B1 is mainly isolated and clearly laterally located. They may be strongly curved, spatulated (*Hoplobunus*), less so (*Paramitraceras* and *Philora*), or substraight and cylindrical (*Karos*).

In *Hoplobunus* (Fig. 1A–C) there are two pairs (A1–A2) of robust setae that are curved and spatulate, set close together in a longitudinal row on the laterals of the truncus (B1, which is identical to them, is also this row). In *Philora* the pattern is very similar, but without any MS B. In *Karos* (Fig. 1D–F) the distinction of groups A, B and C is difficult because the gaps are more subtle, there is the loss of one pair of setae and MS A, B and C are very much alike. There are two pairs, A1–A2, of straight MS (recognizable because they are inserted proximally to D1–D2), with similar sizes. MS B is aligned in the same row as them, but it is smaller. In the *Paramitraceras–Troglostygnopsis* complex there is considerable multiplication in the number of MS A, with at least six pairs (reaching as many as ten pairs) of spatulate slender MS, crowded from latero-ventral to latero-dorsal. MS B1 is very similar in size and shape, but inserted slightly more ventrally.

*Agoristenidae:* MS A (typically two pairs, A1–A2) and B form a continuous equatorial girdle of elongate and bifid/trifid MS that runs from dorsal to ventral on truncus (*Agoristenus*, Fig. 2A–C; *Globibunus*, Fig. 2D–F; see also *Avima*, *Rivetinus* and *Nemastygnus*). The main difference between *Agoristenus* and *Globibunus* is that MS B in the latter are much more distally inserted.

*Stygnidae:* As typically occurs in the MaLP – gonyleptoids with VP divided into a swollen basal part of (malleus) and a lamina parva – MS A and B in Stygnidae do not form a straight longitudinal line laterally on VP, and instead they partly encircle the base of the malleus. MS B usually takes part in a transverse equatorial belt with MS A, girdling the malleus as the ventralmost unit (*Auranus hehu*, Fig. 4;

**Table 4.** Character descriptions and states used in the present analysis

- **1. DS (dorsal scutum), main outline in dorsal view** [Type alpha, beta and gamma as defined in Kury *et al.* (2007). Type epsilon: subrectangular with corners rounded, no constrictions and slightly arched laterals (as in *Agoristenus*). Type zeta: similar to alpha, but narrower, with constrictions and posterior curve less extreme (as in *Hoplobunus*). Type eta: abdominal part size comparable to carapace, steadily growing wider posteriorly, with broad convex posterior margin (typical of Triaenonychidae)]
  - 0 eta (abdominal part size comparable to carapace, steadily growing wider posteriorly, with broad convex posterior margin (typical of Triaenonychidae).)
  - 1 epsilon (subrectangular with corners rounded, no constrictions and slightly arched laterals (as in *Agoristenus*))
  - 2 alpha
  - 3 beta (constricted twice, with coda, widest part on posterior third)
  - 4 gamma
  - 5 zeta [similar to alpha (widest part in the middle), but narrower, with constrictions less extreme (as in *Hoplobunus*)]
  - 6 theta (bell-shaped, without posterior constriction, narrowing gradually)
  - 7 delta
  - 8 iota (subrectangular)
- **2. Posterior margin of DS, shape**
  - 0 convex
  - 1 straight
  - 2 concave
- **3. Carapace outline, sexual dimorphism**
  - 0 same size in both sexes
  - 1 much enlarged in male, groove projectes backwards, squeezing scutal area I
- **4. Ocularium, structure** (Partly corresponding to Kury 1993, cct U4.)
  - 0 high coarsely granular, slanted forward
  - 1 low, may have even median depression
- **5. Placement of the eyes on two separate eyeballs (absence of a common eye mound), presence**
  - 0 eyes placed on a common ocularium
  - 1 2 separate eyeballs
- **6. Frontal hump of carapace, presence** (Yamaguti & Pinto-da-Rocha (2009), cct)
  - 0 absent
  - 1 present
- **7. Scutal area I, presence of median longitudinal groove** (used by Kury, 1992a, cct 10)
  - 0 absent, area I entire
  - 1 present, area I divided into left and right halves
  - 2 secondary effacement
  - 3 Goniosoma-like (area II invading area I)
- **8. Scutal area III, paired armature**
  - 0 unarmed
  - 1 with paramedian pair of tubercles or spines
  - 2 high spines, partially fused
- **9. Median spiniform apophysis of free tergite III, shape**
  - 0 absent
  - 1 stout
  - 2 small
- **10. Median spiniform apophysis of free tergite II, presence**
  - 0 absent
  - 1 present
- **11. Furrow between scutal areas III and IV, degree of effacement**
  - 0 furrow complete
  - 1 furrow effaced in the middle
  - 2 furrow entirely effaced
- **12. Furrow between areas III and IV, shape**
  - 0 straight
  - 1 clearly recurved (pointing forwards)
  - 2 gently procurved (pointing backwards)
  - 3 barely distinct, sinuous-formed by two joined Cs-clearly marked, sinuous
  - 5 entirely effaced

Table 4. *Continued*

- **13. Lateral margins of dorsal scutum, armature**
  - 0 finely granular or without special granulation arranged in a row
  - 1 with longitudinal row of light colored large tubercles, coalescent and flattened
  - 2 with marginal row of light colored tubercles well spaced between them
- **14. Stigmatic area, posterior border**
  - 0 straight or only very slightly concave
  - 1 deeply concave
- **15. Basichelicerite, structure**
  - 0 short, unarmed
  - 1 pre-bulla very long, powerfully armed
  - 2 bulla long, robust, with marginal armature
  - 3 bulla of male attenuate
  - 4 long and very thick
- **16. Posterior margin of cheliceral bulla, ornamentation**
  - 0 smooth
  - 1 with several teeth
- **17. Cheliceral hand of male, sexual dimorphism** (used in Kury, 1992a, cct 7)
  - 0 present, Ch hand balloon-like swollen
  - 1 absent, Ch hand similar in both sexes
  - 2 intermediate, chelicera of male a little larger
- **18. Cheliceral fingers, elaborate dentition, presence**
  - 0 absent, teeth reduced and subequal
  - 1 present, teeth conform to varied categories, fingers often twisted and bent
- **19. Pedipalpal trochanter, modification for locking**
  - 0 without modifications
  - 1 with ventro-basal apophysis interlocking against cavity in coxa 1
- **20. Pedipalpal femur, shape**
  - 0 cylindrical
  - 1 compressed, slightly concave mesally, with ventral row of numerous small spines coalesced into a flap
  - 2 compressed, with ventral row of independent small spines
  - 3 slightly compressed, accommodated wrapping chelicerae
- **21. Pedipalpal femur, disto-mesal setiferous tubercle. presence**
  - 0 absent
  - 1 present
- **22. Pedipalpal femur, ventral row of spines**
  - 0 absent
  - 1 numerous short teeth
  - 2 few stout spines
  - 3 one basal larger and a few smaller in the middle
- **23. Pedipalpal femur, ventro-basal cluster of setiferous tubercles**
  - 0 only one, clearly ventral, outside the 2 rows of ventro-ectal and ventro-mesal ST
  - 1 a cluster of 2 divergent ST
  - 2 none
- **24. Pedipalpal tibia, shape**
  - 0 semi-cylindrical, without flap
  - 1 strongly depressed and concave, all setae fused forming a marginal flap
- **25. Pedipalpal tibia, ventro-ectal setiferous tubercles, size relationship**
  - 0 subequal
  - 1 penultimate or last much larger
- **26. Pedipalpal tarsus, shape**
  - 0 large, subrectangular, with normal claw
  - 1 small, subtriangular with claw much reduced
- **27. Pa and Ti of Pp, granulation of dorsal surface**
  - 0 finely granular
  - 1 with coarse tuberculation



Table 4. *Continued*

- **28. Pedipalp, general size compared to body**
  - 0 as long as scutum
  - 1 extremely elongate and thin
  - 2 robust, clearly larger than scutum
  - 3 stunted, shorter than scutum and thin
  - 4 not comparable, cosmetiform
- **29. Tarsus I, basal articles fused forming spindle**
  - 0 absent
  - 1 present
- **30. Relative thickness of legs I–IV**
  - 0 all subequal
  - 1 III–IV clearly stronger than I–II
  - 2 legs getting steadily stronger from I to IV
  - 3 only leg IV much stouter than the others in the males
- **31. Coxa IV, dorso-apical apophysis only in male**
  - 0 absent
  - 1 present
- **32. Coxa IV of male, armature**
  - 0 weakly developed, armed with small spine or unarmed
  - 1 very robust horn-like apophysis
- **33. Coxa IV of male, position relative to dorsal scutum in dorsal view** [This character was used by Roewer (1923) to separate the Cranaidae-like from the Gonyleptidae-like families of pseudonychiate Laniatores. Discussed in Kury (1992b: 290)]
  - 0 concealed under DS
  - 1 clearly surpassing DS
- **34. Trochanter IV of male, retro-distal region, armature**
  - 0 unarmed
  - 1 stout recurved hook
  - 2 short spiniform apophysis
  - 3 stout procurved hook
- **35. Femur IV of male, structure**
  - 0 elongate, thin, cylindrical, substraight
  - 1 short, slightly sinuous, thickened
  - 2 moderately long, only slightly incrassate sinuous
- **36. Femur IV, sexual dimorphism**
  - 0 absent
  - 1 clearly marked
- **37. Tibia IV, sexual dimorphism**
  - 0 absent
  - 1 clearly marked
- **38. Distitarsus of leg I, segmentation** [This is a classical character, used by Roewer (e.g. 1912) to separate Phalangodinae from Tricommatinae]
  - 0 with 2 articles
  - 1 with 3 articles
- **39. Tarsal claw, legs 3–4, structure** [Character used by Loman (1900, 1902) to define his Insidiatores]
  - 0 median prong, with lateral secondary prongs
  - 1 paired claws
- **40. Tarsal process (Roewerian ‘pseudonychium’)** [Classical character, recurrently present in discussions of systematics of Laniatores. Roewer used the presence of pseudonychium to define, for example Phalangodidae versus Gonyleptidae. This character found its way in different cladistic analyses (Kury, 1992a cct 1)]
  - 0 absent
  - 1 present, similar to the claws
  - 2 present, very thick
- **41. Truncus penis, presence of musculature** [Key character detected by Martens, (1976) and used by Kury (2003b) as a synapomorphy of the Grassatores]
  - 0 present, one muscle along the shaft
  - 1 absent, gland moved by hydraulic pressure

Table 4. *Continued*

- **42. Pars distalis of truncus penis, structure**
  - 0 Distal region of truncus bears MS, but it is not clear-cut defined, being continuous with pars basalis
  - 1 A Ventral plate (VP) is present in the form of a lamina parva, separated from the base by a waist
  - 2 completely defined as a flattened subrectangular VP, clearly separated from truncus
  - 3 Truncus uniform, topped by a tongue-shaped setigerous plate, homology with macrosetae of other Laniatores is uncertain.
  - 4 VP well-defined, immensely developed, complex-shaped, separated from truncus by a neck
- **43. Staff-like break on distal portion of truncus, presence**
  - 0 absent
  - 1 present
- **44. Division of distal setigerous region of truncus (T)**
  - 0 complex system of plates detached from T
  - 1 gradual narrowing of apex without distinction of a podium or a VP
  - 2 Lamina parva well-marked, but extending dorsal – podium absent
  - 3 distal truncus well-cut as a podium and VP well-marked
- **45. Ventral plate (VP), position in relation to truncus**
  - 0 in the same plan
  - 1 bent upon VP
- **46. VP, length**
  - 0 long, at least twice as long as truncus width
  - 1 short, as long as truncus width
- **47. VP, insertion in truncus apex**
  - 0 not sunken into truncus
  - 1 sunken into truncus
- **48. Lateral borders of pars distalis**
  - 0 without keeling
  - 1 distorted, thinner, with setae dislodged from lateral to dorso-lateral insertion
  - 2 flange
  - 3 flange present, but rudimentary only
  - 4 not comparable because flange region completely overwhelmed by immense MS C
- **49. Metasarcine spiny sacs, presence** [Described and illustrated for the first time in Kury (1994)]
  - 0 absent
  - 1 present as a pair of haematodochae latero-subdistally on truncus penis
- **50. VP, overlapping with distal truncus**
  - 0 nor overlapping
  - 1 truncus reaching about half-length of VP
  - 2 truncus overlapping very little, only at base
- **51. Ampycus-like VP, oval, with deep cleft on distal border, presence**
  - 0 absent
  - 1 present
- **52. Glans penis dorsal process, presence**
  - 0 absent
  - 1 present, thumb-like
  - 2 laminar as a keel
- **53. Glans penis ventral process, presence**
  - 0 absent
  - 1 gonyleptid process, formed by stem plus flabellum
  - 2 serrate funnel, arising straight from mid-stylus
- **54. Glans, shape**
  - 0 embodied in the capsula externa
  - 1 as a haematodocha, relatively free in the apical part of truncus
  - 2 mounted atop the follis
- **55. Glans complex, size and position in relation to VP**
  - 0 stylus short, atop a short glans
  - 1 stylus long, in situ surpassing VP because situated on a long podium + glans,
  - 2 stylus very long, atop a short glans, in situ surpassing VP
  - 3 stylus elongate, upon a long column, surpassing VP
  - 4 stylus very short, atop a triangular glans

Table 4. *Continued*

- **56. Sac glans, structure**
  - 0 non-columnar
  - 1 columnar
- **57. Basal glans sac, structure**
  - 0 formed by amorphous folds
  - 1 formed by superimposed rings
- **58. Stylus, distal portion, shape**
  - 0 cylindrical, or otherwise non-compressed
  - 1 somewhat compressed, with small serrate crest and ill-defined carena
  - 2 clearly compressed, with well-developed ventral serrate crest and well-marked carena
- **59. Stylus, structure**
  - 0 cylindrical, with terminal opening
  - 1 strongly flattened and expanded as a serrate keel, with opening as a slit displaced to dorsal
  - 2 Metalibitia-like – sui generis
- **60. Styler cap, presence**
  - 0 absent
  - 1 present
- **61. Ventral plate or ventral surface of penis, microsetae cover**
  - 0 glabrous, microsetae absent
  - 1 covered by one or two fields or isolated clumps of microsetae of varied shapes
- **62. Median field of scale-bristles, shape**
  - 0 absent
  - 1 complete
  - 2 divided in 2 “lungs”
  - 3 extremely reduced to 2 small flecks
- **63. Median field of scale-bristles, structure**
  - 0 formed by T1
  - 1 formed by T2 or T2/T3
  - 2 formed only by T3
  - 3 formed by T5
- **64. Lateral fields of scale-bristles (always formed by type 4 scale-bristles), shape**
  - 0 absent
  - 1 restricted to the corners of VP
  - 2 prominent, occupying most part of VP
  - 3 two wide stripes almost meeting in the center
- **65. Macroseta A, position**
  - 0 inserted on lateral border of VP
  - 1 encircling VP as a girdle
- **66. Macroseta A-B, size and arrangement**
  - 0 all fairly elongate arranged as a girdle, B more ventral
  - 1 lacking entirely
  - 2 A1–A2 forming slanted row, with B extremely reduced
  - 3 all relatively sturdy, forming an arch, B a little weaker, always positioned latero-ventralmost in the arch
  - 4 all a little reduced in size and number, B proximal to A, lateral or ventro-lateral-two A and 1 B forming a triangle, with A lateral in a longitudinal row and B slightly shifted to latero ventral
  - 5 both A and B inserted far distally, all robust and long. B lateral to ventro-lateral.
  - 6 Macroseta A taking part in a equal gap row with C on laterals of VP
- **67. Macroseta A, position**
  - 0 more proximal, with gap between A and C
  - 1 more distal, adjacent to C
- **68. Macroseta B, presence**
  - 0 present
  - 1 absent
- **69. Macrosetae C, basic placement**
  - 0 composing with A an outer girdle to glans, outside D
  - 1 not as a girdle, neither aligned with A, but still dorso-lateral on VP
  - 2 as a longitudinal lateral row distal on VP

Table 4. *Continued*


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- **70. Macrosetae C, shape**
  - 0 short, sturdy, at least partly lanceolate
  - 1 robust, with point lanceolate
  - 2 extremely long and slender
  - 3 very long and flattened
  - 4 robust, buffalo-horn
  - 5 moderately long and twisted, slender, acuminate
- **71. Macrosetae D**
  - 0 1 pair, inserted fully dorsal, at the midway sides of the glans
  - 1 1 pair, inserted much more distally on dorsal surface of VP, shifted more to lateral
  - 2 1 or 2 pairs, well developed, shifted to distal, but still clearly dorsal
  - 3 2 pairs, very small, dorso-basal near the glans
  - 4 2 pairs, forming a mid-dorsal comb, located basal to glans
- **72. Macrosetae D, insertion**
  - 0 1 to 3 pairs fully dorsal, surrounding glans, 1 pair at least as base of glans
  - 1 only one pair, migrated to latero-dorsal among A-C
  - 2 one pair dorso-lateral at base of glans
  - 3 1 or 2 pairs, fully dorsal, much distal
  - 4 1 pair lateral between A and C
- **73. Macrosetae E, position**
  - 0 2 pairs, entirely on the ventral surface of VP, forming a square
  - 1 2 to 4 pairs, strongly reduced, inserted on the latero-distal flange of VP
- **74. Macrosetae E, size**
  - 0 large, size comparable to A, B or C
  - 1 minute, size much smaller than A, B or C
- **75. Macrosetae, pattern**
  - 0 Pattern A–E not recognizable. Not organized in 5 groups and distributed around the VP surface. Homology obscure.
  - 1 Pattern A–E clearly recognizable within the A, B, C, D, E chaetotaxy.
- **76. Tarsal claws of legs III–IV, structure**
  - 0 triaenonychium
  - 1 double claw
- **77. tarsal aggregate pores** (Gainett *et al.*, 2014)
  - 0 absent
  - 1 present

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*Eutimesius* sp., Fig. 5). Sometimes MS A are grouped among them, leaving a gap with MS B (*Jabbastygnus*, some *Protimesius*), or they may be more widely spaced around the truncus.

MS A/B are in most species examined typically short to moderately sized, substraight or slightly curved, sometimes slightly spatulate (*Eutimesius* and *Ricstygnus*, Fig. 5A–F) or foliaceous (*Protimesius*). In *Jime* MS A are exceedingly stout. In *Pickeliana* MS A are short and unequally bifid. In *Stygnoplus* MS A1–A2 and MS B are very short, commonly forming a row. In *Auranus* MS A/B are bifid, agoristenid-like (Fig. 4A–C).

MS A occur mostly as three pairs, A1–A3 (as in *Auranus*, *Jabbastygnus*, Fig. 4A–F). Reduction in number of MS A occurs in *Eutimesius*, *Stygnus*, *Ricstygnus* (Fig. 5A–F), *Stygnoplus* and *Pickeliana*. In some species of *Protimesius* there is a secondary multiplication with *c.* 5–10 pairs of MS A. In *Imeri* and

*Yapacana* there are five pairs of MS A that are slender and not ordered as a row.

*Cryptogeobiidae*: MS A1–A3 are aligned vertically in the laterals of the malleus in *Taquara* (Fig. 3D–F), although this is not typical, because there are also varied arrangements in which MS A + B encircle the malleus as a girdle, or with only two MS, A1–A2 (e.g. *Spinopilar*). Sometimes one MS A is inserted much more distally, already in the lamina parva. The single pair of MS B is always long, prostrate and positioned ventrally on the malleus taking part in an oblique belt with setae A (*Taquara*, Fig. 3D–F).

*Gerdesiidae*: MS A1–A3 are aligned in a line almost transversally on the laterals of the malleus (*Gerdesius*, Fig. 3A–C). In the specimen studied they are asymmetrical; one side has A1 duplicated, resulting in four



**Table 6.** Summary of the results of the four cladistic analyses performed here

Concavity value	No. of trees retained	Length (under equal weights)	Best score – fit
1	1	(296)	30.67655
3	1	(296)	20.86674
6	1	(296)	14.51036
None – equal weights = 1	16	296	n/a

MS A on that side. The pair of MS B1 is part of this row, occupying the innermost (ventral) position.

*Nomoclastinae*: *Nomoclastes* has two pairs, A1–A2 (Fig. 8G–I). In *Quindina* and *Zygopachylus*, MS A is reduced to only one pair, more lightly built. It is a long and robust acuminate seta, out of the typical position (which is associated with the presence of a concave ring encircling the base of VP), shifted to a more latero-ventral and distal insertion (Fig. 8A–F). All MS A form a row with MS C1–C3 at subequal intervals. There is no trace of MS B in any *Nomoclastidae*.

*Zamorinae*: MS A1–A2 are located on the lateral line of the VP, forming a transverse row (Fig. 11D–F). They are long, slender, cylindrical and acuminate. MS B are lacking.

*Cosmetidae*: MS A vary from one to three pairs but mostly two pairs of reduced setae (in stark size contrast especially with the hugely developed C), located latero-basally on VP. This pattern can be easily seen in *Metarhaucus* (Fig. 6A–C), *Protus*, *Gryne* and *Roquettea*, in many Central American species whose generic assignment is unreliable because of Roewer's system (illustrated in Townsend *et al.*, 2010), in the type species of *Cynorta*. *Metalibitia* (Fig. 7A–C) has an aberrant genitalic structure, with all setae, even C, extremely reduced, and A displaced dorsally. MS B1 is only a stump, proximal and latero-ventral instead of lateral as in MS A.

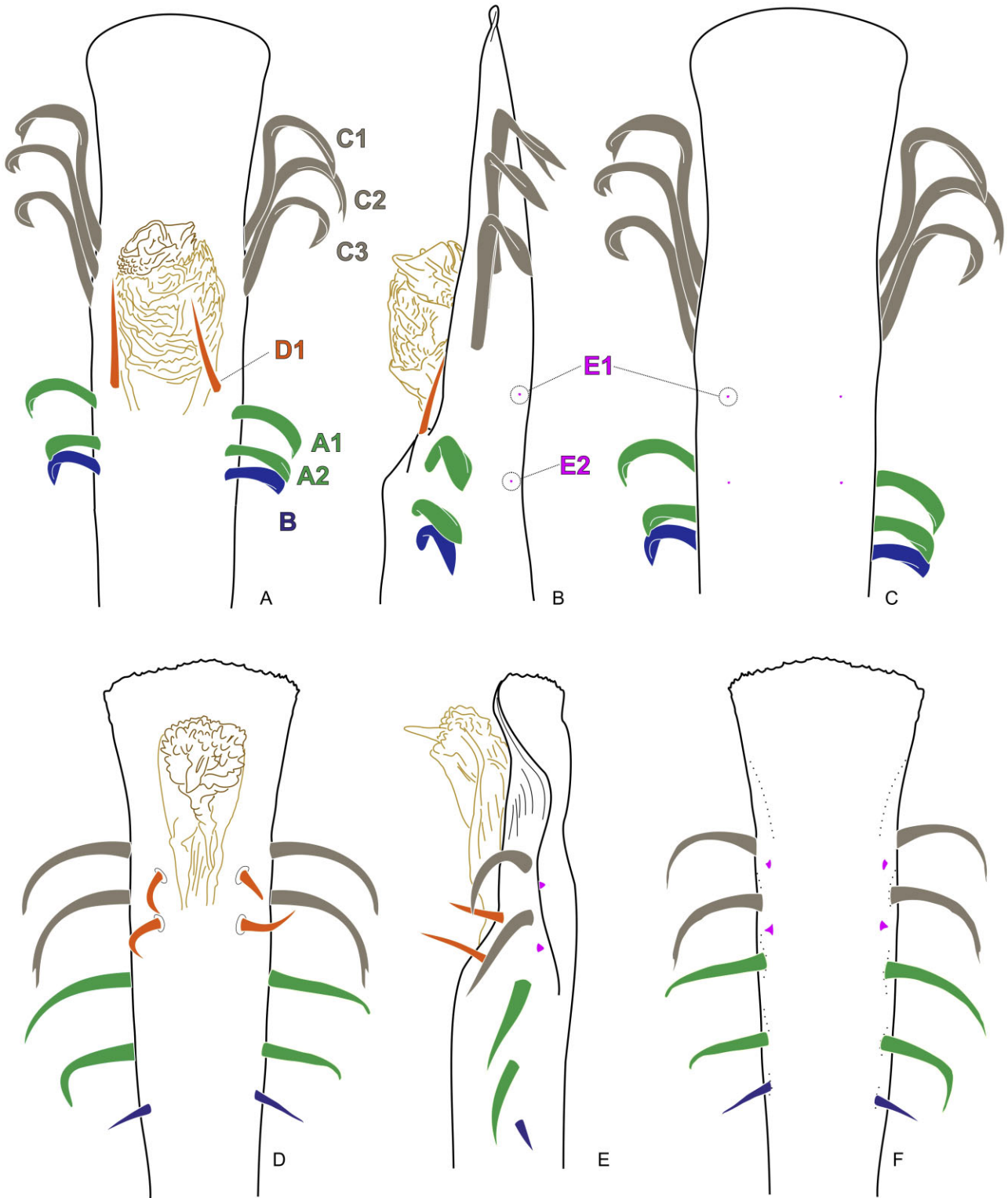
*Metasarcidae*: Here the pattern is similar to that of *Cosmetidae*, with a reduced MS A1 on the lateral border, with a large gap with C. In other species there may be one or two MS A: *Ayacucho*, *Cajamarca* and *Metasarcus*. B1 is minute, shifted ventrally (Fig. 7D–F). In all species, a thin B1 is present more or less close to A1 on the latero-ventral margin of VP. The longitudinal position varies slightly, *Cajamarca* being subdistal and others medial.

*Manaosbiidae*: In all *Manaosbiidae* there are two pairs of MS A, A1–A2, which are very uniform in shape and position. They are long, cylindrical, straight, acuminate,

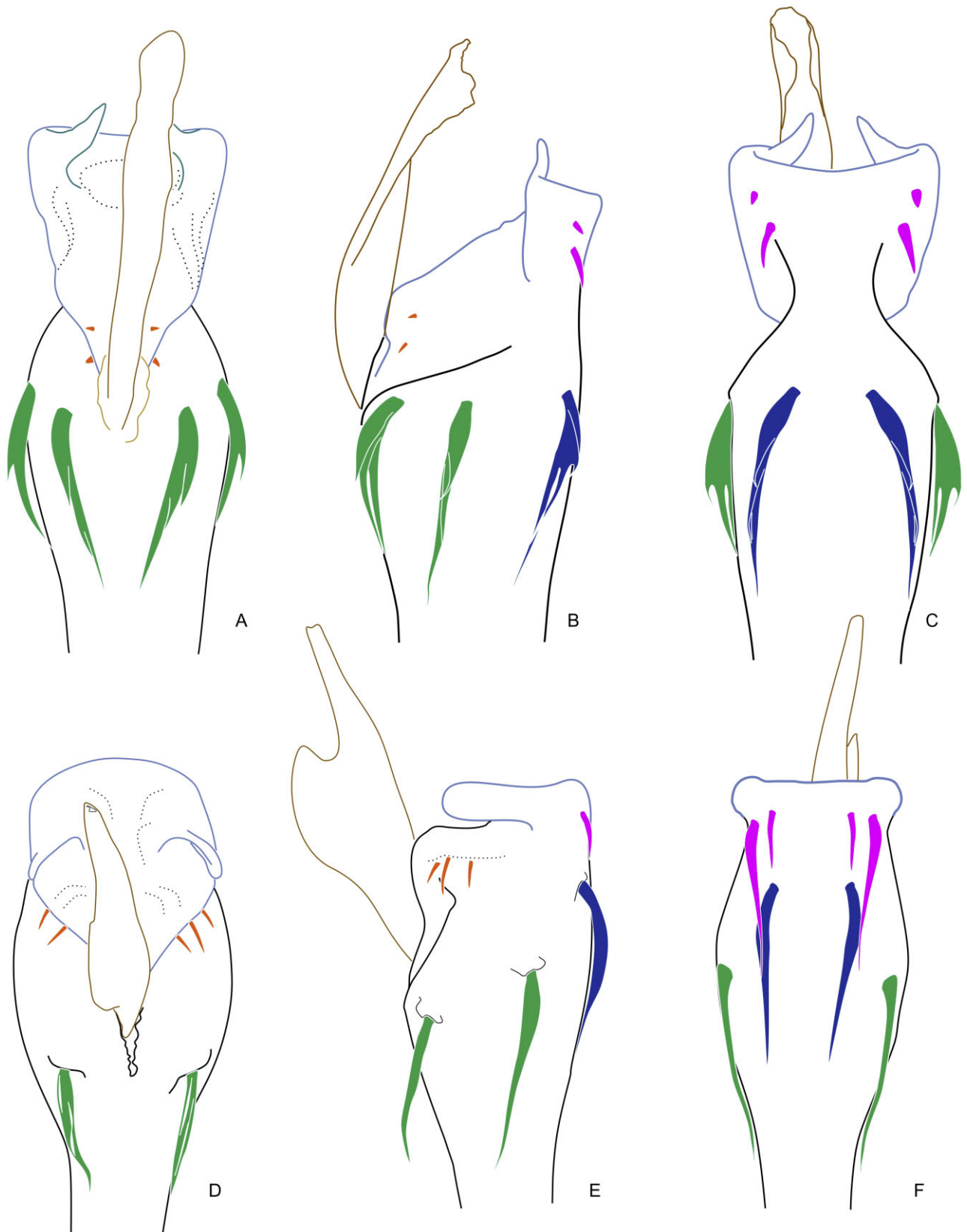
inserted laterally and pointed latero-proximally in *Poecilocranaeus gratiosus* [MNRJ, examined, not figured], *Narcellus*, *Rhopalocranaeus albilineatus*, *Barrona* (Fig. 9D–F) and *Syncranaeus* (Fig. 9A–C). MS B are always shorter than A and located latero-ventrally. They are separated from A1–A2 by a gap (*Narcellus*, *Poecilocranaeus*, *R. albilineatus*), or clustered with A1–A2 (*Barrona*). They are absent in *Rhopalocranaeus* sp. and *Syncranaeus*.

*Cranaidae*: Shapes of MS A are highly variable in this family, although when present they are typically straight and cylindrical (lanceolate in some *Phareicranaeus*, see e.g. González-Sponga, 2003; Villarreal M. & Rodríguez, 2011). As in most other macrosetae groups in *Cranainae*, there is some asymmetry (e.g. Pinto-da-Rocha & Kury, 2003b, fig. 17; Pinto-da-Rocha & Bonaldo 2011, fig. 2A–D). In *Heterocranaeus*, *Chiriboga* and related genera it is hard to homologize the setae because they are all strongly shifted to a distal cluster (Fig. 10D–F). MS A undergo a multiplication resulting in a cluster of A1 to A6 as in *Phalangodus* (Fig. 10A–C), and a common number of two pairs occurs in *Phareicranaeus* (Fig. 11A–C), *Aguaytiella*, *Iquitosa*, *Stygnicranaeus* and *Zannicranaeus*. MS B typically makes part of an arch formed also by A1–A2. Any of the three may be missing (*Agathocranaeus* and *Stygnicranaeus* for example have only A2 and B, lacking A1), but we may observe the full set of three pairs in some *Phareicranaeus*. MS B is often lacking, as in *Chiriboga* and *Metacranaeus*.

*Gonyleptidae (Ampycinae)*: MS A and B are cylindrical, slender and acuminate. MS A are always in two pairs, A1–A2. MS B1 are usually situated far from A, more ventrally (*Hexabunus*, *Hutamaia*, *Pirunipygus*), but in *Licornus* this gap is subtle. MS B are lacking in *Hernandarioides*. MS B are proximal to A in *Hexabunus* and *Pirunipygus*, at the same level as A in *Licornus*, and more distal than A in *Hutamaia*. Size of A and B is variable. In *Hexabunus* and *Pirunipygus*, A is smaller than C, and B much smaller than A. In *Hernandarioides* A is slightly larger than C. In *Hutamaia*, A is subequal to C, while B is the largest. In *Licornus tama*, setae A–C are stout, and A and B are larger than C.

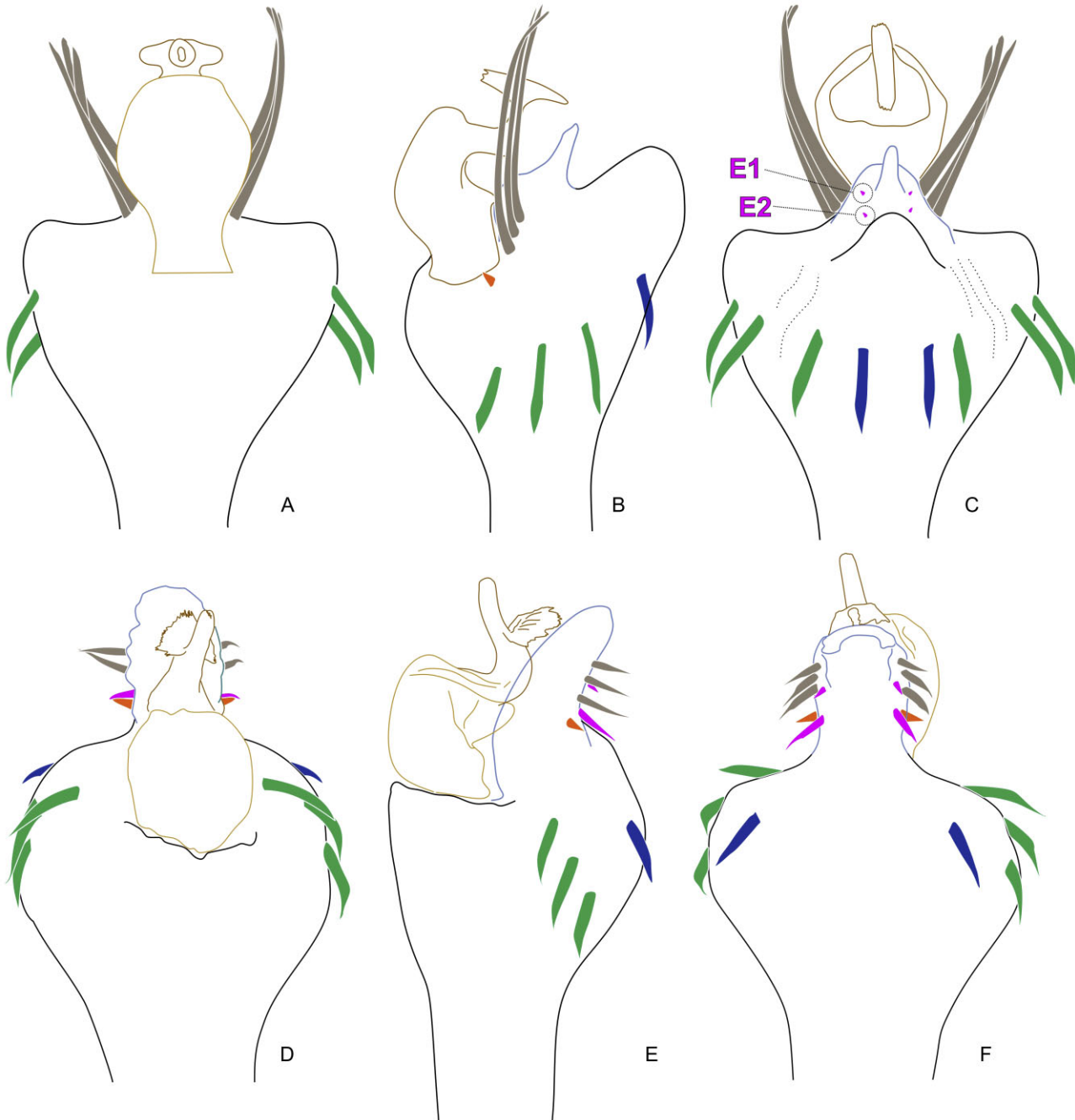


**Figure 1.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Stygnopsidae: A–C, *Hoplobunus boneti*; D–F, *Karos* sp.



**Figure 2.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Agoristenidae: A–C, *Agoristenus* sp.; D–F, *Globibunus rubrofemoratus*.



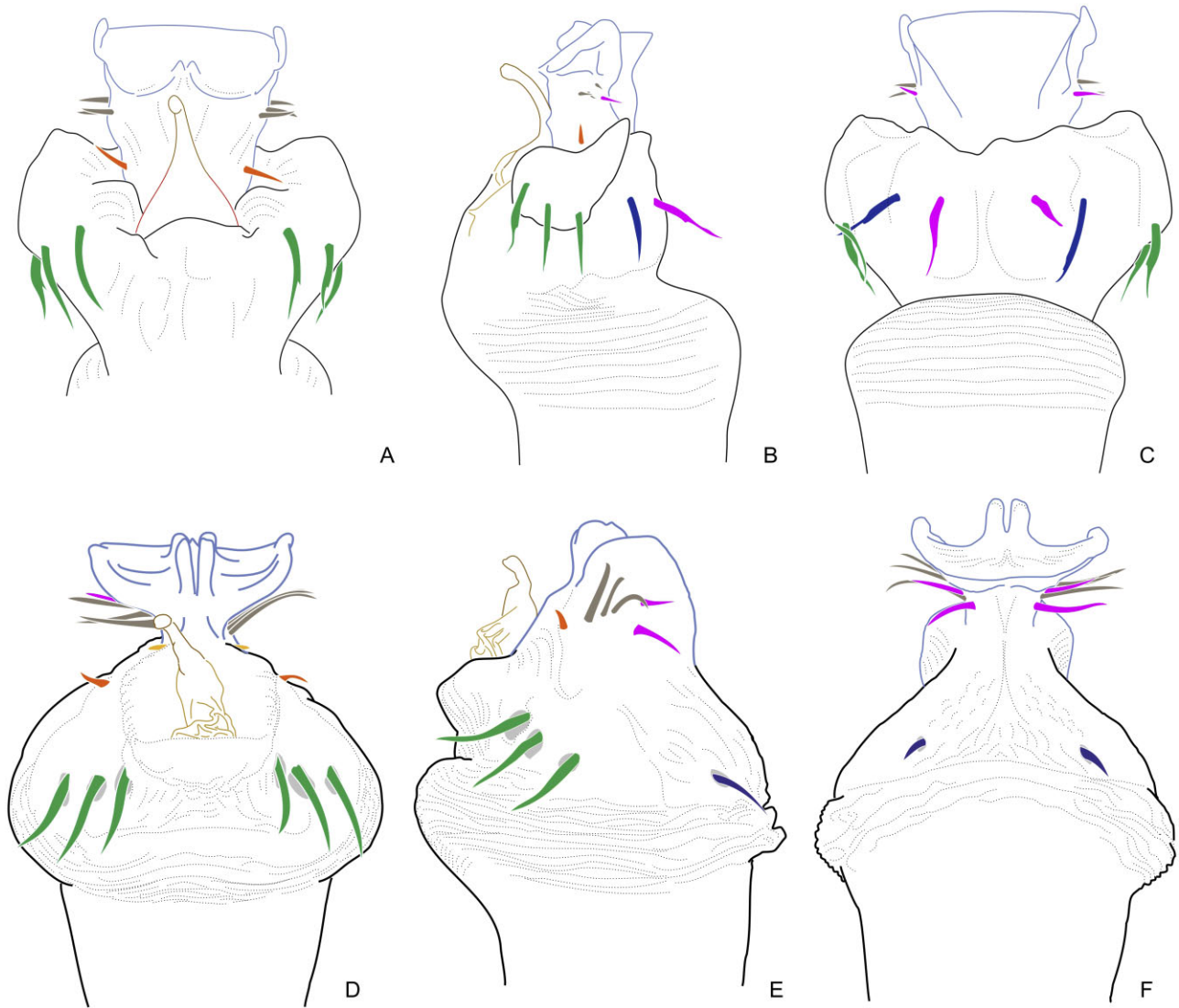


**Figure 3.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in basal Gonyleptoidea: A–C, *Gerdesius mapinguari* (Gerdesiidae); D–F, *Taquara bicoloripes* (Cryptogeobiidae).

*Gonyleptidae* (*Pachylinae* group): Multiplication is very rare in this family. MS A are almost always closely connected to B, with a clear gap between them and C. In this family A and B are not usually aligned vertically; they may form a triangle or an arch.

There are four main patterns: (1) in a few Chilean genera, B is clustered with C, not with A, which re-

sembles other families. An example is provided by *Fonckia*. (2) In the genera *Junicus* and *Marayniocus* only, B is clustered neither with A nor C, and is situated in an intermediate position, close to D. (3) In many genera, a reduced B is placed somewhat ventral to MS A1–3, which may form a slanted line or a triangle. This presumably basal condition in the family

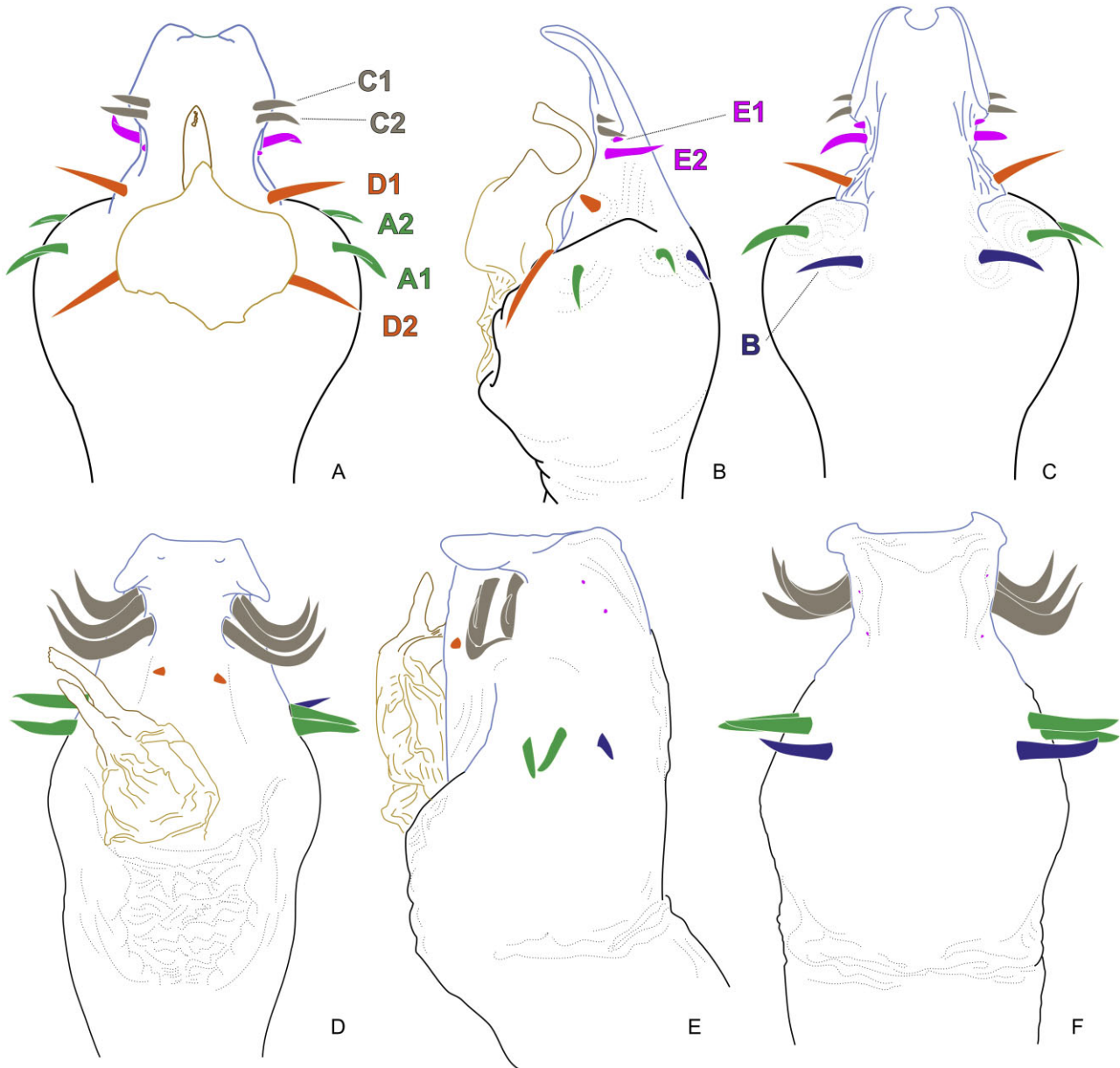


**Figure 4.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Stygnidae: A–C, *Auranus hehu*; D–F, *Jabbastygnus huttonum*.

appears in many variations, and may be seen in *Tricommatum*, *Acanthopachylus* (Fig. 13A–C), *Nanophareus* and *Acrographinotus* – in the last named we also have an example of secondary multiplication of MS A. In Cobaniinae, B is much reduced and displaced ventrally and the three A form a triangle. In Bourguiyinae, MS B is extremely reduced or absent, and there are only two slender A slightly more dorsally inserted. In Mitobatinae there is a reduced B1 + three subequal A1–3, which form a slanted line (e.g. *Encheiridium*, *Longiperna*, *Mitobates*, *Ruschia*) or a triangle (e.g. *Despirus*, *Neoancistrotus*), all from Kury (unpubl. data). (4) A crown, similar to the crescent of K92, is found in some species of Goniosomatinae (*Acutisoma*, *Heteromitobates*, *Serracutisoma*), where a

basal lobe is formed by B + 3 A, pointing proximally, with the co-linear macrosetae very short and lanceolate.

*Gonyleptidae* (K92): The crescent or arch typical of K92 is presumably a derived condition, which features a strong basal lobe of VP, bordered by a curved row of B + 3 A (Fig. 13H). In this crescent, MS A and B are typically short lanceolate and subequal. There are variations in this pattern: B is extremely reduced in Sodreaninae, varying from not reduced to strongly reduced in Caelopyginae. In Hernandariinae, MS B is typically only slightly smaller than the three A or, in a few cases, more strongly reduced. In Gonyleptinae, B + 3 A are not as short, subequal and sometimes B



**Figure 5.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Stygnidae: A–C, *Eutimesius* sp.; D–F, *Ricstygnus quineti*.

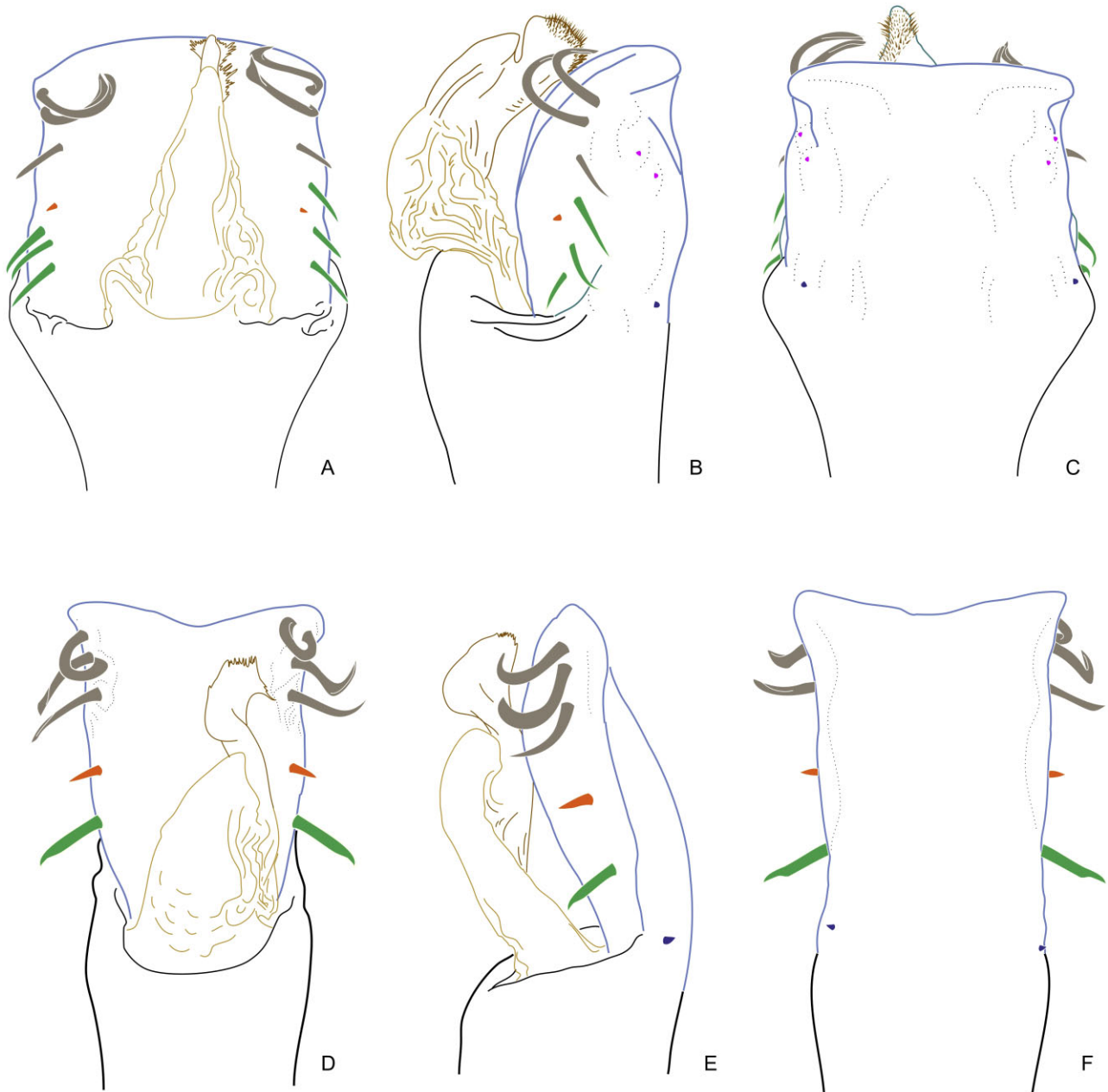
is only slightly smaller. MS A are elongate in some Caelopyginae (*Pristocnemis*, *Garatiba*).

#### GROUP C

These are typically distal or subdistal on the laterals of VP, pointing laterally or more often apically–laterally. May be short and straight, but often are enormously developed, flattened, curved, angled or even twisted to helycoidal. They mostly occur in three pairs, but sometimes they are reduced to two, only one or

lavishly multiplied. Counts on left and right sides may be asymmetrical (e.g. Ampycinae).

*Stygnopsidae*: Setae C are quite variable in shape and position: (1) stout, strongly twisted and spatulate terminally bifid (as in *Hoplobunus*); (2) short, grouped subapically (as in the *Paramitraceras–Troglostygnopsis* complex); or (3) extremely robust, straight, evenly spaced and not clustered (as in *Karos*). No common pattern for the family is discernible other than the number of two pairs C1–C2 and the subdistal insertion.



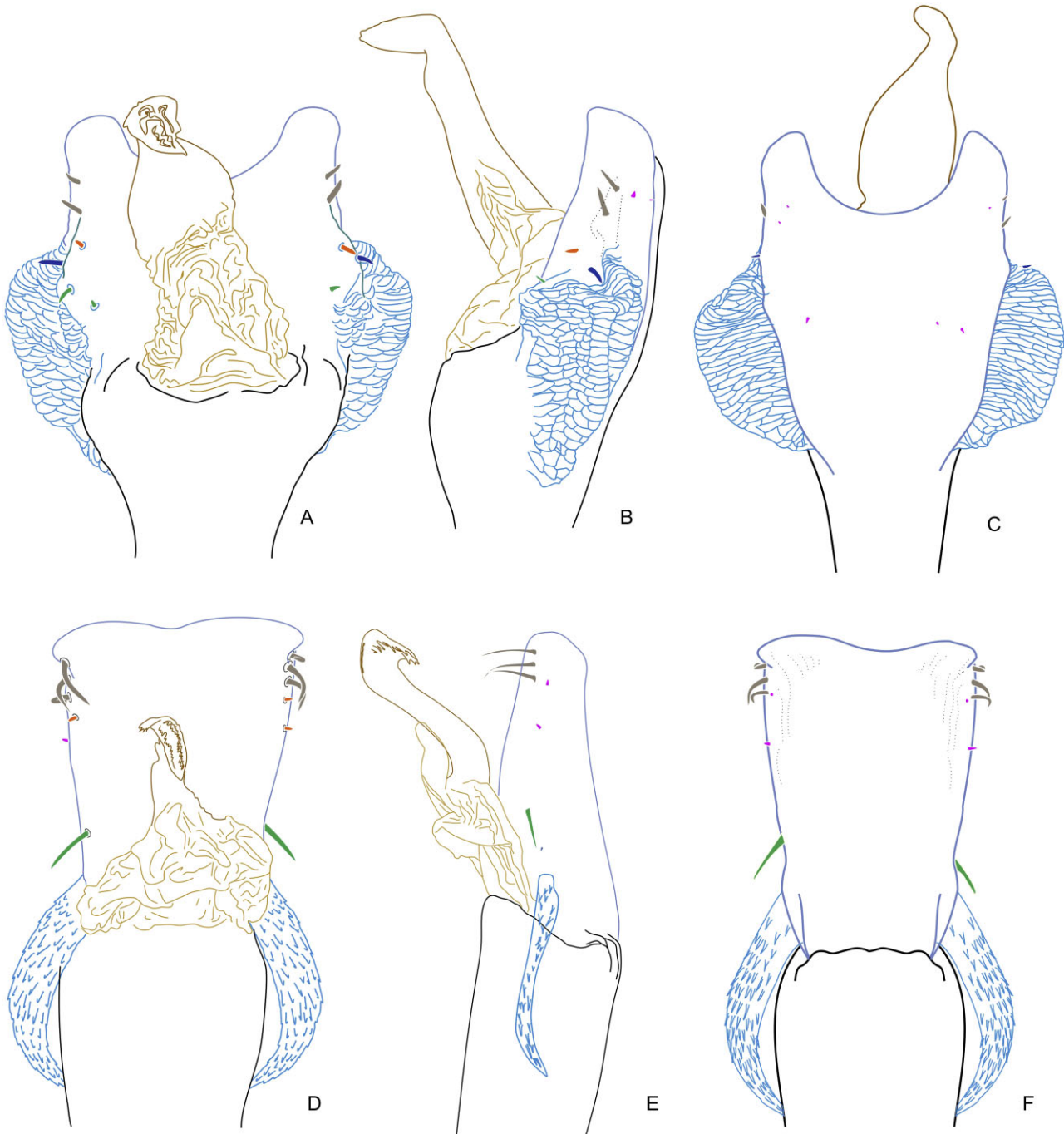
**Figure 6.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Cosmetidae: A–C, *Metarhaucus* sp.; D–F, *Sibambea* sp.

*Agoristenidae*: In this family the distal truncus undergoes drastic deformations, becoming a set malleus + lamina parva, so that it is very difficult to recognize proper homologies. Our interpretation is that MS C are lost in all *Agoristenidae*.

*Stygnidae*: The common pattern of MS C in this family is that they are cylindrical and sharp, sometimes slightly shifted dorsally. Exceptions occur in *Pickeliana*, *Protimesius*, *Ricstygnus* (Fig. 5D–F), *Sickesia* and

*Stygnus* where C1–C3 are immensely developed and curved apically, like African buffalo horns, laterally inserted, grouped closely together and isolated from the others. In some *Stygnoplus* there is an extreme reduction or apparent absence of MS C.

*Cryptogeobiidae*: In all known species of this family, MS C1–C3 are cylindrical, of variable length, from short to elongate, and uniformly arranged in a

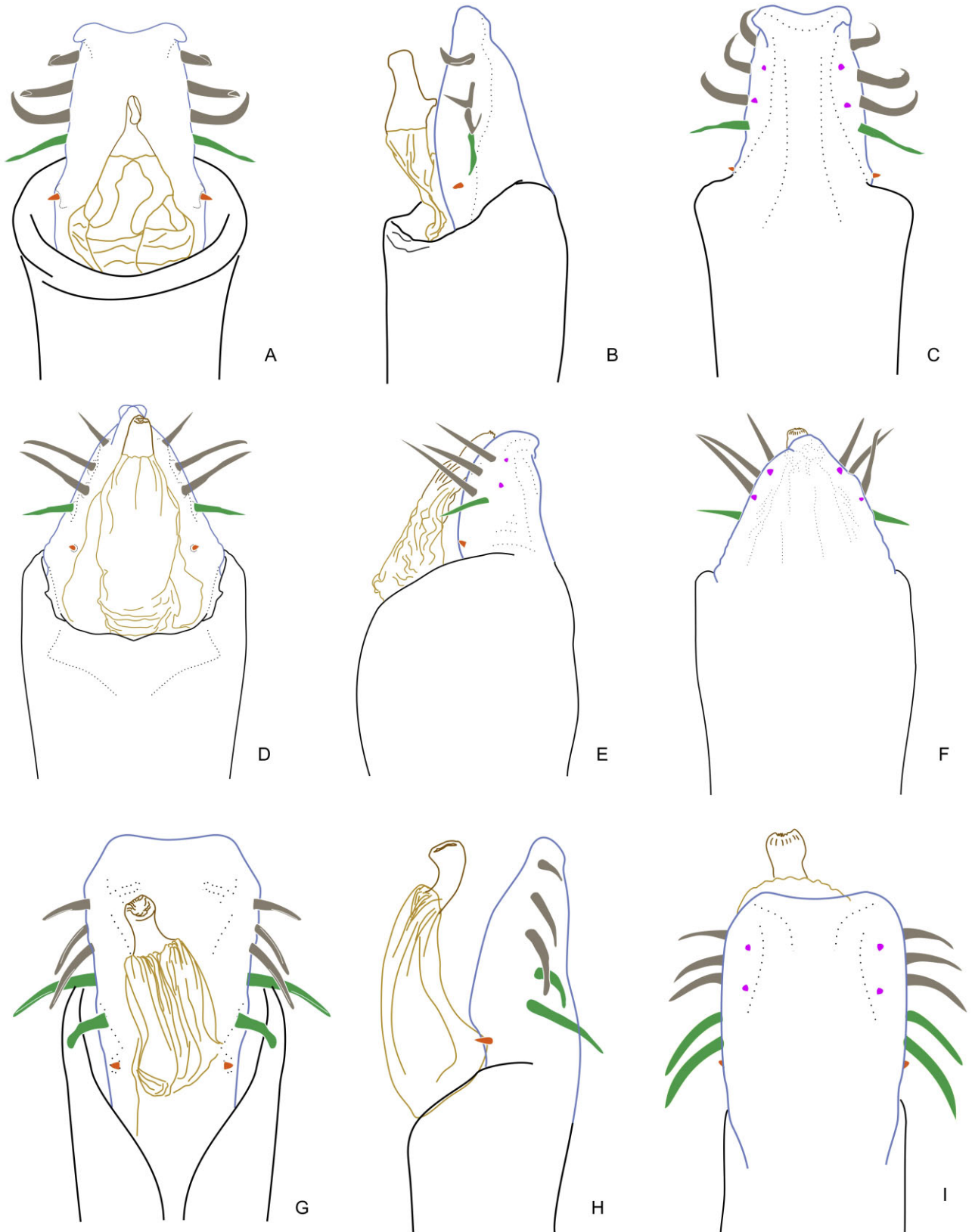


**Figure 7.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Cosmetidae and Metasarcidae: A–C, *Metalibitia paraguayensis*; D–F, *Chacoikeontus clavifemur*.

longitudinal row on the latero-distal part of the lamina parva, as show here in *Taquara* (Fig. 3D–F).

*Gerdesiidae*: MS C1–C3 are highly elongate and slender, pointing apically, inserted in a close tight row at the base of the lamina parva, which is strongly reduced (Fig. 3A–C).

*Nomoclastinae*: This group is represented by three pairs of macrosetae longitudinally aligned on the lateral edge of the VP, but not clustered, instead separated by subequal gaps (Fig. 8A–I). They may be slightly curved (*Quindina*) or almost straight (*Nomoclastes*, *Zygopachylus*). In *Nomoclastes* these setae are subdistally placed and increase subtly in size from C1



**Figure 8.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Nomoclastidae: A–C, *Quindina bella*; D–F, *Zygopachylus albomarginis*; G–I, *Nomoclastes quasimodo*.

to C3. They are straight, not especially elongate, with the tip flattened/spatulate. The distalmost pair is slightly reduced. In *Quindina* they are robust, increasing from C1 to C3, widely spaced, curved and point dorsally. *Zygopachylus* is as in *Quindina*, but MS are more lightly built and straight.

*Zamorinae*: MS C1–C3 are immensely developed, spatulate, tightly clustered on the latero-apical corners on the VP (Fig. 11D–F).

*Cosmetidae*: The common pattern (*Cynorta*, *Eucynortella*, *Metarhaucus*, *Sibambea*, *Taito*) has the full complement of three pairs of MS C1–C3, although C3 is much reduced and straight while C1 and C2 are apical, extremely robust, curved and strongly spatulate/flattened distally. *Cosmetus* is identical, except that C3 is still further reduced. *Metalibitia* possesses only two pairs, C1–C2, of much reduced MS.

*Metasarcidae*: Setae C are mostly very elongate and slender. They are projected primarily laterad, but as a result of strong twisting they may point apicad. In *Cajamarca* C1–C3 are subdistal, clustered together and strongly helycoidal from the base. In *Incasarcus*, C1–C4 or C5 are deeply intertwined but for the most part of their length point laterad. In *Chacoikeontus* C1–C3 are stunted, well separated from each other, not strongly curved and point dorsad (Fig. 7D–F).

*Manaosbiidae*: In all species studied, there are three pairs C1–C3 (in *Poecilocranaus* and *Rhopalocranaus albilineatus* there is a supplementary fourth pair C4). They are comparable to MS A (in size and shape), but they are strongly curved and always inserted latero-distally forming a longitudinal row (Fig. 9A–F).

*Cranidae*: There are typically three pairs of MS C1–C3 located on the latero-distal margin of the VP (as in *Agathocranaus*, *Chiriboga*, *Heterocranaus*, *Stygnicranaus* and *Zannicranaus*). There are also cases of secondary multiplication of setae, attaining 6–12 pairs (e.g. *Phalangodus*) or simply a reduction to a single seta C1 (e.g. many *Phareicranaus*).

The shape of these setae is variable too; some are classically cylindrical, straight and acuminate, while in some *Phareicranaus* they become spatulated and very strong (e.g. *Ph. curvipes*, *Ph. albilineatus*); in another cases these setae are cylindrical but strongly curved (e.g. *Chiriboga* and *Zannicranaus*).

In *Phalangodus* there is a secondary multiplication, they are shorter and straight, and number from C1 to C9 or C10. In *Heterocranaus* they are not as strongly rotated, and C3 is lacking. In *Zamora* C1–C3 are very similar to each other, flattened, much enlarged, only slightly curved and pointed apically.

*Gonyleptidae (Ampycinae)*: Always cylindrical, slender, substraight to curved, and aligned distally on the lateral margin of VP. Highly variable in number: there are one to two asymmetrical pairs (*Hernandarioides*, Fig. 12D–F), three pairs (*Hutamaia*, Fig. 12G–I; *Licornus*), three to four asymmetrical pairs (*Pirunipygus*) or four pairs (*Hexabunus*, Fig. 12A–C). In *Licornus* the robust MS C1–C3 are separated from each other and from A1–A2 by equal gaps, instead of being clustered distally.

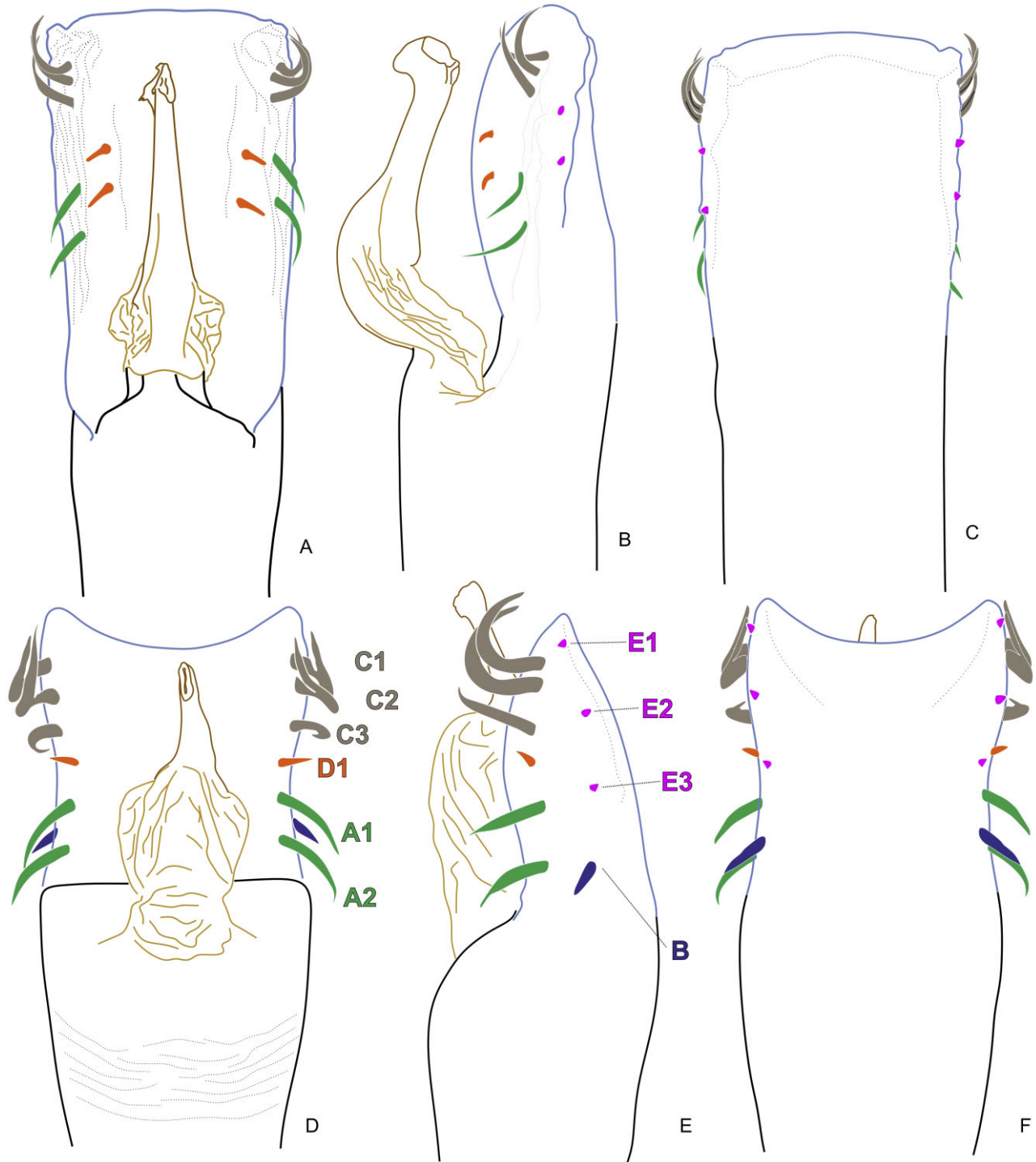
*Gonyleptidae (Pachylinae group and K92)*: In this group MS C1–C3 lie distally on the lateral edge of VP, without variations in number or insertions. *Acanthopachylus* (Fig. 13A–C) has C1–C3 cylindrical, straight, stout, chiselled, slightly increasing from C1 to C3, and with a gap between C2 and C3. In *Gonyleptes* (Fig. 13G–I) C1–C3 are slender, cylindrical, helycoidal, clustered together without a gap and point latero-apicad. In *Mitobates* (Fig. 13D–F), setae C are as in *Gonyleptes*, except that they are only slightly curved and point more laterally.

#### GROUP D

There are two pairs of setae D1–D2, sometimes reduced to only one pair or entirely lacking, typically located between groups A and C, sometimes totally laterally (e.g. *Cosmetidae* and *Gonyleptidae*), sometimes fully dorsally (e.g. in *Stygnidae*). The condition occurring outside *Gonyleptoidea*, in *Epedanidae*, seems to be D1–D2 all aligned forming the inner collar around the glans (whereas the outer collar is formed by MS A + C). It is not known if this is the ancestral state or an autapomorphy of *Epedanidae*. An intermediate position is that of dorso-lateral pairs of D (e.g. some *Cranidae*).

*Stygnopsidae*: What appears to be the primitive pattern, two pairs of well-developed dorsal setae, flanking the glans, occurs only in *Karos* (Fig. 1D–F). In the other taxa sampled here (*Hoplobunus*, the *Paramitraceras–Troglostygnopsis* complex and *Philora*), D1 is reduced and both D1 and D2 are slightly shifted laterally, while D2 is much more distal.

*Agoristenidae*: In this family, as in *Stygnidae* and *Cryptogeobiidae*, the part of the truncus homologous to VP is divided into two parts, the basal part (malleus) being swollen. In the latero-proximal part of the distal part (lamina parva) there are two pairs of extremely reduced setae here interpreted as being D1–D2 in the typical position (*Agoristenus*, Fig. 2A–C). In *Globibunus* (Fig. 2D–F), even with the radical folding of the lamina parva, the two pairs (also asymmetrically three pairs) of slender, quite elongate D can be seen, although pointing proximally.

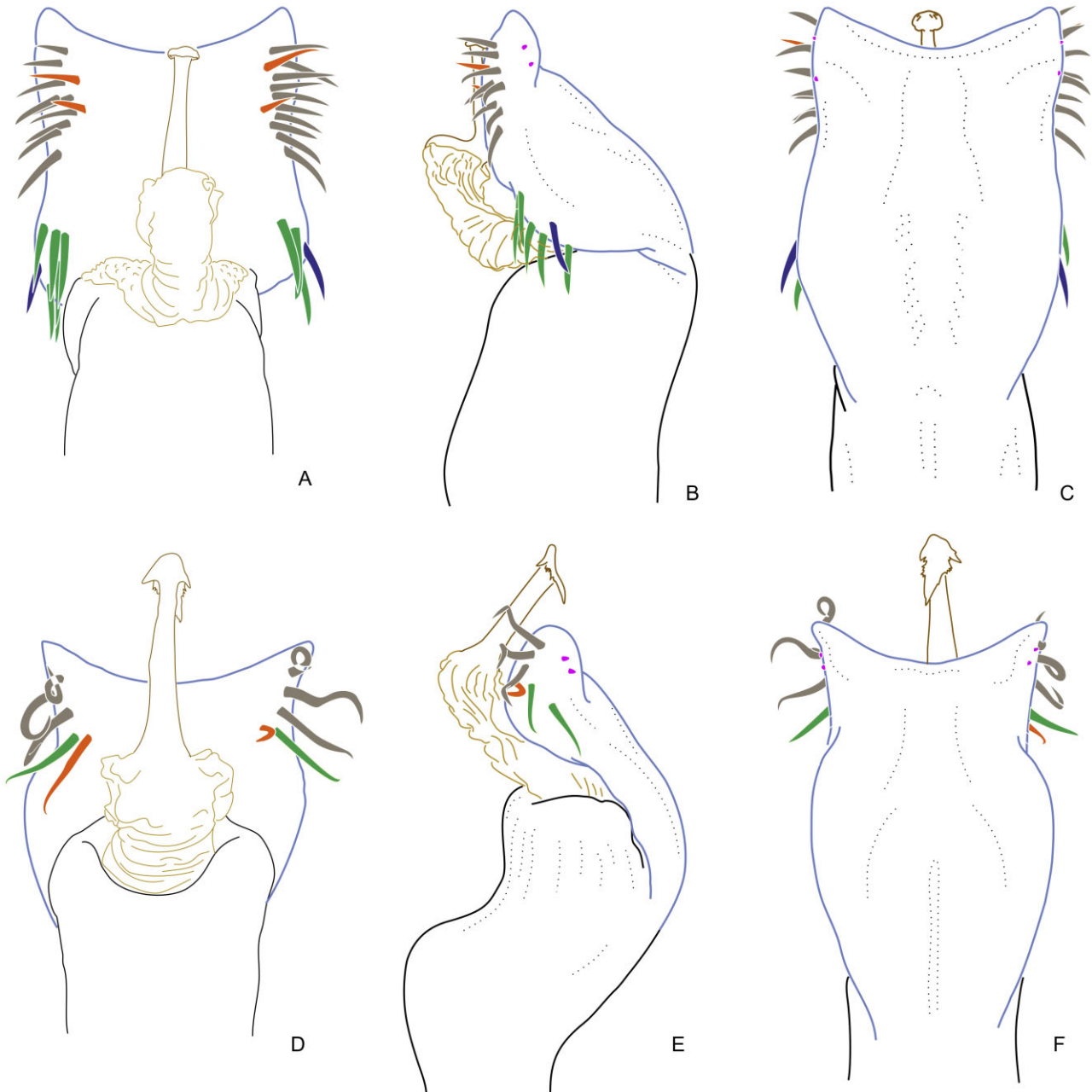


**Figure 9.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Manaosbiidae: A–C, *Syncranaus cribrum*; D–F, *Barrona williamsi*.

*Stygnidae*: Commonly two pairs of MS D are present; in this case they are large and located at the base of the lamina parva: *Stenostygnellus*, *Eutimesius* (Fig. 5A–C) and *Imeri*. In other species there is only one pair

of MS D that are much reduced and shifted distally: *Protimesius*, *Ricstygnus* (Fig. 5D–F) and *Sickesia*. In *Jime* the setae of the basal pair of MS D are immensely developed and very similar to MS C and MS A.





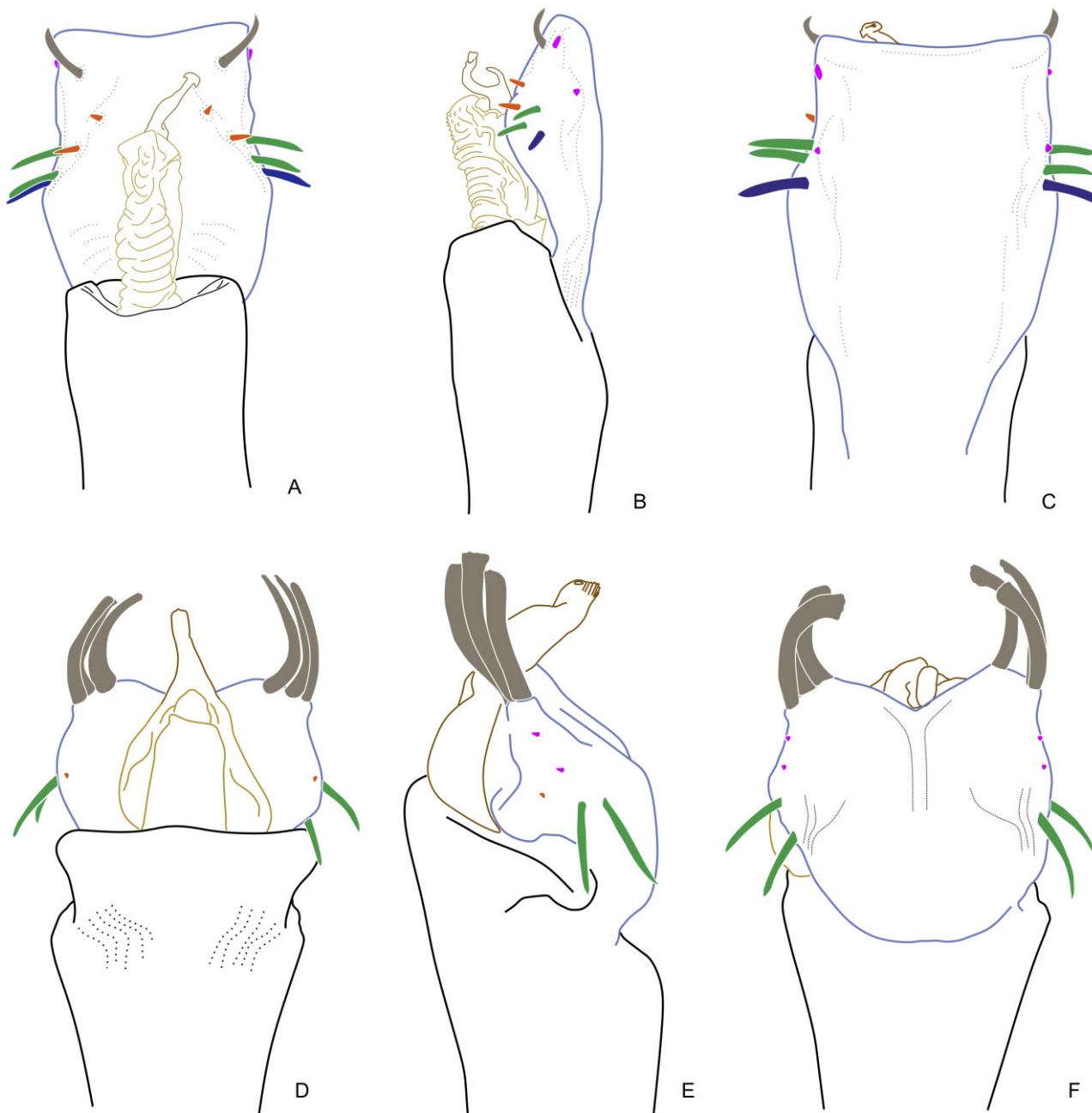
**Figure 10.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Cranaiidae 1: A–C, *Phalangodus* sp.; D–F, *Chiriboga albituber*.

*Cryptogeobiidae*: There is only one pair of small to very small MS D, located on the lateral or latero-dorsal surface of the lamina parva (Fig. 3D–F). Usually it is situated close and proximal to the row of MS C, but in a few species it is much more distally placed.

*Gerdesiidae*: The short MS D1 is located dorsally (contrasting with *Cryptogeobiidae*) near the base of the glans (Fig. 3A–C).

*Nomoclastinae*: Group D always has one pair of strongly reduced dorsal setae, located proximally on VP, close to the base of the glans in *Nomoclastes*, and more distal, near the mid-glans in *Quindina* and *Zygopachylus* (Fig. 8A–I).

*Zamorinae*: There is a single pair of MS D that are extremely reduced, and placed latero-dorsally, next to E2 (Fig. 11D–F).



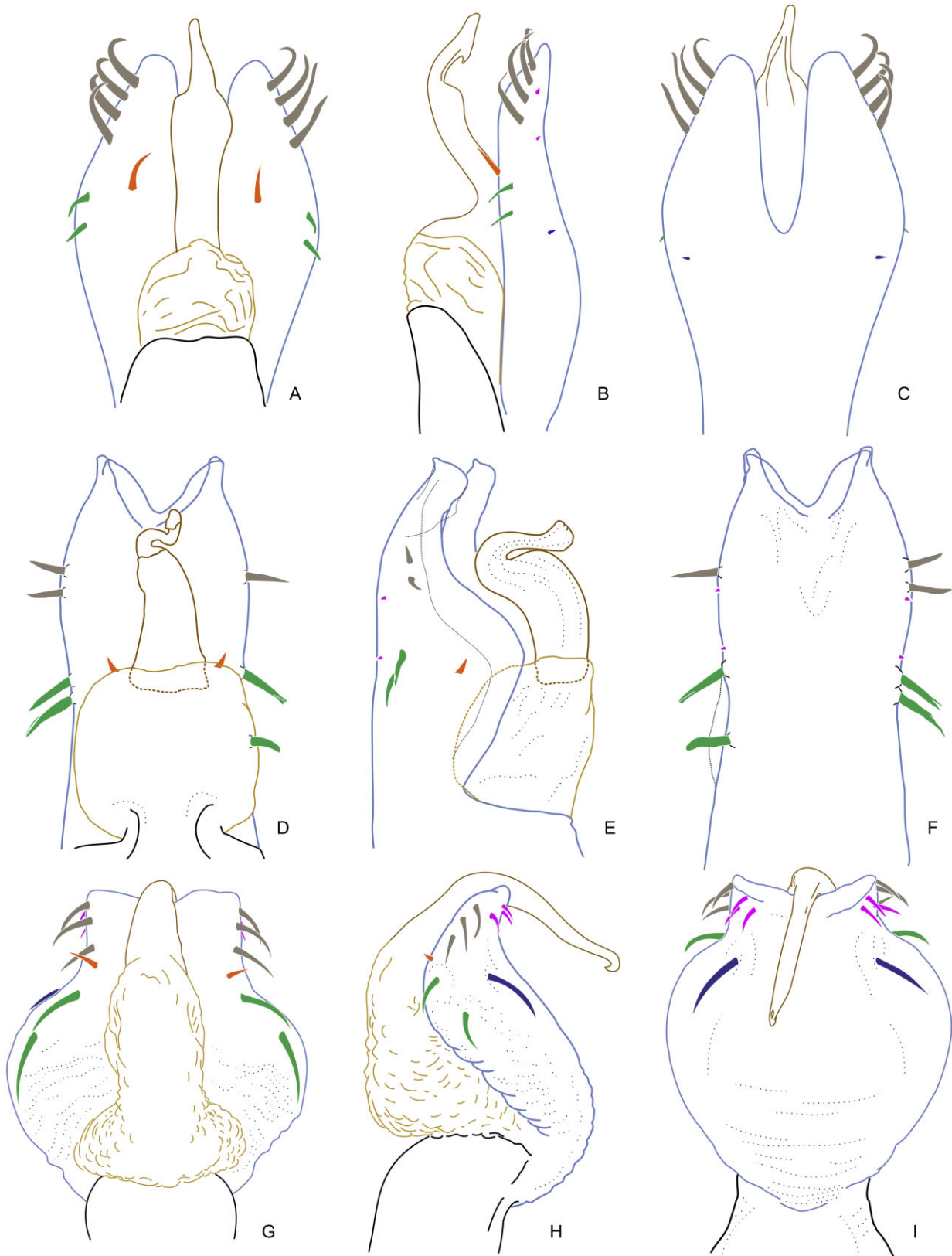
**Figure 11.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Cranaiidae 2: A–C, *Phareicranaus circumlineatus*; D–F, *Zamora granulata*.

*Cosmetidae*: There is only one pair D1 of short setae, placed on the lateral border of VP, much more distally than the base of the glans and co-linear with setae A–C (i.e. inserted laterally) in most species studied (*Cosmetus*, *Cynorta*, *Roquettea*, *Sibambea*). In *Metalibitia* (Fig. 7A–C) and *Metarhaucus* (Fig. 6A–C) D1 is inserted latero-dorsally.

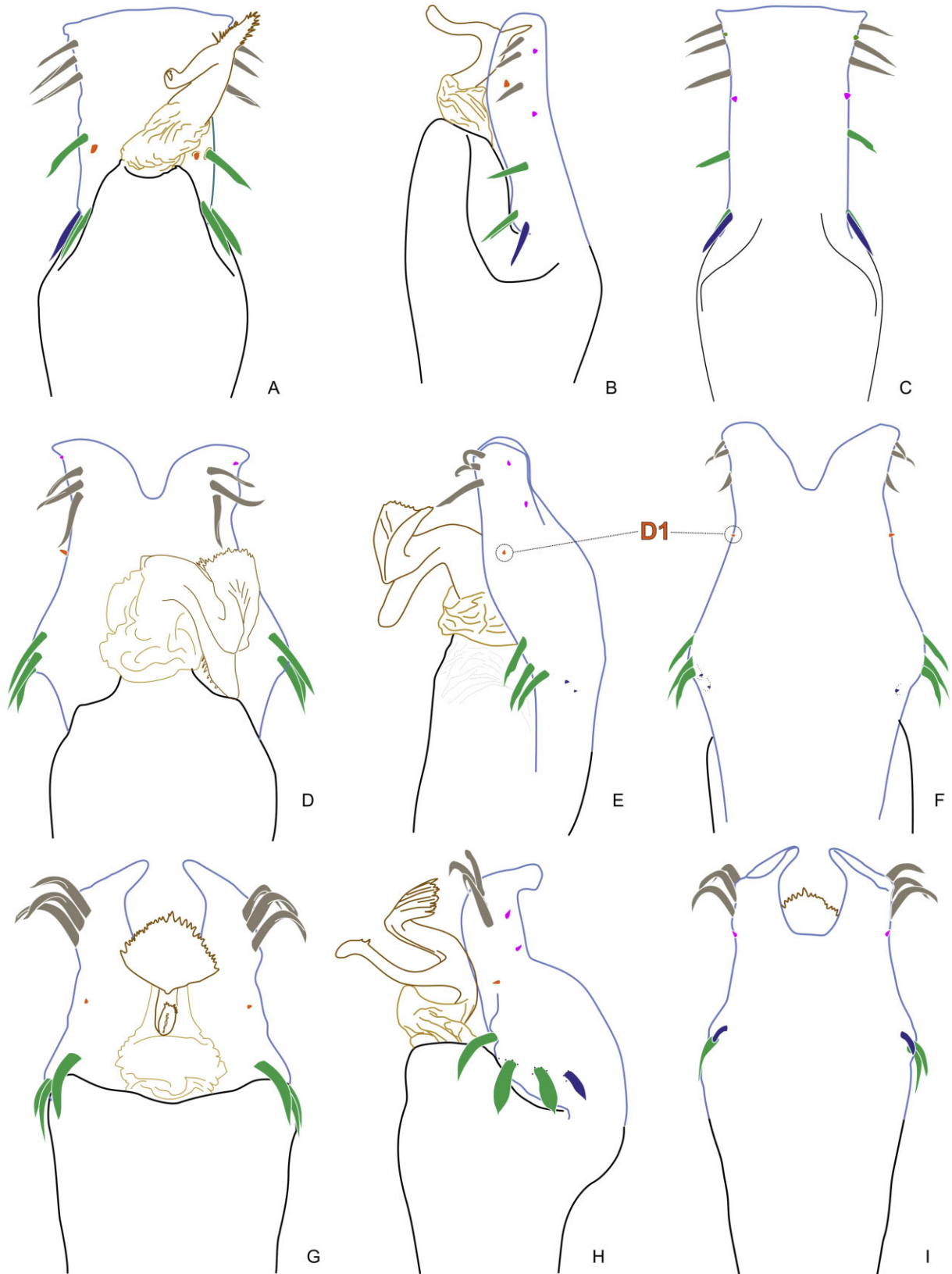
*Metasarcidae*: In this group, there is only one pair of setae, D1, present. Each seta is very small, subdistal

and intermediate in position between fully dorsal and lateral. This pattern is identical for the species illustrated in the literature and *Chacoikeontus* (Fig. 7D–F).

*Manaosbiidae*: In the species studied there may be one or two pairs of MS D, which are straight and shorter than A or C. They are always inserted latero-dorsally (*Barrona*) or fully dorsally (*Cranellus*, *Poecilocranaus*,



**Figure 12.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Ampycinae: A–C, *Hexabunus armillatus*; D–F, *Hernandarioides plana*; G–I, *Hutamaia caramaschii*.



**Figure 13.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Ampycinae: A–C, *Acanthopachylus aculeatus*; D–F, *Mitobates triangulus*; G–I, *Gonyleptes horridus*.

*Rhopalocranaus* sp., *R. albilineatus*, *Syncranaus*). D1 and D2 may be subequal (*Poecilocranaus*, *Syncranaus*) or one clearly shorter (*R. albilineatus*) (Fig. 9A–F).

*Cranaidae*: In this family the primitive condition of two pairs D1–D2 is always maintained, although shifted to the distal half of the VP. In some species D1 is migrated medially (e.g. *Metacranaus*, *Stygnicranaus*). D1–D2 are mostly as long as A or C, although there are examples of reduced size (*Phareicranaus*, *Zamora*).

*Gonyleptidae* (*Ampycinae*): There is only one pair D1, always situated dorsally on VP (Fig. 12A–I). D1 are typically small (slightly larger in *Hexabunus*) and situated more distally in mid-stylus (*Hexabunus*, *Hutamaia*) or more proximally at glans (*Hernandarioides*, *Licornus*). MS D are indistinct in the published illustration of *Pirunipygus*.

*Gonyleptidae* (*Pachylinae* group and *K92*): Configuration is very uniform. There is only one pair D1 of very short setae, placed on the lateral border, mostly colinear with setae A–C (Fig. 13A–I). In general there are gaps between C/D and D/A–B.

#### GROUP E

These are two pairs of setae, mostly small or even minuscule (and because of their size they have previously largely gone unnoticed), in many species forming a ventral rectangle or trapeze (e.g. *Ampycinae*, *Cosmetidae*, *Cryptogeobiidae*, *Nomoclastidae*), in others located subapical lateral on the flanges of VP (e.g. *Cranaidae*, many *Gonyleptidae*, *Manaosbiidae*).

*Stygnopsidae*: As with most setae in this family, size and position of MS E are variable, but they are always clearly inserted on the ventral side of the truncus. In *Hoplobunus* (Fig. 1A–C) and *Karos* (Fig. 1D–F) a pattern occurs of a rectangle, formed by four minute setae situated at the same height as MS C or even more proximally. In all other genera, there is one pair of large, more external E2 contrasting with a pair of minuscule E1. In *Troglostygnopsis* they form a trapeze, the small setae closer to each other. E1 and E2 are colinear in *Paramitraceras* and *Philora*.

*Agoristenidae*: E1 is smaller and simple, while E2 is longer and bifid in most species. In *Agoristenus* (Fig. 2A–C), both pairs of MS E1–E2 form a wide, low rectangle on the ventral surface of lamina parva. In *Globibunus* (Fig. 2D–F) they form a wide, low trapeze.

*Stygnidae* (Figs 4, 5): MS E1–E2 are typically well developed (*Auranus*, *Eutimesius*, *Jabbastygnus*), al-

though they may be short in *Protimesius* and in a group of genera they are much reduced to minute stumps (*Ricstygnus*). They are mostly subequal (*Jabbastygnus*, *Protimesius*), but sometimes E2 is much larger than E1 (*Eutimesius*). The locus of insertion varies, and in some genera (*Imeri*, *Jime*, *Stygnoplus*) E1–E2 are inserted much basally in the LP. In *Auranus* this is taken to the extreme, with E2 inserted in the malleus.

*Cryptogeobiidae*: The two pairs of MS E1–E2 are relatively well developed (Fig. 3D–F), even as robust as MS C and D in some species where these distal MS are all subequal in size. They are always situated in the ventral surface of the lamina parva, forming a rectangle, and in some cases, e.g. *Bissulla* (Kury, 2014), basalmost MS are strongly displaced basally, elongate and point apically.

*Gerdesiidae*: There are two pairs of extremely reduced MS E1–E2 located in a square on the tiny ventral surface of the lamina parva (Fig. 3A–C).

*Cosmetidae*: There are two pairs of extremely tiny setae E1–E2, latero-ventral, near the edges of VP. This pattern occurs in all species studied here (*Cosmetus*, *Cynorta*, *Eucynortella*, *Metalibitia*, *Roquettea*) except in *Sibambea*, where both E are lost.

*Metasarcidae*: The species illustrated here has two pairs E1–E2 of small setae on the lateral flange (Fig. 7D–F), but in *Incasarcus* there seem to be four pairs.

*Nomoclastinae*: Two pairs of short stump setae E1–E2 occur, forming a ventral rectangle (*Nomoclastes*) or trapeze due to the tapering shape of VP (*Quindina*, *Zygotachylus*) (Fig. 8A–I).

*Zamorinae*: MS E1–E2 are extremely reduced and form a very wide rectangle because the setae are strongly displaced to lateral instead of latero-ventral or ventral. Although they are fully lateral, there is no flange associated (Fig. 11D–F).

*Manaosbiidae*: In this family there is a very uniform scheme with two pairs of very short setae E1–E2 present on the latero-distal flanges of VP, often blunt-rounded instead of acuminate. This scheme is illustrated here in *Poecilocranaus*, *Rhopalocranaus* sp. and *Syncranaus* (Fig. 9A–C), but see also the same in *Barrona* (although this species has three pairs E1–E3), *Narcellus* and *Rhopalocranaus albilineatus* Goodnight & Goodnight, 1947.

*Cranaidae*: In this family, the E group is represented by two pairs of very small setae, frequently rounded, mostly located on a flange in ventro-lateral position

in a distal portion of the VP. They are sometimes difficult to see, located in a depression and covered by many microsetae. An example is provided by *Zannicranus*.

*Gonyleptidae (Ampycinae)*: Although a typical flange is lacking, MS E1–E2 are GG-like: reduced, and placed distally at laterals of VP. In *Hutamaia* there is a supernumerary E3 along the usual rectangle E1–E2 (also visible in other *Hutamaia* in Tourinho & Mendes, 2014).

*Gonyleptidae (Pachylinae group and K92)*: There are generally two pairs of short setae E1–E2, located on a flange in ventrolateral position in a distal portion of the VP (Fig. 13A–I). In Bourguiinae, there is no flange, probably lost because of the abnormal development of C, and MS E migrated more proximally.

#### MAIN RESULTS OF THE ANALYSIS

All three analyses using implied weight were extremely similar, producing only one most-parsimonious tree each (Table 6). The one with concavity 3 is used to illustrate (Figs 14, 15) the phylogenetic hypothesis discussed here. As may be seen from the numerical values (Fig. 15), Gonyleptidae, Metasarcidae/Cosmetidae (Me/Co) and Microsetata have only moderate support, while GG and its interrelationships are only weakly supported. On the other hand, each of the other families is strongly supported, such as the Ampycinae and ampycine-less Gonyleptidae. The equal weight analysis yielded 16 equally most parsimonious trees and their strict consensus (Fig. 16) is notably congruent with the tree above, only failing to recover the Me/Co and GG clades (Navajo rugs in Fig. 15). The main results and taxonomic implications are:

- 1 the Microsetata of Kury (2014) are recovered including Me/Co sister to an expanded GG;
- 2 the genera *Quindina* (Cranidae) and *Zygopachylus* (Manosbiidae) are transferred to Nomoclastidae rank nov., hitherto regarded as a subfamily of Stygnidae, now a sister group of the Microsetata;
- 3 Zamorinae, currently placed in Cranidae, is the sister group to Nomoclastidae, and is therefore transferred to this family;
- 4 an expanded Gonyleptidae is recovered, including Manosbiidae and Cranidae, but the independence of these families is also recovered because the Gonyleptidae *stricto sensu* do form a clade;
- 5 the Ampycinae, in spite of many particularities, are recovered inside Gonyleptidae;
- 6 the zamorine-less Cranidae are recovered as a monophyletic sister group to Gonyleptidae, but not nested inside it.

## TAXONOMIC RESULTS

### SUPERFAMILY GONYLEPTOIDEA SUNDEVALL, 1833

*Diagnosis*: Distitarsus of leg I with 3 articles (with secondary regressions to 2 articles in some species). Tarsal aggregate pores widespread (uninvestigated in many species). A distinct setigerous plate recognizable (except in Stygnopsidae) either as a set malleus + lamina parva or as a ventral plate. Glans as a haematodocha free on apical truncus (except on Stygnopsidae). Pattern A–E of macrosetae recognizable on penis. MS C forming a longitudinal row on latero-distal region of penis (except in Stygnidae).

*Subtaxa included*: Agoristenidae, Cryptogeobiidae, Gerdesiidae, Laminata, Stygnopsidae, Stygnidae.

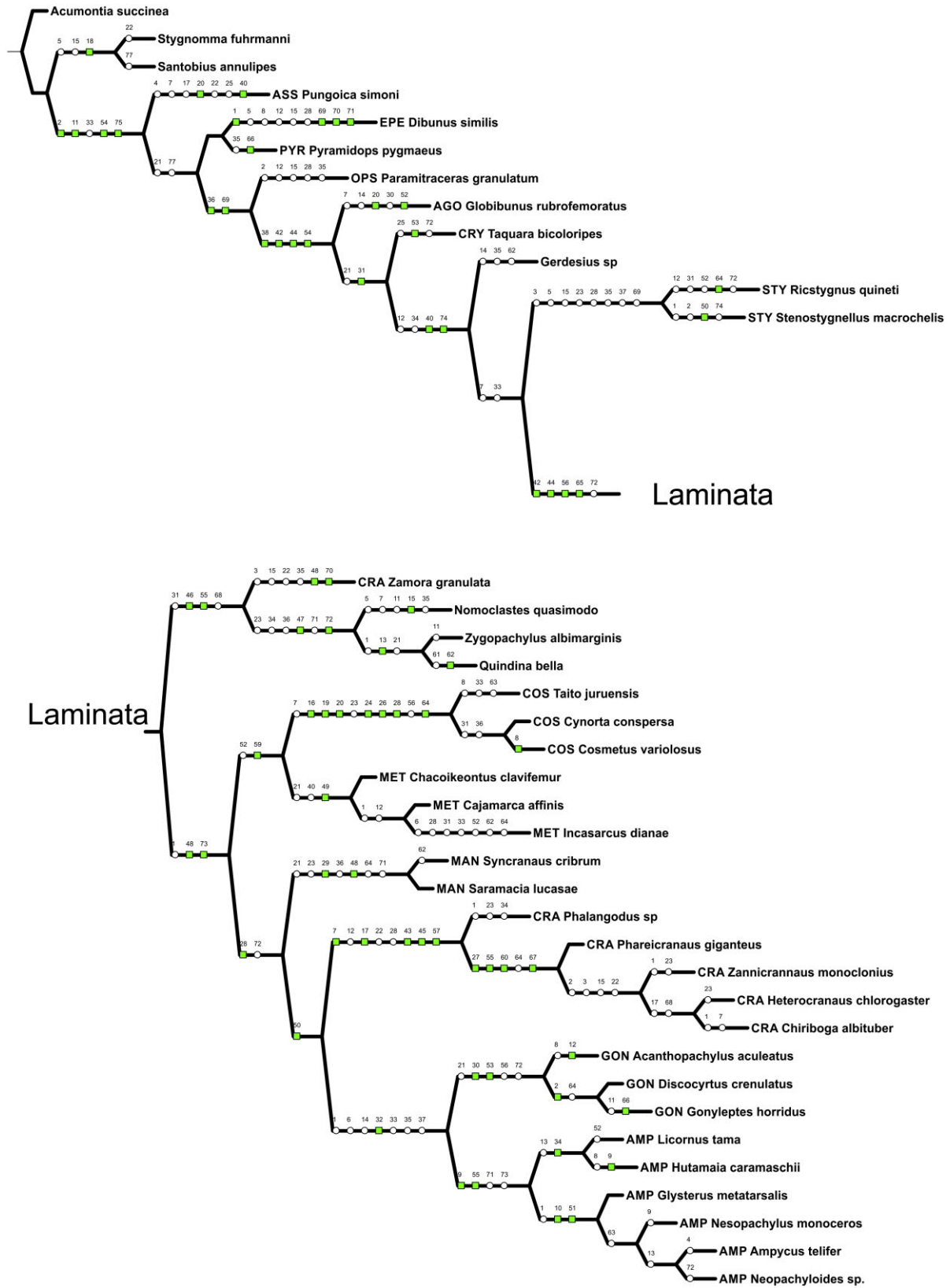
### FAMILY STYGNIDAE SIMON, 1879

#### *JABBASTYGNUS* GEN. NOV.

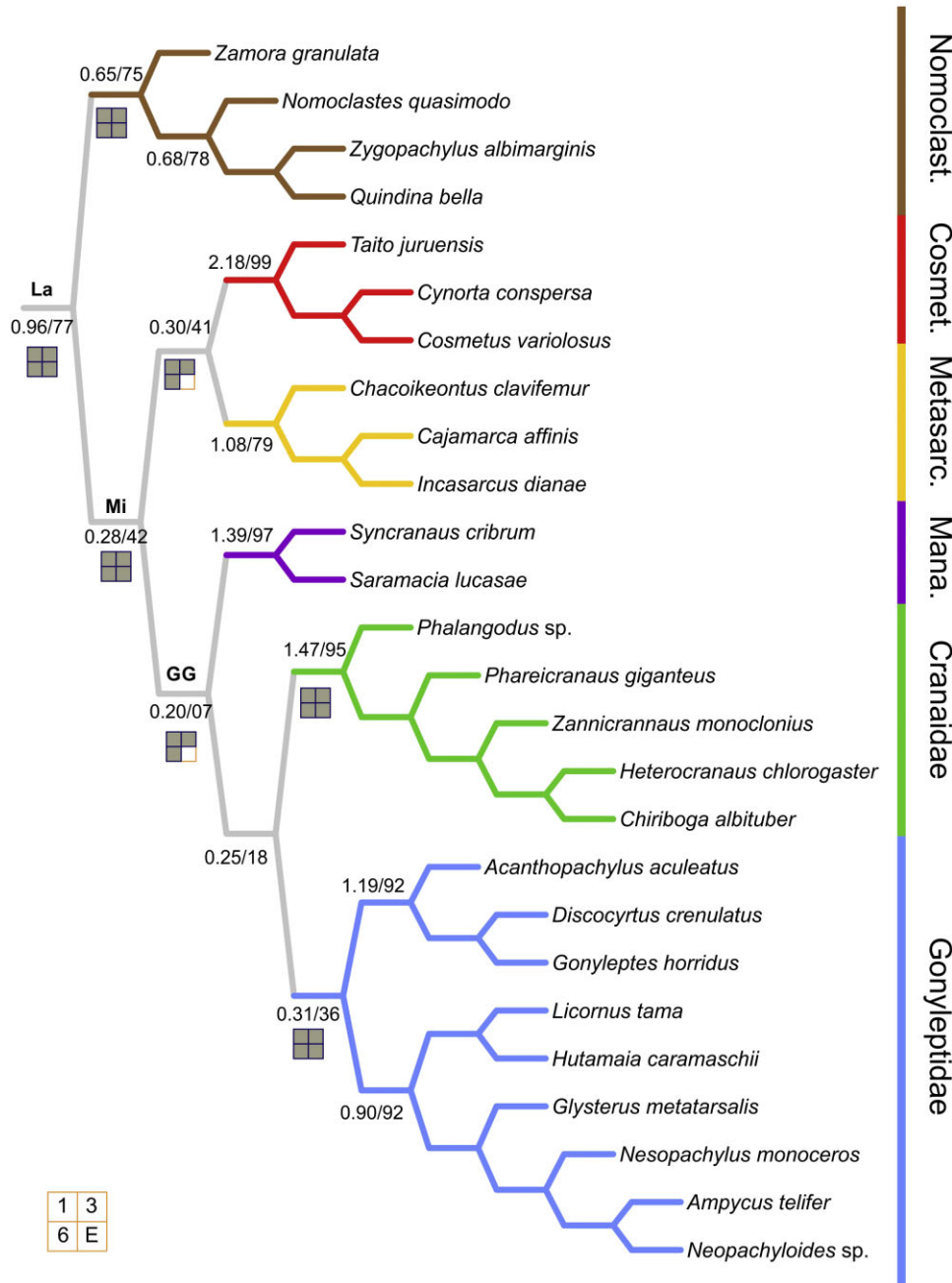
*Etymology*: Genus name is derived from Jabba the Hutt, a character from *Star Wars*, complemented by the pre-existing genus *Stygnus* Perty, 1833. This refers to the shape of male genitalia which resembles the grotesque face of this character. Gender masculine.

*Type species*: *Jabbastygnus huttoni* sp. nov.

*Diagnosis*: The new genus is here primarily compared with three other genera of Stygninae (see Discussion for details). Dorsal scutum outline alpha, but with posterior margin widened (like *Ricstygnus*, unlike *Auranus*, rectangular or *Stygnus*, pyriform or convex without constrictions); interocular mound high, with two short spines in longitudinal row (unlike *Ricstygnus*, high, with one high spine; *Stygnus*, only the spine without mound; *Auranus*, without interocular mound, but with the whole carapace strongly convex); mesotergum divided into 4 areas (as in *Ricstygnus*, unlike *Auranus*/*Stygnus* with 3 areas); scutal area III unarmed (as in *Ricstygnus*, unlike *Auranus*/*Stygnus*, with a pair of high acuminate spines); basitarsomeres IV thickened (unlike *Auranus*, *Ricstygnus*, *Stygnus*); VP separated from truncus by a deeply multi-wrinkled toroidal region (as in *Auranus hehu*; unlike *Ricstygnus*/*Stygnus*); complex truncus-glans co-linear (as in all other Stygninae, except *Auranus*, where VP arises after an abrupt change in the direction of truncus); lamina parva strongly thickened dorso-ventrally (as in *Auranus*, *Ricstygnus*, *Stygnus*); lamina parva with a flat, rounded, subquadrangular platform + a pair of erect mid-dorsal lobes (as in *Auranus hehu* and *A. parvus*, unlike any other Stygninae); MS A1–A3 forming slanted row widely separated from B, which is ventrally inserted (as in *Auranus*; unlike *Ricstygnus*/*Stygnus*, with A1–A2 transverse, contiguous with B); MS C1–C3, slender,



**Figure 14.** Cladogram depicting proposed phylogenetic relationships for Gonyleptoidea. This tree was the only one obtained with concavity = 3, and the characters are mapped in the unambiguous optimization.



**Figure 15.** Cladogram depicting proposed phylogenetic relationships for Laminata. The small ‘Navajo rugs’ at selected branches indicate which of the four analyses supports a given clade. A key to the analyses is given in the set of four squares at the bottom left, abbreviated as: 1 = implied weights, concavity 1; 3 = same, concavity 3; 6 = same, concavity 6; E = strict consensus of the analysis under equal weights. Numerals at branches represent absolute Bremer support/standard Bootstrap resampling percentage values. GG, Greater Gonyleptidae; La, Laminata; Mi, Microsetata.

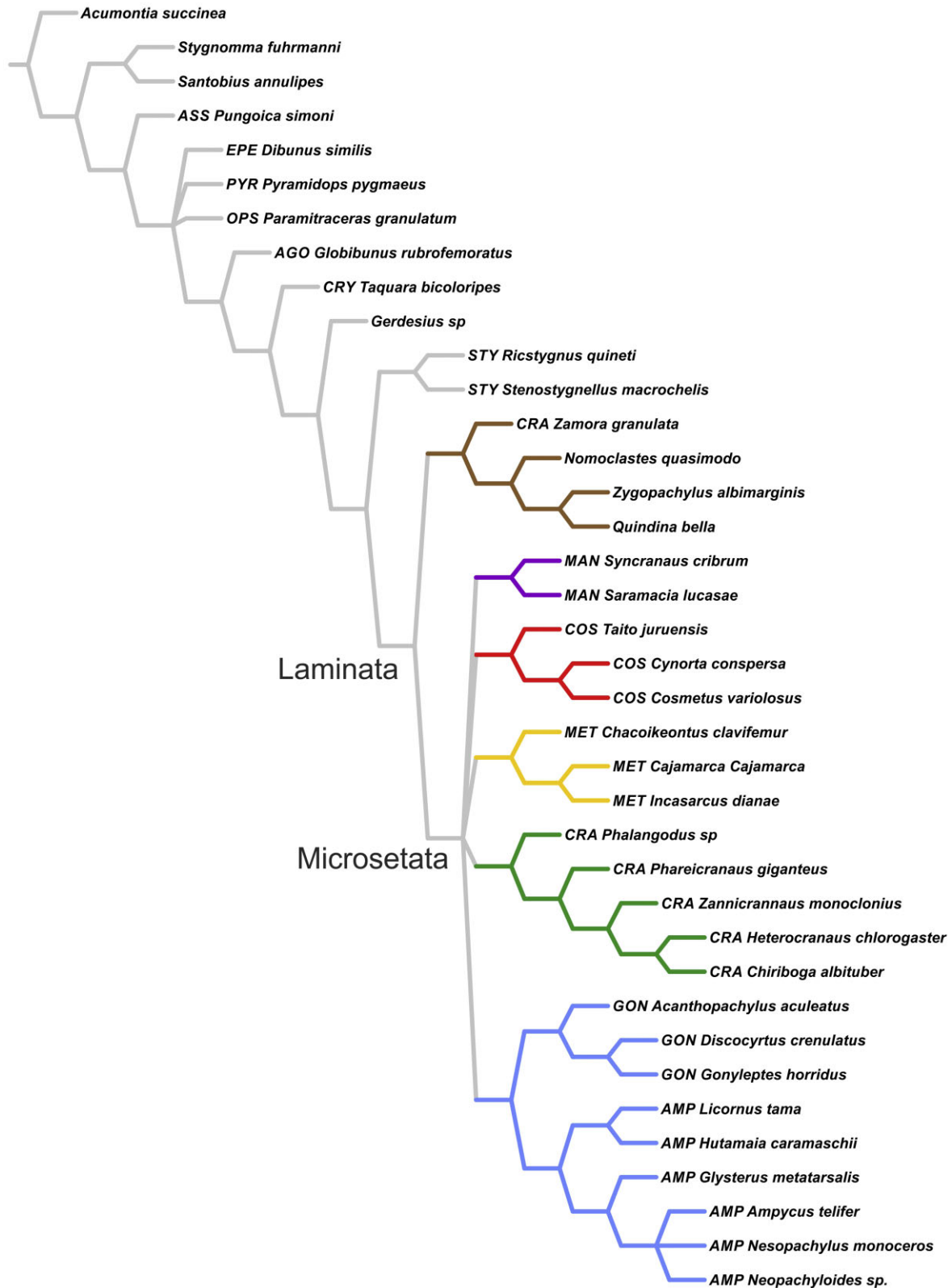
in transverse sub-distal row (as in *Auranus*; unlike most other Stygninae shaped like immense buffalo-horns in longitudinal row); MS E1–E2 elongate, closely set (unlike *Ricstygnus/Stygnus*, with minuscule E1–E2 inserted close to each other; unlike *Auranus*, with E1 widely separated from E2, both elongate).

**JABBASTYGNUS HUTTORUM SP. NOV.**

*Etymology:* The Hutts are a fictional alien species in the *Star Wars* universe.

*Type data:* ♂ holotype (IAvH 3000110) Colombia, Boyacá, San Pedro de Iguaque, Morro Negro, Transecto





**Figure 16.** Cladogram depicting proposed phylogenetic relationships for Gonyleptoidea. This is the strict consensus of the 4th analysis (under equal weights). Colour code for branches represent the families and are the same as in Figure 15. Three relevant clades not recovered under equal weights are Gonyleptoidea, Me/Co and GG (see Discussion for details).

**Table 7.** Body and appendage measurements of *J. huttonum*

CL	1.7 (1.8)	Ti I	1.1 (1.1)
AL	1.9 (1.8)	Ti II	1.8 (1.7)
CW	2.4 (2.3)	Ti III	1.5 (1.3)
AW	2.7 (2.8)	Ti IV	2.0 (2.0)
ID	1.4 (1.4)	Fe I	1.7 (1.5)
Pp Fe	2.1 (1.9)	Fe II	2.5 (2.3)
Pp Pa	1.2 (1.1)	Fe III	2.1 (2.0)
		Fe IV	2.5 (2.4)

♂ holotype and ♂ paratype (in parentheses). A, abdomen; C, carapace; Fe, femur; ID, interocular distance; L, length; Pa, patella; Pp, pedipalpus; Ti, tibia; W, width.

1, secondary forest, pitfall trap 3245 m (05°38'32.1"N, 73°28'58.7"W), 13–15.v.2003 Elvia Lucía González & Claudia Reina leg.; 1 ♂ paratype (IAvH 3000042) Colombia, Boyacá, Villa de Leyva, Santuario de Fauna y Flora Iguaque, Sitio Laguna Iguaque 3450 m (5°38'N, 73°29'W), 16.x.1998, D. Forero leg.

*Description of male holotype:* Measurements of body and appendages of both holotype and paratype males in Table 7.

*Body (Fig. 18A, B):* Dorsal scutum outline alpha (subrectangular with rounded sides and widened at mid-length), posterior margin slightly convex. Cheliceral sockets shallow, flanked by two pairs of small triangular processes. Anterior corners of carapace each with two setiferous tubercles. Eyes placed on separate individual mounds, space between them and interocular mound densely covered with minute granules. Interocular mound elevated, bearing two acuminate spines in longitudinal row, and placed very close to anterior margin of carapace. Posterior half of carapace strongly convex. Mesotergum divided into four areas, area I divided into left and right halves, its outline distorted both by scutal groove and by projection of area II, so both halves touch each other only at a small point. Areas III and IV partially fused in the median portion. Mesotergal area I with pair of granules, areas II–IV each with a transverse row of granules accompanied by supplementary median ones. Posterior margin of scutum and free tergites I–III each with a transverse row of acuminate setiferous tubercles.

*Appendages:* Cheliceral bulla with two pairs of ectal tubercles, cheliceral hand kidney-like, swollen (Fig. 17A–C). Pedipalpal femur and patella short, the former with longitudinal ventral row of setiferous tubercles, otherwise entirely unarmed (Fig. 18C). Pedipalpal tibia and tarsus each with ventro-ectal and ventro-mesal row of spines, spine count tibia (v-e IiIiIiI and v-m IiIi), tarsus (v-e IiiiI and v-m IiIiii) (Fig. 18C, D). Legs I–IV short

(Fig. 18A). Tr II with dorso-apical tubercle. Tr III subcubic, robust, with large retro-apical tubercle (Fig. 17A). Fe III with pro-dorsal, pro-ventral and retro-ventral rows of acuminate setiferous tubercles, the two last growing distally. Fe III also with stout proximal retro-dorsal setiferous tubercle. Ti III uniformly thick, with longitudinal rows of setiferous tubercles, the retro-dorsal and retro ventral stouter. Cx IV armed with strong dorsal and pro-dorsal acuminate tubercles. Tr IV with two larger dorsal tubercles amidst smaller ones, and one retro-ventral setiferous tubercle. Fe IV (Fig. 18E–G) with pro-ventral and retro-ventral rows of acuminate setiferous tubercles, divergent distally and one stout retro-dorsal setiferous tubercle. Ti IV with six longitudinal rows of strong setiferous tubercles, retro-ventral the strongest. Basal tarsomeres IV thickened (Fig. 18H). Tarsal claws III–IV subparallel, unpectinated, tarsi without scopulae. Penultimate and antepenultimate tarsomeres of leg IV short, wedge-shaped. Last tarsomere of leg IV moderately elongate, intermediate in shape between the short wedge of Heterostygninae and the elongate foot of Stygninae. Tarsal counts: 6(3)–6(3)/10(4)–10(3)/6–6/7–7.

*Genitalia (Fig. 19A–D):* Truncus apical inflated as a torus encircled by multiple small wrinkles dorsal and lateral plus a few thick ventral folds. Malleus hemispherical, projected mid-dorsally as a podium where the glans rests. Malleus contains MS A1–A3 forming a dorso-lateral arch and B, making part of the same arch, but separated by a wide gap and inserted ventrally. Lamina parva complex-shaped, formed by: (1) a columnar base, compressed laterally bearing MS C–E; (2) a flat subquadrangular platform projected laterally into two wide lobes; and (3) a pair of erect mid-dorsal lobes. MS D1 small, dorso-lateral, inserted distally, at the junction glans/stylus; MS C1–C3 forming a transverse row just below platform; MS E1–E2 long, forming a longitudinal ventro-lateral row.

*Variation:* Paratype has only one spine atop the interocular mound. Tarsal counts of paratype: 5(3)–5(3)/9(3)–8(3)/6–5/6–6.

#### UNRANKED TAXON LAMINATA NAME NOV.

*Etymology:* The name refers to the evolutionary novelty of the formation of a *lamina ventralis* (or ventral setigerous plate), different from other setigerous plates in Laniatores.

*Cladistic node-based definition:* The last common ancestor of *Quindina* (oldest genus of Nomoclastidae) and *Gonyleptes* (oldest genus of Microsetata), and all descendants of that ancestor.



**Figure 17.** *Jabbastygnus huttoni* sp. nov., male holotype (IAvH 3000110): A, habitus, dorsal view; B, same, lateral view; C, carapace, pedipalpi and chelicerae, frontal view; D, free tergites and sternites, posterior view. Scale bars = 1 mm.

*Diagnosis:* Distal truncus well cut as a podium and flattened rectangular VP well marked. Glans columnar (except in Cosmetidae and Gonyleptidae). MS A–B inserted on lateral border of VP, not forming a girdle around truncus.

*Included subtaxa:* Microsetata, Nomoclastidae.

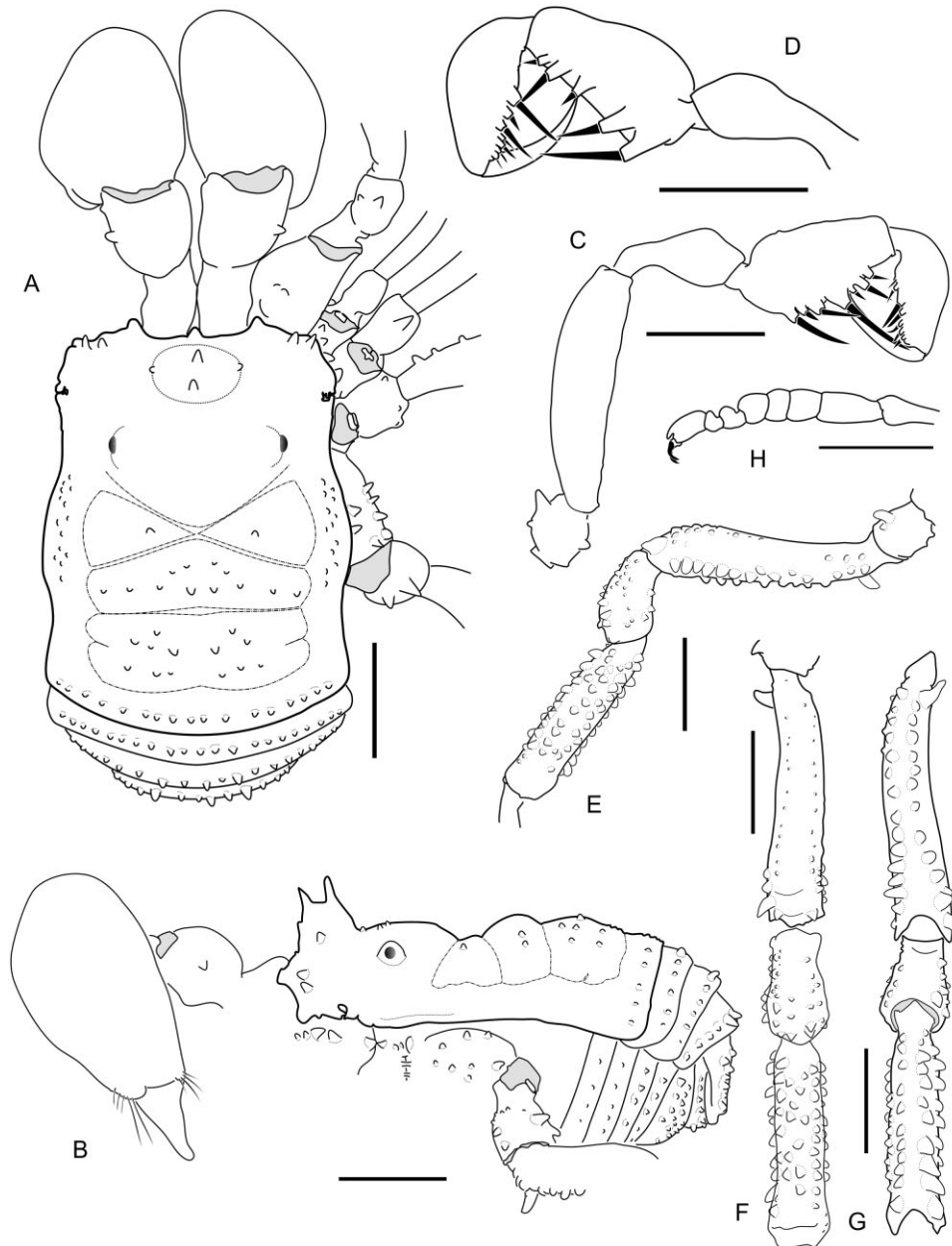
FAMILY NOMOCLASTIDAE ROEWER, 1943 RANK NOV.  
Gonyleptidae Nomoclastinae Roewer 1943: 14.

*Diagnosis:* Outline of dorsal scutum beta or zeta. Coxa IV dorso-apically unarmed. Ventral plate short, as long as truncus width. Latero-distal borders of VP without flange. Macrosetae B lacking. Macrosetae E small, inserted ventrally, forming distal rectangle. Paired latero-distal patches of scale-bristles (type 4) absent. Glans

penis without dorsal process. Stylus very short atop a triangular glans.

*Combined distribution:* Colombia, Ecuador and Panama.

*Remarks:* Male genitalia of *Nomoclastes* were studied in detail for the first time for this project and we found that (1) the basic structure strikingly resembles those of *Quindina* and *Zygobunus* and (2) there is no compelling evidence to include Nomoclastinae as Manaosbiidae or Stygnidae. That motivated a cladistic analysis. The *Zygobunus*-like manaosbiids were already informally recognized by some researchers as departing from the typical manaosbiid facies as established in Kury (1997a) while *Nomoclastes* looks awkward inside Stygnidae. *Quindina* is still officially in Cranida as of 2003 (Kury, 2003a). Giribet *et al.* (2010) recognized a more restricted Gonyleptoidea, excluding the Assamiidae and Stygnopsidae, Manaosbiidae



**Figure 18.** *Jabbastygnus huttoni* sp. nov., male holotype (IAvH 3000110): A, habitus, dorsal view; B, same, lateral view; C, right pedipalpus, ectal view; D, right pedipalpus Pa–Ta, mesal view; E, right leg IV, prolateral view; F, same, dorsal view; G, same, ventral view; H, tarsus IV, lateral view. Scale bars = 1 mm.

appeared as polyphyletic, the classic *Rhopalocranaus* appeared as a sister group to all the remaining families, while *Zygopachylus* grouped with Cosmetidae. In Sharma & Giribet (2011) the internal relationships of Gonyleptoidea were radically different from previous studies, and they did not include any typical Manaosbiidae, only *Zygopachylus*, which appeared in a wide polytomy including also Cosmetidae, Cranaiidae and Gonyleptidae. None of these analyses included *Nomoclastes*.

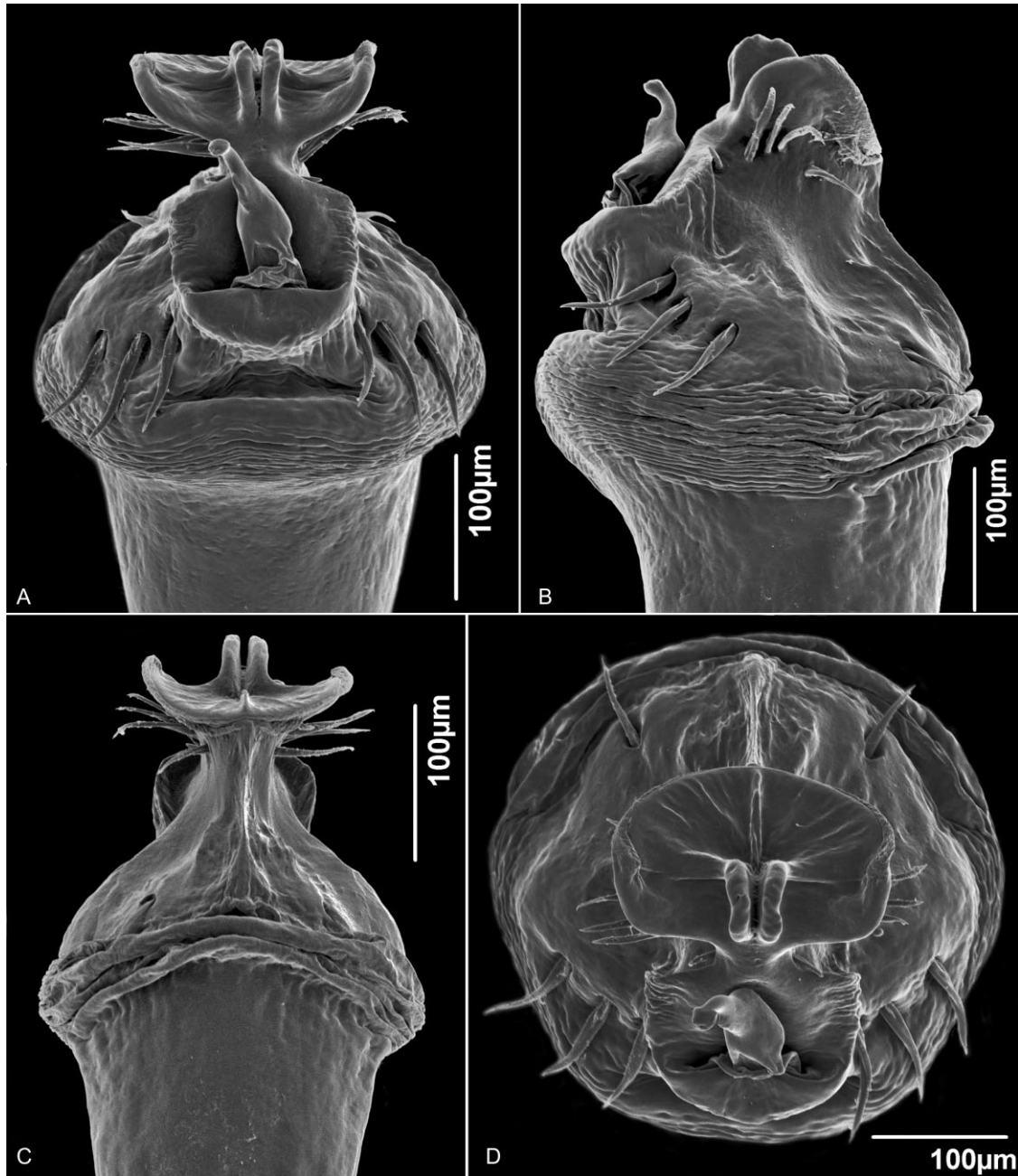
SUBFAMILY ZAMORINAE KURY, 1997 NEW  
FAMILIAL ASSIGNMENT

Agoristenidae Zamorinae Kury 1997b: 339; Kury 2003a: 34; Pinto-da-Rocha & Hara 2009: 36.

Cranaiidae Zamorinae: Kury 2012b: 35.

*Diagnosis:* As in Kury (2012b).

*Distribution:* Ecuador.



**Figure 19.** *Jabbastygnus huttoni* sp. nov., male holotype (IAvH 3000110), distal part of penis: A, dorsal view; B, lateral view; C, ventral view; D, apical view. Scale bars = 0.1 mm.

#### SUBFAMILY NOMOCLASTINAE

Gonyleptidae Nomoclastinae Roewer 1943: 14, 36.

Stygnidae Nomoclastinae: Mello-Leitão 1949: 31; Pinto-da-Rocha 1997: 170; Kury 2003a: 228.

**Diagnosis:** Gonyleptoidea without marked dimorphism in chelicerae and pedipalps. Ocularium either low, elliptical, with median depression (*Quindina*, *Zygopachylus*) or lacking, eye sessile on carapace

(*Nomoclastes*). Anterior margin of carapace without frontal hump. Dorsal scutum either entirely smooth and unarmed (*Nomoclastes*) or with a pair of robust paramedian spiniform processes on area III (*Quindina*, *Zygopachylus*). Legs I–IV unarmed, slender, but not extremely elongate. Coxa IV of male with immense ventral spur (*Nomoclastes* only). Basitarsus I not spindle-like swollen as in Manaosbiidae. Tarsal claws III and IV with well-developed median tarsal process. Ventral

plate subrectangular to trapezoid, arising from inside a rounded cavity on dorsal side of apical truncus penis. Patches of laminar scale-setae on the ventro-latero-distal borders of VP absent (Fig. 20H). Macrosetae C1–C3 laterally inserted, well developed, only slightly curved, MS A1–A2 or only A1 following the same lateral row as MS C1–C3. MS D1 small, inserted dorsally or dorso-laterally on the basal third of VP. MS E1–E2 as small stumps located ventrally on VP forming a quadrangle. Stylus short and sturdy, with rounded head, mounted atop a long columnar glans.

*Included genera:* *Nomoclastes* Sørensen, 1932 (type genus), *Quindina* Roewer, 1915, *Zygopachylus* Chamberlin, 1925. There are other genera of Gonyleptoidea currently in Cranaidae and Manaosbiidae that probably belong here, but this placement awaits further studies on them. For example, *Napostygnus* Roewer, 1929, recently allocated to Cranaidae by Pinto-da-Rocha *et al.* (2012), could be a member of the Nomoclastinae based on the short stylus associated with a columnar glans, lack of MS B, and MS C not clustered forming a spaced lateral row. However, there are some important diagnostic characters regarding microsetae and MS E unknown. Moreover, the presence of a dorsal process of stylus, otherwise unknown in Nomoclastidae, is puzzling.

*Earlier placement of genera:* *Nomoclastes* was originally in Stygnidae, not placed in any subfamily. Transferred to Gonyleptidae, which then included the present-day Stygnidae by Roewer (1943) into the new monotypic subfamily Nomoclastinae. With the recognition of Stygnidae by Mello-Leitão (1949), Nomoclastinae was again carried into the latter family, where it was confirmed by Pinto-da-Rocha (1997). *Quindina* was originally in Gonyleptidae Cranainae. *Zygopachylus* was originally in Gonyleptidae, assigned to Pachylinae by Roewer (1929), to Cranainae by Goodnight & Goodnight (1947) and to Prostygnae by Juberthie (1970). Transferred to Manaosbiidae by Kury (1997a).

*Combined distribution:* Colombia and Panama.

UNRANKED TAXON MICROSETATA KURY, 2014

Microsetata Kury 2014: 12.

*Etymology:* The name refers to the cover of microsetae present on the penis VP on most species of this group.

*Cladistic node-based definition:* The last common ancestor of *Cosmetus* and *Gonyleptes*, and all descendants of that ancestor.

*Diagnosis:* Distal margin of lateral borders of VP with well-developed flange, typically bearing MS E1–E2. MS A–B forming a triangle (or an arch in K92). Macrosetae E strongly reduced, inserted on the latero-distal flange of VP (except in Ampycinae, which have a ventral rectangle). Ventro-lateral fields of scale-bridles (type 4) often present, at least on distal corners of ventral surface of VP. Median field of scale-bridles (types 1–3) often present on VP.

*Included families:* Cosmetidae, Greater Gonyleptidae (GG), Metasarcidae.

UNRANKED TAXON GREATER GONYLEPTIDAE (GG),  
KURY, 2014

Gonyleptidae (expanded concept): Pinto-da-Rocha *et al.* 2014: 12.

Greater Gonyleptidae (GG) Kury 2014: 12.

*Etymology:* This name refers to the original conception of this group as an expanded Gonyleptidae.

*Cladistic node-based definition:* The last common ancestor of *Camelianus* (oldest genus of Manaosbiidae) and *Gonyleptes*, and all descendants of that ancestor.

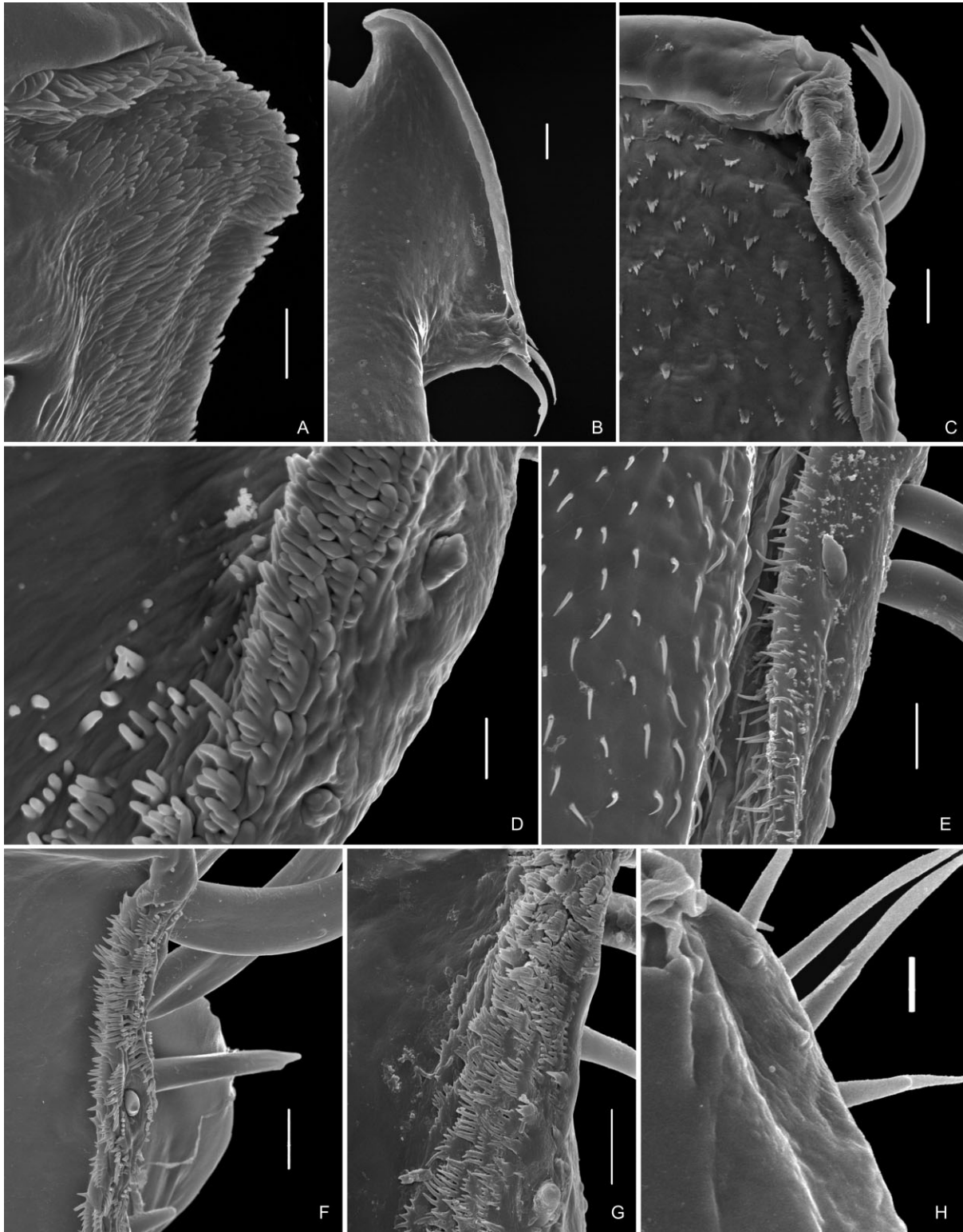
*Diagnosis:* Pedipalpus short and weak (except in Cranaidae where it is robust and some species of Cranaidae and Gonyleptidae where it is extremely elongate). VP elongate, overlapping with distal truncus (except in Manaosbiidae). Paired latero-distal patches of scale-bridles (type 4) mostly present (absent in some Gonyleptidae). Median field of microsetae (mostly type 1) present (absent in some Ampycinae). Stylus not compressed, without wattle. Stylus and glans length highly variable.

*Included families:* Cranaidae, Gonyleptidae, Manaosbiidae.

## DISCUSSION

### SYSTEMATIC PLACEMENT OF *JABBASTYGNUS*

There is a phylogenetic analysis of Stygnidae published almost 20 years ago (Pinto-da-Rocha, 1997), which is now outdated owing to the great amount of new information gathered since then. Likewise, the lack of a hypothesis of homology for the macrosetae hindered many of the character interpretations. In spite of the recognition of two symmetrical subtaxa in Stygnidae (Pinto-da-Rocha, 1997), there is no strong support for the monophyly of Stygninae, which might be paraphyletic with respect to Heterostygnae. *Jabbastygnus* may be included in the Stygninae (or at least not in Heterostygnae) because it shares the



**Figure 20.** Lateral borders of ventral surface of ventral plate of assorted Gonyleptoidea, showing presence/absence of mat of scale-bristles: A, *Ricstygnum quineti* (MNRJ 2112); B, *Stenostygnellus macrochelis* (MNRJ-HS 691); C, *Syncranus cribrum* (MNRJ-HS 692); D, *Zannicranus monoclonius* (MNRJ 19322); E, *Yraguara fleuryi* (MNRJ 4415); F, *Gryne marginalis* (MNRJ 17579); G, *Gnidia holmbergi* (MNRJ 5520); H, *Zygopachylus albimarginis* (CAS AK 049). Scale bars = 0.05 mm (A, D), 0.1 mm (B, C, E–H).

following character states with most genera in the subfamily: (1) LP thickened dorso-ventrally; (2) presence of two patches of scale-setae on ventral surface of LP; (3) tarsal claws divergent, unpectinated; and (4) last tarsomere of leg IV rod-shaped. The presence of strongly developed MS C1–C3 as buffalo-horns is apomorphic and appears to be synapomorphic for a group of genera, including *Protimesius*, *Ricstygnus*, *Sickesia* and *Stygnus*, but neither *Jabbastygnus* nor *Auranus*. *Jabbastygnus* is quite similar to *Ricstygnus* in external morphological features, whereas genital morphology indicates a closest proximity with *Auranus* (see individual character in the ‘Diagnosis’ section).

#### HOMOLOGY OF MS A–E IN NON-GONYLEPTOIDEA

We have not studied in detail the pattern of macrosetae outside Gonyleptoidea, but we did examine other related families (using the phylogenetic scheme proposed by Sharma & Giribet, 2011). In Tithaeidae and Petrobunidae we were unable to recognize any similar pattern. On the other hand, in Epedanidae and Pyramidopidae, some correspondence with the A–E paradigm could be seen. Assamiidae MS morphology is quite diverse and the A–E pattern may be estimated only in a few species.

#### *Epedanidae* (Figs 21A–F, 22A–C)

The pattern A–E is recognizable, with the groups of MS arranged in concentric rings around the glans socket (two of the examples here are adapted from Weber, 1988, and additional examples are taken from the literature).

In Epedanidae two main patterns of truncus structure may be recognized:

- 1 In *Pseudobiantes japonicus* Hirst, 1911 the distal truncus is concave as a spoon, and the follis is based on a socket on this concavity. The same configuration may also be observed for example in *Epedanellus tuberculatus* Roewer, 1911 and *Takaoia sauteri* Roewer, 1911. Also, *Parabeloniscus* sp. matches this pattern, although the spoon is not as much projected apically.
- 2 In *Epedanus pictus* Thorell, 1876 the truncus is not projected apically, but truncated. There is a dorso-subapical concavity which lodges the follis and a ventro-subapical canyon, with a tubular fold to the side. Also this group of species possesses a sixth group of setae, apparently absent in Gonyleptoidea, which may be called macrosetae F1–F2. They are similar to MS B, arranged in the same way, but much more proximal on the ventral surface of the truncus. The same arrangement and these F setae can also be seen in *Dibunus similis* Roewer, 1912, *Toccolus javanensis* Kury, 2008, *Pasohnus bispinosus* Suzuki,

1976 and *Plistobunus columnarius* Lian, Zhang & Zhang, 2011.

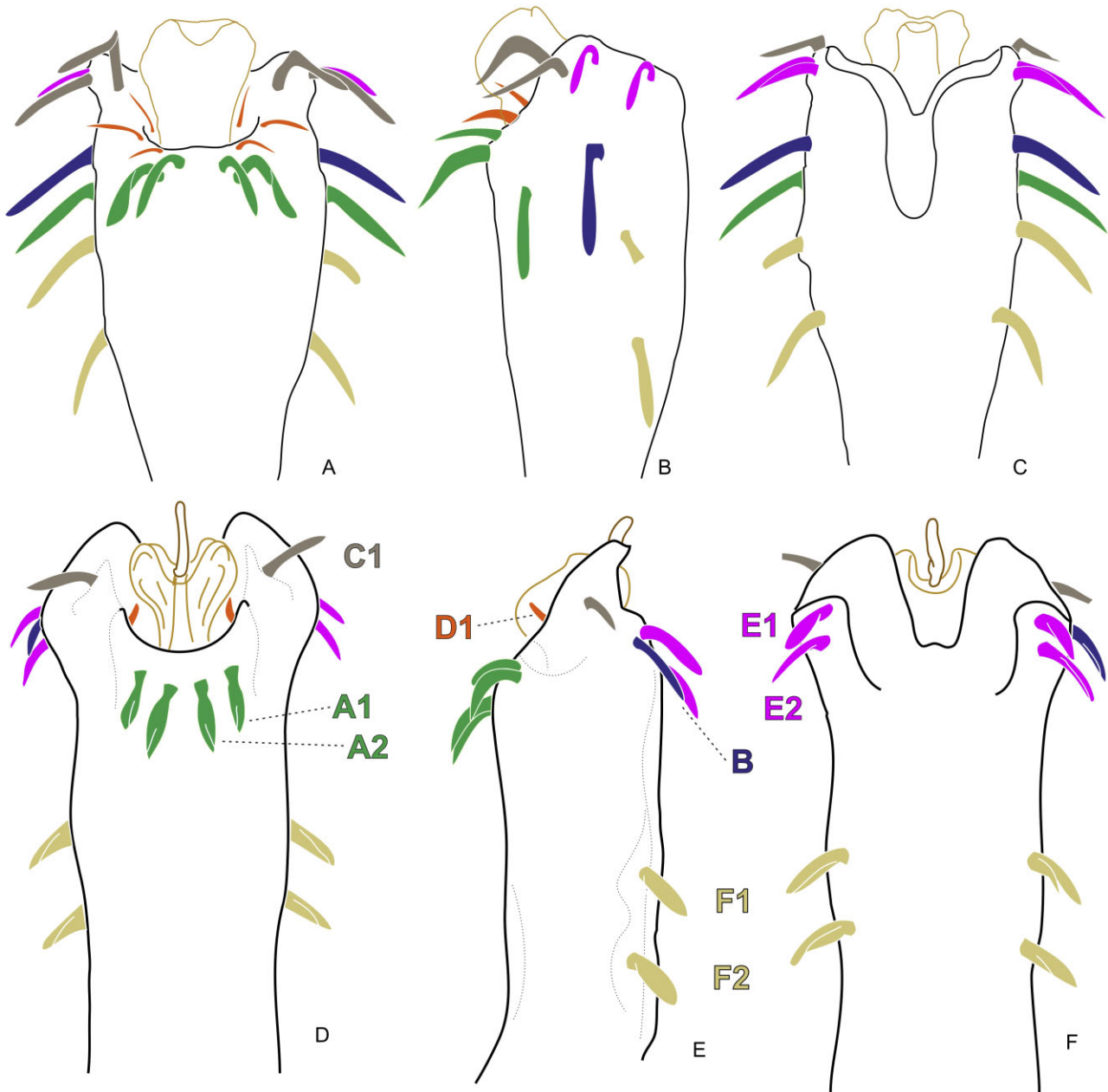
Starting with MS A1–A2, which are very typical of all Epedanidae studied here (and loosely resemble the set of four central incisor teeth of most mammals): they are well developed, curved, spatulate and inserted close to each other, on the dorsal surface of the truncus, mostly immediately basal to the follis socket (except in *Parabeloniscus*, where they are more proximally inserted, far from the glans socket). These MS A comprise part of the girdle surrounding the follis socket along with MS C. In *Epedanellus*, *Pseudobiantes* and *Takaoia* MS C1–C3 are well developed, spatulate and form a tight row aligned with A1–A2 on the rim of the follis socket, separated from those by a noticeable gap. MS B1 comprise part of the girdle surrounding the follis socket, but they are inserted remotely from A in a more ventral position. In *Parabeloniscus*, this A–C ring is more loosely marked, with A much more proximal, and C diminished to C1–C2 and migrated to more ventral. In *Toccolus* MS A1–A3 (or A1–A2) comprise part of a girdle surrounding the follis socket. Macrosetae B1 are located ventrally over the tubular fold. *Epedanus* shows the same, with B more lateral and only two pairs C1–C2. *Dibunus* has only one pair C1. MS D always make the innermost, distalmost ring around the socket. They are often extremely thin (e.g. *Epedanus*, *Pseudobiantes*) or very short (*Dibunus*) and their number varies from one to three pairs. They are seldom as robust as MS A or C (e.g. *Toccolus*). MS E1–E2 are often arranged in a ventral trapeze (e.g. *Dibunus*, *Epedanellus*, *Pseudobiantes*, *Takaoia*, *Toccolus*), but in *Epedanus* they are apically inserted.

#### *Pyramidopidae* (Fig. 22D–F)

It will be some time before the highly diverse morphology of Pyramidopidae can be fully understood. The sample illustrated by Sharma, Prieto & Giribet (2011), in spite of the very poor resolution, shows extreme plasticity, but we limit our description to the single species we have examined by SEM. In *Pyramidops pygmaeus* Loman, 1902 the truncus has a sub-distal neck that leads to a huge concave, flattened distal head with a discoid base (Fig. 22D–F). There is a full complement of short, lanceolate macrosetae. MS A1–A3 are arranged proximally in a longitudinal row on the laterals of the head. Macrosetae B1 are fully ventral, inserted well distally. Macrosetae C1 are much reduced and located dorso-apically. Macrosetae D1 are also short, inserted near the rim of the glans. Macrosetae E1–E2 are close together subapically.

Regarding the grammatical gender of *Pyramidops*, it is masculine, derived from the Greek *pyramis* = ‘pyramid’ + *ops* = ‘eye’ (M.-A. Alonso-Zarazaga, pers.





**Figure 21.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Epedanidae: A–C, *Epedanus pictus*; D–F, *Dibunus similis*. All adapted from Weber (1988).

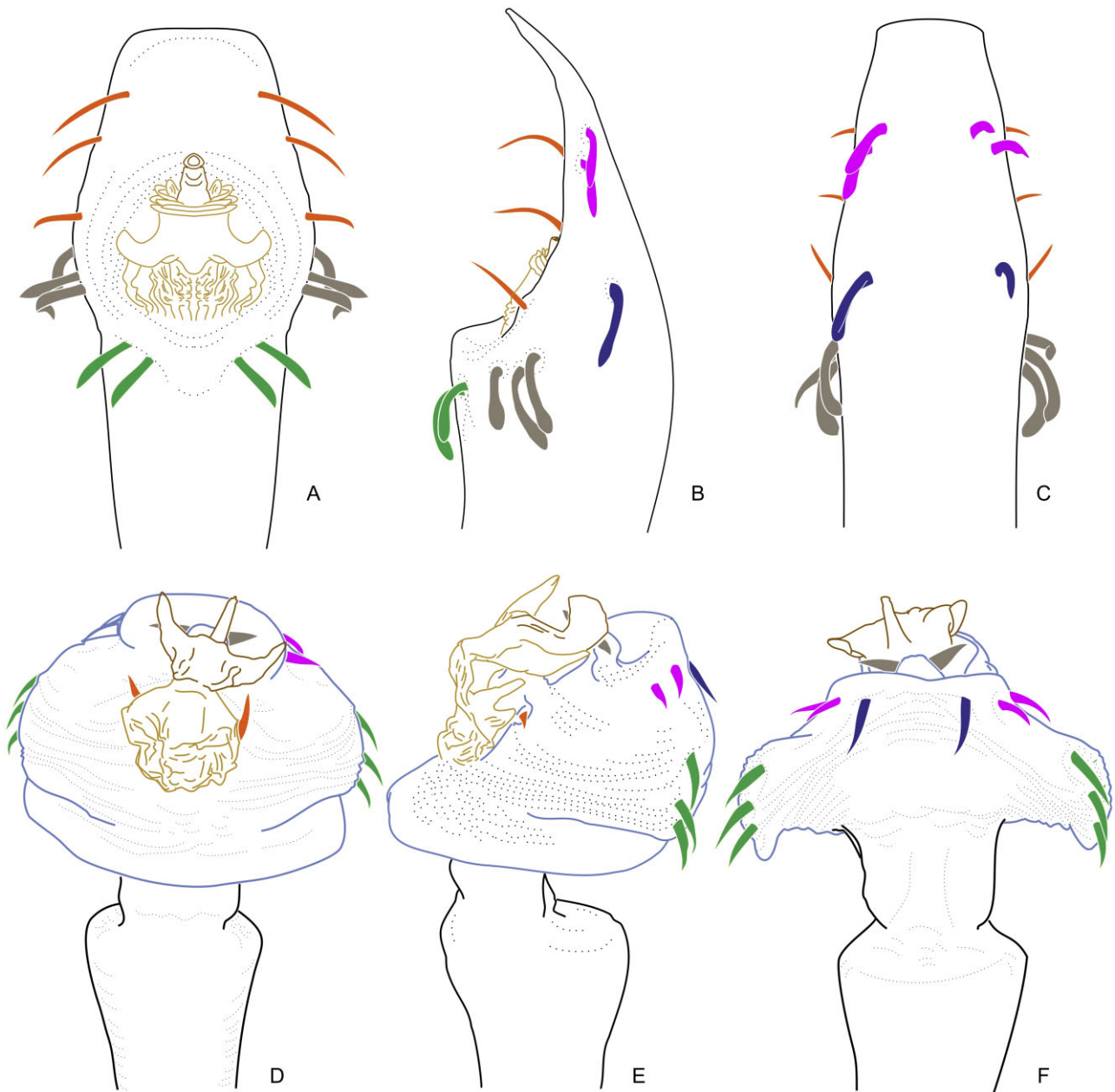
comm.). Therefore, the correct inflection of the scientific name is *Pyramidops pygmaeus*. Roewer was inconsistent in the usage, sometimes regarding it as feminine. Sharma *et al.* (2011) followed the interpretation of do Amaral (1975) that this name should be feminine.

#### *Assamiidae* (Fig. 23A–F)

Penial morphology is copiously multiform in this family. For most species illustrated by Suzuki (1969), Martens

(1977), Kauri (1985) and Santos & Prieto (2010), the pattern A–E cannot be clearly recognized. There are sets of macrosetae shifted, clustered, reduced, multiplied and otherwise modified (e.g. *Niefanga*, *Rhabdopygus*).

Nevertheless, a few species match the A–E pattern proposed here, as exemplified by *Pungoica* and *Sermowaius* (Fig. 23A–F). As in Epedanidae, MS D1–D2 or D1–D3 are more slender and form the innermost ring around the glans. However, the outer ring



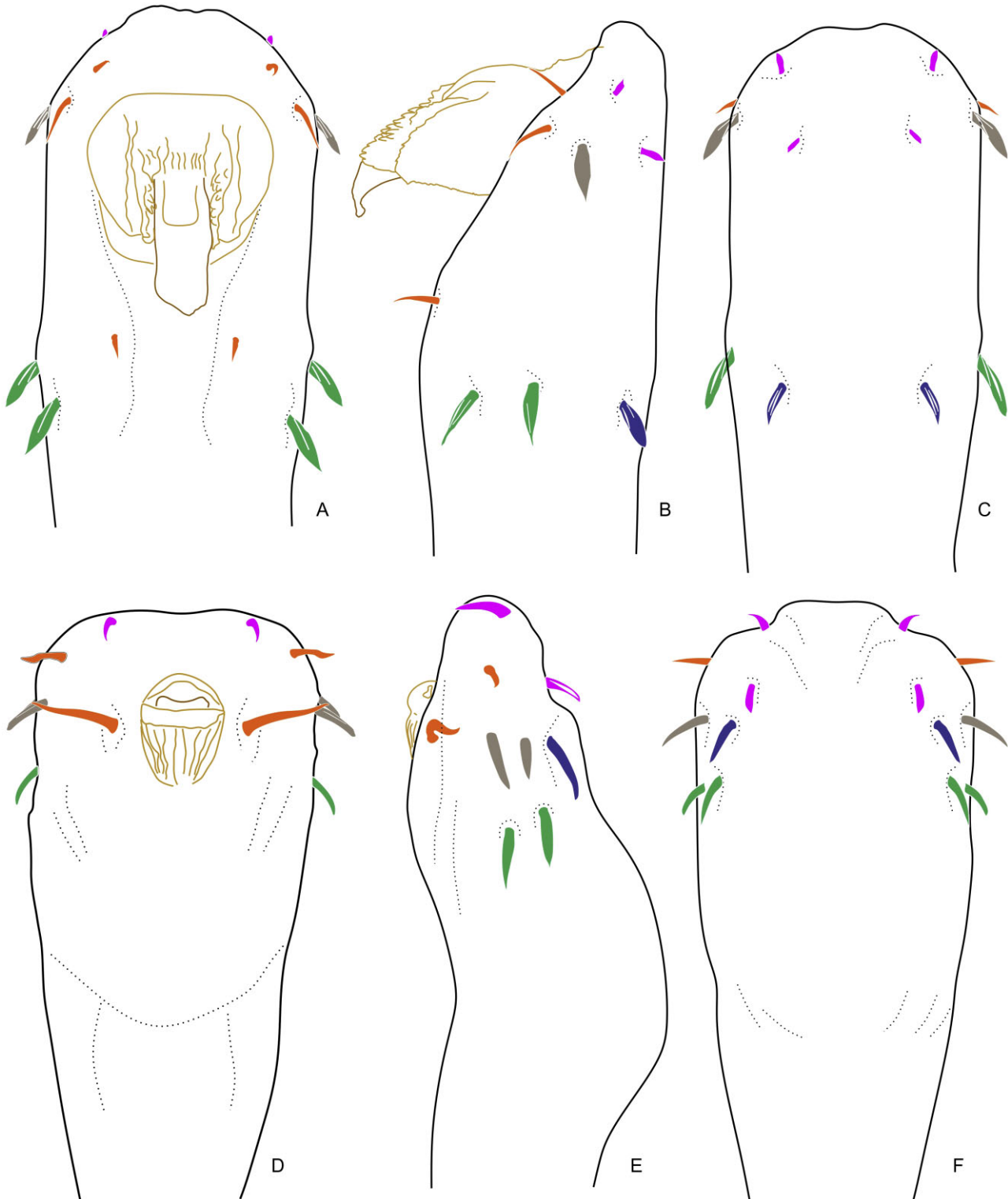
**Figure 22.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Epedanidae and Pyramidopidae: A–C, *Pseudobiantes japonicus*; D–F, *Pyramidops pygmaeus*.

that is well defined in Epedanidae is not clear here. MS C1 or C1–C2 are fully lateral, well distal on the truncus. MS A1–A2 + B1 do form a ring much more proximal than C. Well-developed MS E1–E2 form a ventro-distal quadrangle, with E1 inserted ventro-apically instead of ventrally (as in *Epedanus*).

#### ACKNOWLEDGEMENTS

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**Figure 23.** Distal part of penis, dorsal, lateral and ventral views, showing patterns of macrosetae in Assamiidae: A–C, *Pungoica simoni*; D–F, *Sermowaius* sp.

graciously shared results of his unpublished 1988 monograph and allowed the use of his illustrations of the genitalia of *E. pictus* and *D. similis*. Claudia Medina (IAvH) provided loans of Colombian Opiliones and facilitated A.B.K.'s trip to Leyva. Norman Platnick (AMNH), Charles Griswold (CAS), Petra Sierwald (FMNH), Herbert Levi (MCZ) and Jonathan Coddington (USNM) provided a variety of specimens of different families of harvestmen for comparison.

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