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A new genus of cyphophthalmid from the Iberian Peninsula with a phylogenetic analysis of the Sironidae (Arachnida : Opiliones : Cyphophthalmi) and a SEM database of external morphology

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Abstract. A new species of sironid from Portugal is described based on a single male specimen collected over half a century ago. The unique combination of character states and phylogenetic comparison with representatives of all sironid genera justifies the erection of a new genus, the fourth one found in the Iberian Peninsula. Phylogenetic analysis is conducted using equal weights and the implied weighting method as a means of testing the stability of clades with respect to parameter variation, in a similar fashion to the sensitivity analysis commonly performed in molecular data analyses. Results suggest that the new genus is sister to *Paramiopsalis* Juberthie, 1962, although nodal support for this relationship is low. The morphological data matrix is accompanied by scanning electron micrographs of most characters for 24 species to make the morphological coding as explicit as possible. Comparison of these images fostered the discovery and proper interpretation of characters and their states.

Additional keywords: Arachnida, cladistic analysis, *Iberosiro*, Portugal, Sironidae.

Introduction

The cyphophthalmid fauna of the Iberian Peninsula is not extraordinary from the standpoint of species-diversity, but it hosts an unusual amount of disparity (body plan diversity) (Fig. 1). All our prior knowledge of the Iberian Cyphophthalmi can be attributed to two of the most prominent European opilionologists: Christian Juberthie, from France, and Maria Rambla, from Spain. The three known species from the Iberian Peninsula were described by Juberthie and placed in three distinct genera, two of which are monotypic (Juberthie 1956, 1961, 1962). *Parasiro coiffaiti* Juberthie, 1956 is endemic to the north-east Iberian Peninsula (provinces of Girona and Barcelona) and south-east France (Pyrénées-Orientales) (Juberthie 1956, 1957, 1958; Rambla 1974, 1986; Rambla and Fontarnau 1984) with a more or less widespread distribution. This species is supposedly related to *Parasiro corsicus* (Simon, 1872) and *Parasiro minor* Juberthie, 1958, from Corsica, Sardinia (Brignoli 1968; Juberthie 1958; Simon 1872) and the Italian Peninsula (specimens reported here).

Odontosiro lusitanicus Juberthie, 1961 was originally described from specimens collected by M. H. Coiffait in Guimarães, Portugal (Juberthie 1961), and given its own generic status because of the unique combination of type 1 ozophores (as in *Parasiro* Hansen & Sørensen, 1904) and the presence of a complete *corona analis* (as in *Siro* Latreille, 1796). (Juberthie only mentioned that the specimens were collected from Guimaraes [sic.] by Coiffat in the north of Portugal. There are two localities in the north of Portugal named Guimarães, one in the province of Braga, and another in the province of Viseu.) Rambla and Fontarnau (1984) reported two new localities for *Odontosiro lusitanicus*, this time from Galicia and León in Spain. The details were to be presented '*dans un prochain travail*' [in a forthcoming paper] (Rambla and Fontarnau 1984: 146); however, no additional information was ever published. We have been unable to locate these specimens in the collection of Maria Rambla, deposited at the Departament de Biologia Animal, Universitat de Barcelona, Barcelona, Spain (DBAUB). *Odontosiro* Juberthie, 1961 remains a monotypic genus.

The third species described from the Iberian Peninsula, *Paramiopsalis ramulosus* Juberthie, 1962, was described originally from Pessegueiro, in the Aveiro Province of

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Portugal (however, there are two localities named Pessegueiro in the Aveiro province). Its range was later extended to the north-west Iberian Peninsula with several localities in the provinces of A Coruña, Pontevedra, and León in Spain (Rambla and Fontarnau 1984). We have collected several females in one of these localities.

Paramiopsalis Juberthie, 1962 also constitutes a monotypic genus, and shows a remarkable combination of characters. In fact, this species was originally described as belonging to the subfamily Stylocellinae (*sensu* Hansen and Sørensen 1904) for having the coxa of leg II fused to that of leg III as do the members of the currently recognised families Stylocellidae, Ogoveidae, and Neogoveidae (Hansen and Sørensen 1904; Shear 1980). Its taxonomic position was later revised by Shear (1980), and *Paramiopsalis* was placed within its current family, Sironidae. The unique plumose adenostyle (that gives origin to the specific epithet) (see Rambla and Fontarnau 1984: plate I, figs 4–6 and fig. 32i), the typical *Siro* ozophores, anal plate, and anal gland, and the typical *Parasiro* anal region (with sternites 8 and 9 fused, but not fused with tergite IX) together constitute an original combination of characters that provide justification for the unique generic status of this species. *Paramiopsalis* and *Odontosiro* clearly overlap in their areas of distribution, but they are obviously different morphologically.

Besides these three species, the only other report of Iberian cyphophthalmids is that of a *Siro duricorius* (Joseph, 1868) from Lovios in the province of Ourense (Galicia, Spain) (Kraus 1961), however, this proved to be an erroneous identification of *P. ramulosus*, as later correctly identified by J. Gruber (see Rambla and Fontarnau 1984: 146–147).

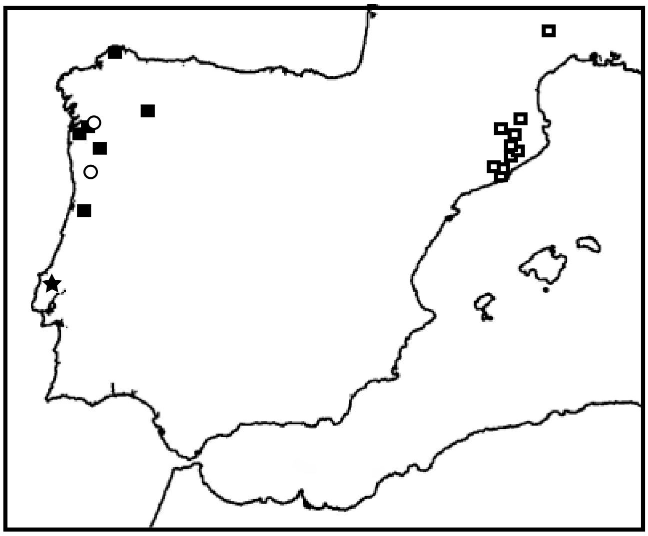

Fig. 1. Map showing the distribution of cyphophthalmid collection localities across the Iberian Peninsula. ★, *Iberosiro distylos,* sp. nov.; ■, *Paramiopsalis ramulosus*; ○, *Odontosiro lusitanicus*; □, *Parasiro coiffaiti*.

The only parsimony analysis of the cyphophthalmid genera (Giribet and Boyer 2002) included representatives of *P. ramulosus* and *P. coiffaiti*, but data on *O. lusitanicus* were not coded due to the impossibility of observing any material of the species. The morphological data placed *Paramiopsalis* within a clade containing members of the genera *Siro* and *Marwe* Shear, 1985, and separated from the other Iberian genus, *Parasiro*. A relationship between *Paramiopsalis* and *Siro* is also suggested by molecular data (Giribet and Boyer 2002), whereas *Parasiro* remains outside of this clade. The position of *Odontosiro* needs critical examination within a phylogenetic framework.

A collection from a cave in the district of Lisboa (Algarve da Terra da Rolha, Portugal) yielded a single male specimen of a small cyphophthalmid with a combination of character states observed in *Paramiopsalis*, *Parasiro* and *Odontosiro*. This specimen has the coxa of the second pair of legs fused to the third coxa, a unique trait within the Sironidae, only shared with *Paramiopsalis*. This unique combination of characters justifies the erection of a new genus.

This paper describes this new genus and species of Cyphophthalmi from Portugal, and reexamines the phylogeny of the family Sironidae following the analysis of 46 morphological characters in all species of the Sironidae (with the exception of the diverse genus *Siro*, for which representatives from two European clades and from all North American species have been chosen). All the species analysed, with three exceptions, have been studied in detail using scanning electron microscopy (SEM); we present the first morphological analysis with comprehensive illustrations of all character states for almost all analysed taxa to create a new standard in morphological analysis of cladistic matrices. Our goal is to provide detailed illustrations, of the 'hard data' used in morphological cladistic analyses. This can be studied and interpreted by all researchers, not just those with privileged access to the studied specimens. As work proceeds in future, we expect to add to this database of Cyphophthalmi images.

Methods and abbreviations

A total of 27 species of sironids and relevant outgroup taxa were studied (Appendix 1). Twenty-four of these species were examined using a FEI Quanta 200 or a Hitachi S4700 FE-SEM. The single specimen of the new species was embedded in glycerin as a temporary mount and studied under a Leica MZ 12.5 stereomicroscope and a Leica DMRB compound light microscope. The holotype has been photographed in ventral and dorsal views using a JVC KY-F70B digital camera mounted on a Leica MZ 12.5 stereomicroscope. A series of 10 to 20 images were taken at different focal planes and assembled with the dedicated software package Auto-Montage *v.* 4.01.0085 by Synoptics Ltd. Drawings of the holotype were made using compound and steromicroscopes, with grid coordinates used to ensure correct proportions.

Measurements were mostly taken using the stereomicroscope. Total body length refers to the distance between the midpoints of the anterior and posterior margins of the carapace. Lengths of leg and palp articles were measured on their dorsal sides, from the midpoints of the anterior and posterior margins. Tarsal length does not include the claw. The position of the adenostyle on tarsus IV is given at the more clearly marked distal point, where it abruptly rises from the dorsal surface of the tarsus.

Specimens cited herein are housed in the following institutions:

AMNH	American Museum of Natural History, New York, USA
CAS	California Academy of Sciences, San Francisco, USA
Ccol	James Cokendolpher private Collection, Lubbock, USA
DBAUB	Departament de Biologia Animal, Universitat de Barcelona, Barcelona, Spain
FMNH	Field Museum of Natural History, Chicago, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA
MHNG	Muséum d'histoire naturelle, Genève, Switzerland
MNHN	Museé National d'Histoire naturelle, Paris, France
MRAC	Royal Museum of Central Africa, Tervuren, Belgium
ZMB	Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Berlin, Germany
ZMUC	Zoological Museum, University of Copenhagen, Denmark
WAM	Western Australian Museum, Perth, Australia

Phylogenetic analyses

Morphological characters used in the phylogenetic analyses are listed in Appendix 2. The data matrix is given in Table 1.

Phylogenetic analyses of morphological characters were executed in NONA (Goloboff 1998), Pee-Wee (Goloboff 1997), and Winclada (Nixon 2002). Parsimony analyses using equal weighting and implied weighting for six values of concavity (the maximum allowed in Pee-Wee) were explored to test the stability of the results with respect to parameter variation, in a similar fashion to the analyses of Prendini (2003). We intended to emulate the sensitivity analysis frequently used in molecular data analyses (Wheeler 1995). Analyses were conducted holding up to 10,000 trees (*hold 10000*) and searching for 100 replicates under tree-bisection-and-reconnection (TBR) branch swapping, holding up to 10 trees per replicate (*hold/10, mult* 100*). The resultant trees were subjected to TBR branch swapping (with the 10,000 trees upper bound) (*max**).

The strict consensus of the cladograms obtained under all analytical conditions was calculated to summarise the conflict among the fundamental trees, and to illustrate those nodes that are stable to parameter variation (Giribet 2003). We also tested for nodal support using parsimony jackknifing (Farris 1997; Farris *et al*. 1996) for the equally weighted analysis with 1,000 replicates.

Characters were optimised using the 'unambiguous changes only' function, and were considered homoplastic when any extra step made them homoplastic. This seems the most conservative way of optimizing unambiguous characters.

Table 1. Coding for the 46 morphological characters discussed in Appendix 2

Taxa	Characters				
	1	1111111111	2222222222	3333333333	444444
	1234567890	1234567890	1234567890	1234567890	123456
Stylocellus globosus	1110110101	010500-000	1010100100	0020000010	100101
Stylocellus ramblae	1110010111	011500-010	1010101100	0020000000	0-0???
Ogovea cameroonensis	0130000100	011500-000	3010101100	1101103-00	0-010?
Paragovia sironoides	0101000110	0115011000	5110101111	1-01003-00	0-0001
Huitaca ventralis	0100002110	0113111000	0100101011	1-01003-00	0-?10?
Metagovea philipi	0100002110	0113011110	0100101011	1-01003-00	0-0101
Troglosiro sp.	0101012110	0113011000	0001011000	1001003-00	0-0???
Karripurcellia peckorum	0320001110	010200-000	0000011000	0110010100	0-0101
Chileogovea oedipus	0320001110	011400-110	0010011000	1110000111	11011?
Suzukielus sauteri	0120100000	0102110111	0000011000	1000000110	120111
Paramiopsalis ramulosus	0100100000	100100-000	4001101000	1000001010	100111
Iberosiro distylos	0100110000	100100-000	6001101000	3000001000	0-????
Parasiro coiffaiti	0000110100	0002010110	0001010000	1000001000	0-0110
Parasiro minor	0000110100	0102011110	0001010000	1000001000	0-0110
Parasiro corsicus	0000110100	0102111110	0001010000	1000001000	0-0110
Odontosiro lusitanicus	00??110100	1105110110	001?0???0?	????003-00	0-0111
Siro duricorius	0101110000	010100-000	0001011000	2000003-11	100111
Siro serbicus	0101110000	010100-000	0001011000	2000003-11	100???
Siro rubens	0101100000	010100-000	0001011000	2000003-10	101111
Siro valleorum	0101100000	010100-000	0001010000	1000003-10	101?11
Tranteeva paradoxa	0100100000	000100-000	0001011000	2000003-11	100111
Siro exilis	0101100000	000100-000	0001000000	1000003-11	10011?
Siro sonoma	0101100100	000100-110	0001000000	1000003-11	100??1
Siro acaroides	0101100000	000100-110	0001010000	1000003-01	100111
Siro kamiakensis	0101100000	000100-001	0001000000	1000003-11	10010?
Metasiro americanus	0100002110	0103111100	2100001001	1000004-01	110101
Marwe coarctata	0040100000	000000-000	000110-000	000?003-00	0-0??1

Order **OPILIONES** Sundevall

Suborder **CYPHOPHTHALMI** Simon

Family **SIRONIDAE** Simon

Genus ***Iberosiro***, gen. nov.

Diagnosis

Sironid without eyes. Ozophores of type 2, conical, with terminal plug-shaped structure and without spiral cuticular ornamentation. Transverse prosomal sulcus absent. Transverse opisthosomal sulci inconspicuous. Mid-dorsal, longitudinal opisthosomal sulcus absent. Coxae of leg I movable; coxae of legs II and III fused. Ventral prosomal complex with left and right coxae I, II and IV meeting in midline, but coxae III not so. Endites of coxae II and III running along their sutures, giving coxae III endites a V-shaped appearance; coxae IV endites widening anteriorly to contribute to the broad sternal region, not running parallel to coxae IV suture for a distance longer than the gonostome. Coxal endites forming smooth broad sternal plate. Pores of coxal glands clearly visible at inner corners of coxae III. Sternum absent. Gonostome semicircular, wider than long and delimited anteriorly by coxae IV. Spiracles circular. Without sternal opisthosomal glands. Sternites 8 and 9 fused medially; tergite IX free, not forming a complete corona analis. Tergites IX and VIII lacking anal gland pores. Anal plate without modifications.

Chelicerae relatively short and strong, with few setae; without conspicuous granulation. Proximal article without prominent dorsal and ventral processes. Second article robust, its widest portion near articulation with the mobile digit; ornamented by small scale-like projections. Palp with ventral process on proximal end of rectangular trochanter. Legs with all claws smooth, long and hook-like, lacking dentition or lateral pegs. Metatarsi of legs I and II smooth; granulated on legs III and IV. Tarsus of leg I lacking distinct solea. Tarsi of legs I and II sparsely ornamented with brown granules; smooth in legs III and IV. Tarsus IV entire, carrying lamelliform adenostyle with a bilobed tip ending in dorsal position and second adenostyle-like structure present on ventral surface of tarsus IV.

Genitalia not studied. Female unknown.

Assigned species

A single species, *Iberosiro distylos*, sp. nov.

Etymology

The generic name is derived from the Iberian Peninsula and the generic name *Siro* and refers to the geographical distribution of the genus and its phylogenetic affinity. Gender masculine.

Iberosiro distylos, sp. nov

(Figs 2–6, Table 2)

Material examined

Holotype. ♂, Algarve (cave) da Terra da Rolha, Rocha Forte, Serra de Montejunto (Estremadura, Portugal), leg. A. de Barros Machado, 16.iv.1941, MNHN.

Diagnosis

As for generic diagnosis.

Description

Male

Total length 1.37 mm, width across ozophores 606 µm, greatest width 766 µm; length-width ratio 1.79. Body pale yellowish-white, with patches of darker brown sclerotisation (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without lateral projections; prosomal region trapezoidal. Eyes absent. Ozophores conical, with plug-shaped structure at tip posterior to ozopore, emerging from dorsal scutum laterally, but elevated from margin of scutum (type 2 of Juberthie 1970) (Fig. 4*a*); ornamentation uniform and non-directional. Transverse prosomal sulcus absent (Figs 2*a*, 3*a*). Transverse opisthosomal sulci inconspicuous. Mid-dorsal, longitudinal opisthosomal sulcus absent (Figs 2*a*, 3*a*). Dorsal scutum flat; maximum width at prosomal area.

Coxae of leg I movable, coxae of legs II and III fused. Ventral prosomal complex with left and right coxae I, II and IV meeting in the midline, but coxae III not so, suture between coxae II and III joining suture between coxae III and IV (Figs 2*b*, 3*b*). Endites of coxae II and III running along their sutures, giving coxae III endites a V-shaped appearance; coxae IV endites widening anteriorly to contrib-

Table 2. Leg measurements (in µm) of *Iberosiro distylos*, sp. nov. male holotype
Length : width ratio in parentheses

Leg	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Sum
I	121 / 94 (1.29)	420 / 98 (4.3)	174 / 94 (1.86)	270 / 80 (3.37)	176 / 84.9 (2.07)	383 / 103 (3.71)	1544
II	109 / 90 (1.21)	354 / 99 (3.57)	150 / 102 (1.47)	219 / 91 (2.42)	153 / 76.2 (2.01)	339 / 88 (3.85)	1324
III	121 / 90 (1.35)	367 / 98 (3.76)	163 / 99 (1.64)	199 / 95 (2.09)	142 / 74.6 (1.90)	282 / 79 (3.59)	1273
IV	172 / 80 (2.15)	360 / 100 (3.6)	190 / 98 (1.93)	219 / 98 (2.23)	169 / 79.4 (2.13)	383 / 141 (2.71)	1493

ute to broad sternal region, not running parallel to coxae IV suture for a distance longer than gonostome. Coxal endites forming smooth sternal plate with greatest width 370 µm between coxae III and IV. Pores of coxal glands clearly visible at inner corners of coxae III. Sternum absent. Gonostome region with horn-like projections adjacent to suture between coxae IV. Gonostome semicircular, wider than long, and delimited anteriorly by coxae IV. Lateral walls formed by elevated endites of coxae IV.

Spiracles circular, small, with maximum diameter 38 µm (Fig. 4*b*). Sternal opisthosomal glands absent. Sternites 8 and 9 fused medially; tergite IX free, not forming a complete corona analis (Fig. 5*a*). Tergites IX and VIII lacking anal gland pores. Tergite IX constricted in middle, appearing bilobed. Anal plate without modifications, measuring 123 × 174 µm (Fig. 5*a*). Cuticle with granular surface in all ventral areas including coxae and anal plate, except on coxal endites (Fig. 2).

Chelicerae relatively short and strong, with few setae, appearing without conspicuous granulation using light microscopy (Fig. 4*c*). Proximal article without prominent dorsal and ventral processes. Second article robust, subcylindrical, its widest portion near articulation with mobile digit; ornamented by small scale-like projections. Proximal article 368 µm long, 123 µm wide, second article 480 µm long, 106 µm wide, movable finger 180 µm long, 45 µm wide. Dentition uniform and similar on both cheliceral fingers, with 10 denticles on each finger.

Palp with ventral process on proximal end of rectangular trochanter (Figs 4*d*, 6*a*). Length/width in µm (length to width ratio in parentheses) of palpal articles from trochanter to tarsus of male: 139/73 (1.91); 325/67 (4.88); 178/60 (2.95); 259/54 (4.79); 200/47 (4.27); total length 1.102 mm. Palpal claw 38 µm long.

Legs (Figs 4*e–h*, 6*b–c*; Table 2) with all claws smooth, long and hook-like, with lateral cuticular ridges, lacking dentition or lateral pegs (Figs 5*b–e*). Surfaces of all trochanters, femurs, patellae, and tibiae clearly ornamented with granules. Metatarsi of legs I and II (Fig. 6*b*) smooth; granulated in legs III and IV (Fig. 6*c*). Tarsus of leg I lacking distinct solea. Tarsi of legs I and II sparsely ornamented by brown granules; smooth in legs III and IV. Tarsus IV entire (Fig. 6*c*), carrying an adenostyle with robust bilobed tip; in normal dorsal position; approximate length 84 µm; bearing four setae not clustered at tip (Fig. 6*d*); distal margin at 46% of tarsal length. Second sub-cylindrical adenostyle-like structure present on ventral surface of tarsus IV, approximate length 26 µm, with five setae emerging from tip; distal margin at 61% of tarsal length (Fig. 6*e–f*).

Penis not studied.

Female

Unknown.

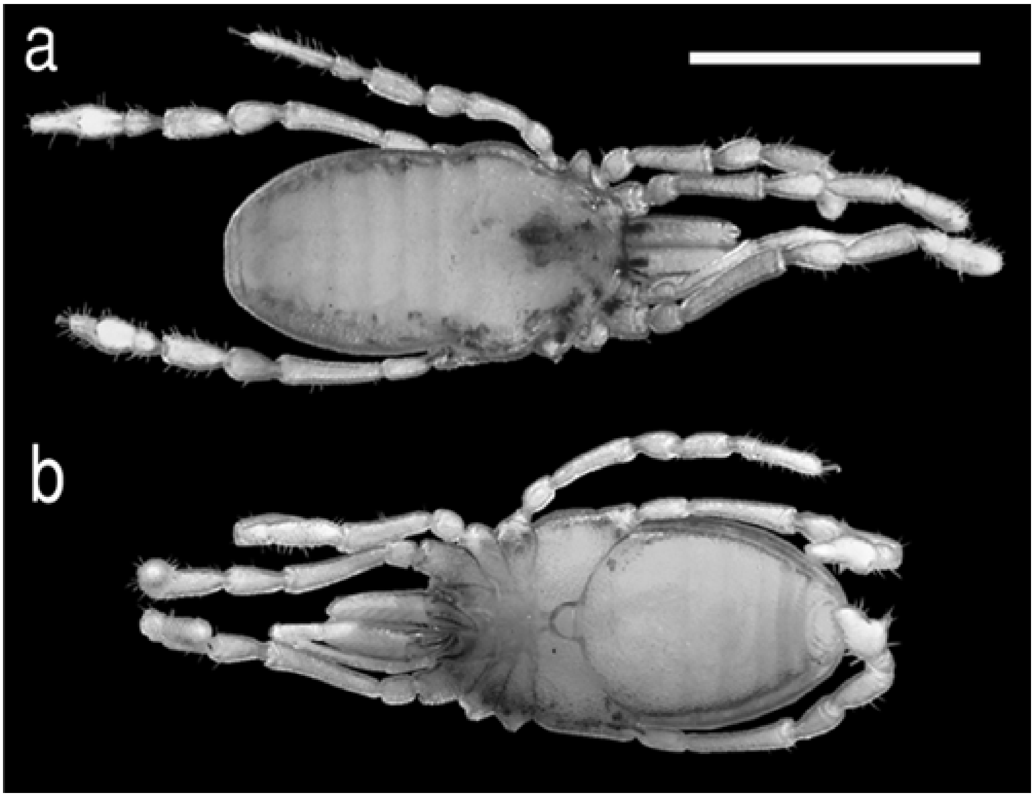

Fig. 2. *Iberosiro distylos*, sp. nov., photographs of holotype. *a*, Dorsal, and *b*, ventral view. Scale bar = 1.0 mm.

Remarks

This species is unique due to the rare combination of character states and the presence of several autapomorphic features. The vial found at the MNHN was labelled: '*Paramiopsalis* n.sp. (W. Shear det. 1993)', probably due to the presence of type 2 ozophores, a ventral process in the palp trochanter, the presence of fused coxae of legs II and III, and the unique coxal endites forming a broad smooth plate. These characters certainly suggest a relationship among these two species, as illustrated in the phylogenetic analysis presented here (Figs 7–9). However, both species have important differences that have been used to diagnose other cyphophthalmid genera, such as the type of ornamentation of the chelicerae, or the very unique adenostyle and associated structures in both species. Furthermore, *Paramiopsalis ramulosus* has three conspicuous anal gland pores and a prominent carina in the anal plate (Fig. 38*i*) that makes it easily distinguishable from *Iberosiro distylos*, which has a smooth anal plate and no anal gland pores (Fig. 5*a*).

When compared to the other geographically close species, *Odontosiro lusitanicus* and *Parasiro coiffaiti*, the ozophore position differs (type 1 in *Odontosiro* and *Parasiro*), as does the presence of the dorsal crest in the cheliceral basal article; the claw ornamentation; the fusion of coxae II and III, and the types of adenostyles. Furthermore, *Parasiro* can be distinguished by the lack of a ventral process in the palp trochanter, although it shares the unique type of anal region (without corona analis) found in *Paramiopsalis* and *Iberosiro,* gen. nov. On the contrary, *Odontosiro* has the ventral process in the palp trochanter, but differs in the anal region because it presents a complete corona analis.

Habitat

The only specimen known was found in a cave. No further information is available.

Distribution

Only known from the type locality.

Etymology

The specific epithet *distylos* originates from the Greek, *dís* (two) and *stŷlos* (column or pointed instrument for marking or engraving), referring to the presence of two adenostyle organs in the fourth tarsus of the male.

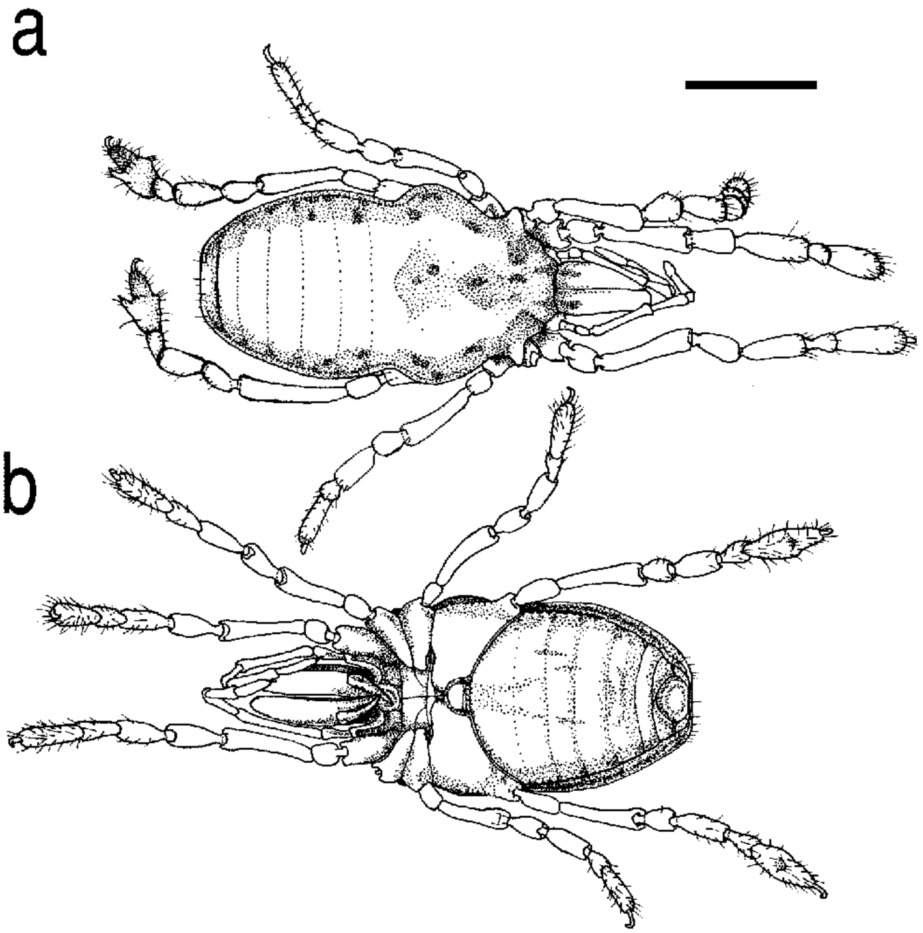

Fig. 3. *Iberosiro distylos*, sp. nov., line drawings of holotype. *a*, Dorsal, and *b*, ventral view. Scale bar = 500 µm.

Results and discussion

In total we coded 46 morphological characters, all of which are unordered (non-additive). Missing data accounted for 2.9% of the total character states scored, and most of the missing data refer to the genitalia, which has not been studied in all species, and to *Odontosiro lusitanicus* for which no material was available for study. The repository institution of the *Odontosiro lusitanicus* type material is supposedly the MNHN, but the material has not been located in that collection. Furthermore, efforts to collect this species in the north-western Iberian Peninsula, both in Spain and Portugal, yielded no specimens.

Equally weighted parsimony

Phylogenetic analysis of the morphological matrix conducted using equal weights (EW) yielded six trees of length 142 ($CI = 0.46$; $RI = 0.68$); the strict consensus of these trees is shown in Fig. 7. This tree, arbitrarily rooted with Stylocellidae (following one of the rooting options for the Cyphophthalmi according to Giribet and Boyer (2002) and Boyer and Giribet (unpublished data)), shows a clade that includes a paraphyletic Sironidae, with Pettalidae nesting as sister-group to *Suzukielus* Juberthie, 1970. As in previous phylogenetic analyses of Cyphophthalmi, *Metasiro* Juberthie, 1960 does not cluster with the sironids, unlike *Marwe*. The new genus *Iberosiro* is sister to *Paramiopsalis*; this relationship based on the presence of two characters that optimise as homoplastic: the presence of a ventral process in the palp trochanter (character 11) (also present in *Odontosiro*) and the medially fused sternites 8 and 9 (character 37) that are also present in *Parasiro*. Jackknife support for the clade uniting *Iberosiro* and *Paramiopsalis* is below 50% (jackknife values for this tree are plotted in Fig. 9).

Relationships among other sironid taxa show jackknife support values below 50%, with the exception of the clade including *Odontosiro* and *Parasiro*, with a jackknife value of

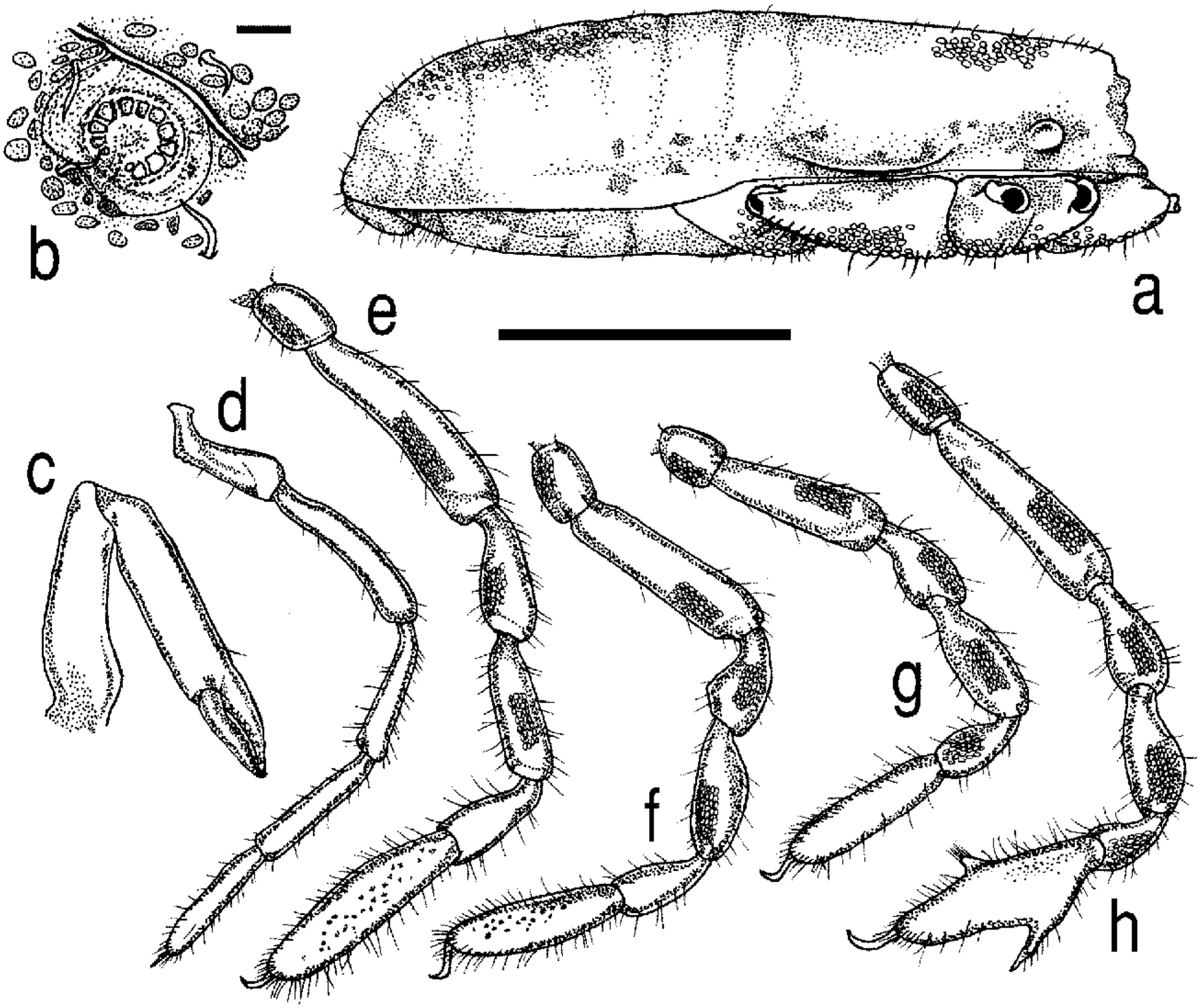

Fig. 4. *Iberosiro distylos*, sp. nov., line drawings of holotype. *a*, Lateral view of body; *b*, left spiracle; *c*, right chelicer; *d*, right palp; *e*, right leg I; *f*, right leg II; *g*, right leg III; *h*, right leg IV. Scale bars: *a, c–h* = 500 µm; *b* = 20 µm.

67%, and the monophyly of *Parasiro*, with a value of 72%. A clade formed by *Siro duricorius* and *S. serbicus* Hadži, 1973 has a jackknife value of 57%. This analysis also supports a monophyletic genus *Siro* (that includes the 'genus' *Tranteeva* Kratochvíl, 1958), as well as monophyly of the North American *Siro* species. *Tranteeva* has been considered a junior synonym of *Siro* in several publications, as shown in our cladistic analysis. The genus *Siro* is sister-group to a clade composed of (*Marwe* (*Iberosiro* + *Paramiopsalis*)), with these taxa sharing a unique state within the non-tropicophthalmid families: fusion of coxae II and III (Tropicophthalmi *sensu* Shear 1980 includes the families Stylocellidae, Ogoveidae and Neogoveidae).

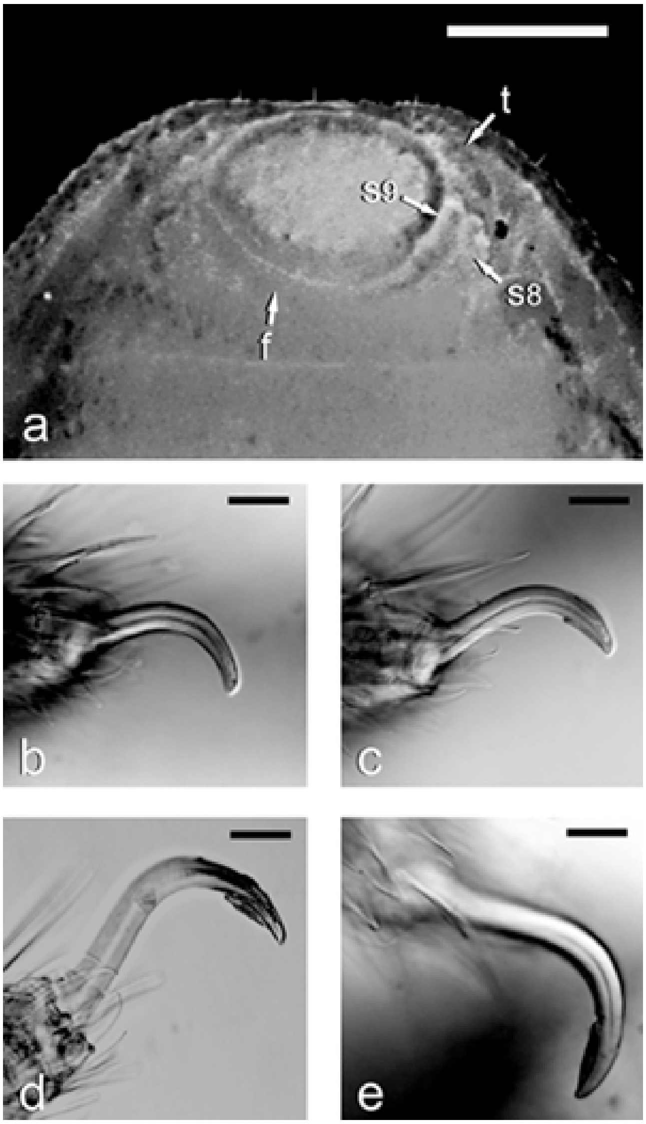

Fig. 5. *Iberosiro distylos*, sp. nov., compound light microscopy photographs of holotype. *a*, Anal region; *b*, claw of left leg I; *c*, claw of left leg II; *d*, claw of left leg III; *e*, claw of left leg IV. Scale bars: *a* = 100 µm; *b*–*e* = 20 µm. Symbols and arrows indicate: *t*, tergite IX; S8, sternite 8; S9, sternite 9; f, medial fusion of sternites 8 and 9.

Interestingly, the clade formed by *Odontosiro* + *Parasiro* is sister to a clade grouping *Suzukielus* + Pettalidae. The sister-group relationship of *Suzukielus* and Pettalidae was already suggested in a previous cladistic analysis of the cyphophthalmid genera (Giribet and Boyer 2002). *Troglosiro* Juberthie, 1979 forms the sister-group to the Sironidae–Pettalidae clade (as originally suggested by Shear 1993), followed by *Metasiro* and by a grade of neogoveid species. Basically, these relationships, although better resolved, are in agreement with those proposed by Giribet and Boyer (2002).

Reanalysis of the data without *Odontosiro* (that has 24% missing data, contributing a total of about 31% of the missing data in the matrix) did not change the results in any significant way.

Implied weights and sensitivity analysis

The analysis under implied weighting (IW) for the values of the concavity function ranging from 1 to 6 is illustrated in Table 3. Under $k = 1$, one tree with fit considerably lower than those of other k values (fit = 222.2) was obtained, this tree being 16 steps longer than the EW tree. Other k values gave trees with fit ranging from 267.8 to 342.0; these corresponding to EW costs of 144 to 145. The IW analyses give the tree shown in Fig. 8, found under k values of 4, 5, 6 and, in one of the two trees obtained, for $k = 3$. This tree shows a monophyletic clade composed of *Troglosiro*, *Metasiro* and Neogoveidae, as the sister-group to a clade containing *Suzukielus*, Pettalidae and (*Odontosiro* + *Parasiro*). The genus *Siro* (again, including *Tranteeva*) is monophyletic, as are the pairs *S. rubens* Latreille, 1804 + *S. valleorum* Chemini, 1990, *S. duricorius* + *S. serbicus*, and the North American species of *Siro*. In this tree *Tranteeva* appears as the sister-group to the North American species. Finally, (*Marwe* (*Iberosiro* + *Paramiopsalis*)) form the sister-group to the remaining taxa (except *Ogovea* Roewer, 1923).

The IW tree (Fig. 8) with the highest fit includes a clade formed by *Troglosiro*, *Metasiro*, and Neogoveidae. A similar result supporting monophyly of *Troglosiro* + *Paragovia* was suggested previously based on molecular data (Giribet and Boyer 2002), and is further corroborated by the addition of molecular data from a South American neogoveid (Boyer and Giribet, unpublished data). This result needs to be further tested by adding *Metasiro* to the molecular dataset.

The strict consensus of all the trees obtained under IW and EW analyses is presented in Fig. 9. This tree corroborates the monophyly of Pettalidae under all analytical conditions, even considering that both represented species are very distinct in their morphologies. We suspect that the addition of pettalid taxa with greater morphological diversity would contribute to make the group even more stable and well supported. Other clades that have jackknife support values above 50% and that are stable to parameter variation are: Stylocellidae; *S. duricorius* + *S. serbicus*; *Parasiro*, and the clade composed of *Parasiro* + *Odontosiro*. The relationship between jackknife support and stability has been shown in other studies (Giribet 2003).

Interestingly, there are two clades obtained in all analyses that do not have jackknife values above 50%: the clade containing the North American *Siro*, and the clade containing the genera *Paramiopsalis* and *Iberosiro*.

Iberosiro *as a new genus*

All analyses suggest that *Iberosiro* and *Paramiopsalis* are sister taxa. The fact that both genera are monotypic may raise suspicion about the justification of a new generic category for the new species here described. However, no unambiguous synapomorphies uniting these two species have been found. Complete rediagnosis of *Paramiopsalis* would be required if the new species were included within it. The new species differs considerably from *Paramiopsalis* in fundamental characters, such as the unique adenostyles and the lack of male exocrine anal glands and a carina in the anal plate of *Iberosiro*.

Analysis of the variation among sironid (and selected outgroup) characters shows that most characters are homoplastic according to the topologies here presented. The unique ozophore position, a trait uniting *Odontosiro* and *Parasiro*, is homoplastic when considering *Marwe*, also with type 1 ozophores (character 2). The presence of a cheliceral dorsal crest in *Odontosiro* and *Parasiro* (character 8) is also found in *Siro sonoma* Shear, 1980 and in *Metasiro*. Among sironids, the presence of a ventral process in the palp trochanter (character 11) is restricted to the genera of the north-west Iberian Peninsula, but the current cladistic analysis does not support a monophyletic north-western Iberian clade. The ornamentation of legs I and II (character 14) is (in general) conserved, and within the sironids *Siro* (including *Tranteeva*), *Paramiopsalis* and *Iberosiro* share the same type of smooth metatarsus and tarsus, but *Odontosiro* and *Parasiro* each have a unique type of ornamentation. Claw modification (characters 15–19) frequently occurs in *Parasiro* and *Odontosiro*, but not in *Paramiopsalis*, *Iberosiro*, and the genera *Siro* and *Tranteeva* (Figs 22–29). Conversely, *Iberosiro* and *Paramiopsalis* share a type of II coxa that is fused to coxa III (character 25), a trait that is generally found among the members of the families Stylocellidae, Ogoveidae and Neogoveidae, as well as in the mysterious *Marwe coarctata*. The anal region (character 37) of *Iberosiro*, *Paramiopsalis* and *Parasiro* is unique among all cyphophthalmids for having a free tergite IX and sternites 8 and 9 fused medially, whereas other sironids (including *Odontosiro*, but not *Suzukielus* or *Metasiro*) have a complete corona analis. One last character that deserves further comment is the lack of anal glands in the Iberian genera of sironids, with the exception of *Paramiopsalis*, in which the anal glands are very conspicuous (character 41) (as found in most other sironids), and accompanied by a conspicuous longitudinal carina (character 39). The current analyses suggest that the taxonomy of the family Sironidae

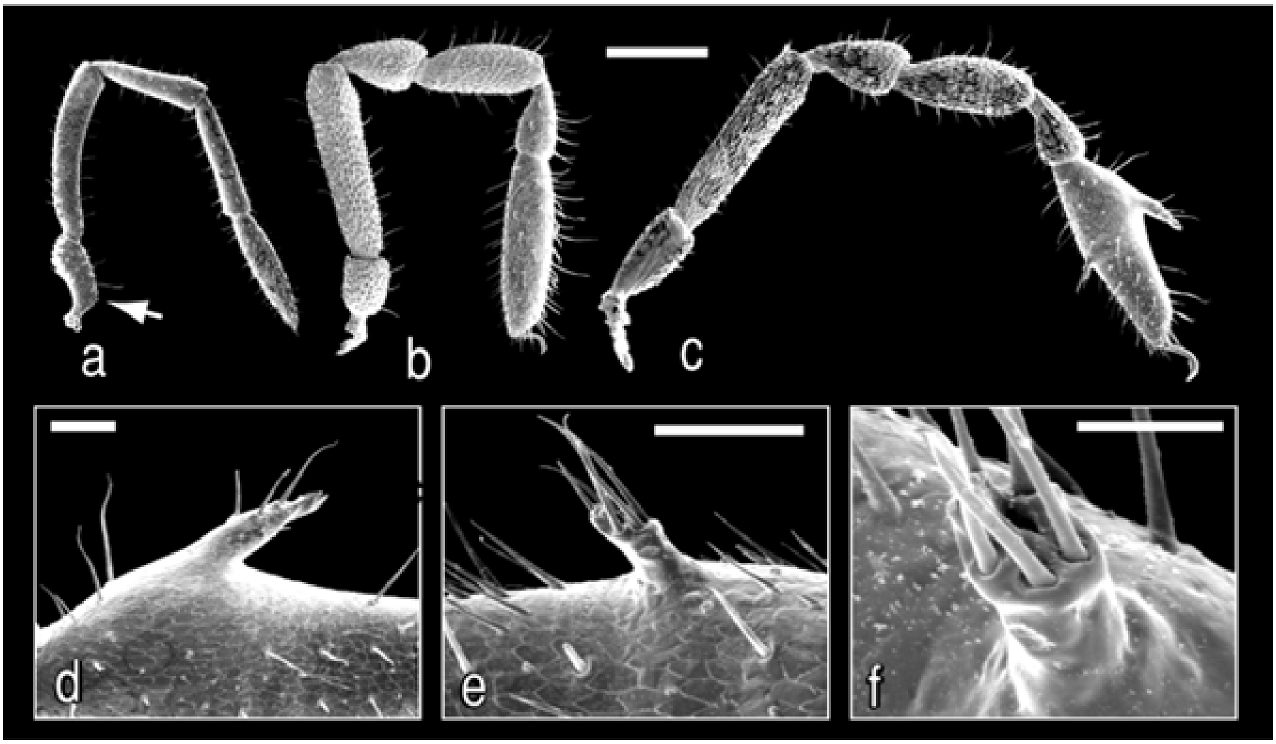

Fig. 6. *Iberosiro distylos*, sp. nov., electronmicrographs of holotype. *a*, Left palp, lateral view; *b*, right leg II, lateral view; *c*, right leg IV, lateral view; *d*, detail of right adenostyle; *e*, detail of second adenostyle-like structure; *f*, detail of second adenostyle-like structure showing apical pore. Scale bars: *a*–*c* = 200 µm; *d*, *e* = 50 µm; *f* = 20 µm. Arrow indicates ventral process of palp trochanter.

may need reorganisation, but we feel that at this point we prefer not to propose a new taxonomy for the group until molecular data are collected for most species and analysed together with the morphological characters here presented.

Summarising, the Iberian genera of sironids (*Parasiro* is also found in Corsica, Sardinia and the Italian peninsula) show an astonishing variability in their character states, often equivalent to those found across large geographical distances. This fauna also includes some of the poorest known cyphophthalmid species (in terms of numbers of specimens collected); some are restricted to areas where commercial logging and reforestation with non-

Fig. 7. Strict consensus of six trees of length 142 (*CI* = 0.46; *RI* = 0.68) for the parsimony analysis under equal weights. Character optimisations are based on unambiguous optimisations, where characters are considered ambiguous (homoplastic) when they change more than once in the tree. Numbers above marks indicate which character is changing; hollow marks are ambiguous characters, filled marks are unambiguous.

Table 3. Tree length and fit for the parsimony analyses under equal weights (EW) and implied weights for *k* values ranging from 1 to 6

The number of most parsimonious trees (MPTs) for each analysis is indicated

	Length	Fit	MPTs
EW	142		6
k = 1	158	222.2	1
k = 2	144	267.8	2
	145	267.8	
k = 3	144	297.1	2
	145	297.1	
k = 4	144	316.9	1
k = 5	144	330.8	1
k = 6	144	342	1

autochthonous species, especially of eucalyptus, may threaten the persistence of such species. *Parasiro coiffaiti* and *Paramiopsalis* have been collected more or less frequently during the last few decades, but the fate of *Odontosiro*, and especially *Iberosiro*, may require especial attention. The case of *Odontosiro* is challenging because details of its type locality (Portugal) are not well specified (see Giribet 2000), the type specimens have not been located at the MNHN (Muñoz-Cuevas, personal communication 2002), and the only modern report of new localities indicates its presence in the provinces of Pontevedra and León in north-west Spain (Rambla and Fontarnau 1984). However, these authors never published the specific localities, and no specimens of *Odontosiro lusitanicus* were found in the M. Rambla collection, currently deposited at the DBAUB. Two attempts to collect the species in northern Portugal and north-western Spain during July 2001 and September 2002 did not yield any specimens of *Odontosiro lusitanicus*, although *Paramiopsalis ramulosus* was found.

The status of *Iberosiro* is even more challenging since only one specimen, the holotype, has ever been reported and it was collected in 1941 in a cave at the Serra de Montejunto preservation area, near Lisbon (Portugal). To date we have

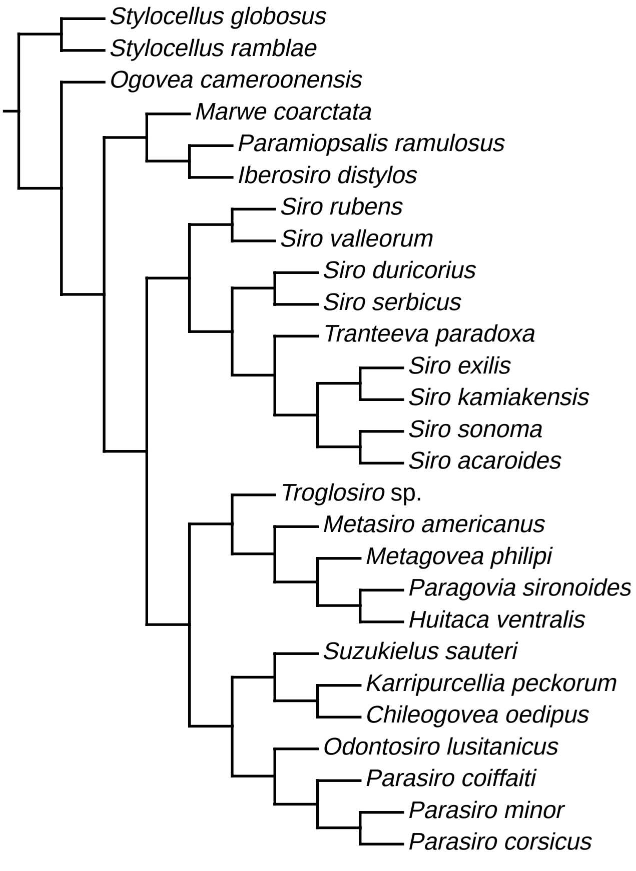

Fig. 8. Tree obtained under implied weights for k values ranging from 3 to 6 (see Table 3 for specific fit values). This tree requires 144 steps under equal weights.

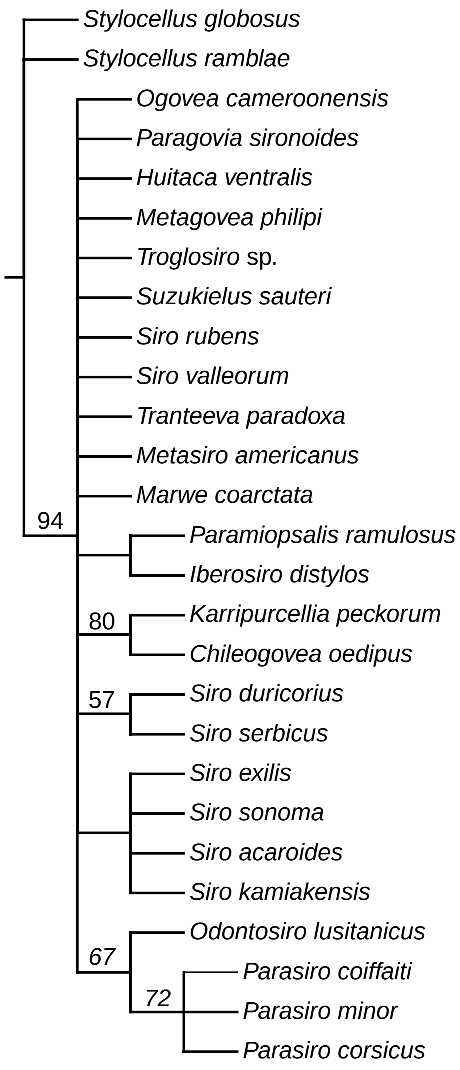

Fig. 9. Strict consensus tree of 14 cladograms obtained under equal weights and under implied weights for *k* values ranging from 1–6. Numbers on branches reflect the jackknife proportions for the equally weighted analysis.

not been able to obtain information about the cave where the animal was collected more than half a century ago, but it will be very important to prospect the area for new individuals for scientific study, as well as for assessing the status of the population of this rare species.

Acknowledgments

Arturo Muñoz-Cuevas (MNHN) kindly provided the specimens of *Iberosiro* and the types of *Parasiro* for study. Michele K. Nishiguchi, David Posada and Mónica Poubes assisted in collecting trips to Galicia and Portugal. James Cokendolpher allowed us to scan his only male specimen of *Suzukielus*. Maria Rambla and Eduardo Mateos allowed access to collections of Iberian cyphophthalmids. Carlos Prieto provided specimens from Cameroon and Equatorial Guinea. Jason Dunlop (ZMB), Mark Harvey (WAM), Rudi Jocqué (MRAC), Lorenzo Prendini & Norman Platnick (AMNH), Nikolaj Scharff (ZMUC), Peter Schwendinger (MHNG), Petra Sierwald (FMNH), Darrell Ubick & Charles Griswold (CAS) arranged the loans of specimens. We are indebted to Gary Alpert (MCZ) for his assistance photographing the holotype of the new species using Automontage, and to Richard Schalek (CIMS and OEB) for his assistance with the SEM facility. Mark Harvey and an anonymous reviewer provided comments that helped to improve this manuscript. Funding for this study was provided by NSF Award #0236871 to G. Giribet and NSF Graduate Research Fellowship to B. L. de Bivort.

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Appendix 1. List of material examined (other than for *Iberosiro distylos*, sp. nov)

Stylocellus ramblae Giribet, 2002

SEM from ♀ paratype (MCZ 35137) from the Singapore Botanical Gardens (Singapore), 8.iv.1981, leg. J. Kethley.

Other material examined. Holotype and remaining paratypes (FMNH, WAM).

Stylocellus globosus Schwendinger & Giribet, 2004

SEM from ♂ paratype (MCZ 44693) from Gua Puncak (04°31.536′N, 101°09.000′E) (Malaysia), 21.xi.2001, leg. J. Segl.

Other material examined. Holotype and remaining paratypes.

Ogovea cameroonensis Giribet & Prieto, 2003

SEM from ♂ (MCZ 55738) from the forêt d'Ototomo, Région de Yaoundé (Cameroon), December 1968, leg. J.-L. Amiet.

Other material examined. ♂♂ and ♀♀ from the same locality (MHNG, MRAC 134.818).

Paragovia sironoides Hansen, 1921

SEM from ♂ (MCZ DNA100462) from Edyabe (Río Campo) (2°19′59″N, 9°48′11″E) (Equatorial Guinea), 6.viii.2001, leg. J. Lapuente, in leaf litter.

Huitaca ventralis Shear, 1979

SEM from ♂ paratype (MCZ 30323), 30 km south of Chinácota, Provincia Norte de Santander (Colombia), 320 m (8000′), 14.v.1974, leg. S. Peck.

Other material examined. Holotype ♂ (MCZ 14835).

Metagovea philipi Goodnight & Goodnight, 1980

SEM from ♂ and ♀ paratypes (AMNH) from Los Taxos Cave (3°6′S, 78°12′W), Morona Santiago Province (Ecuador), 12.vii.1976, leg. N. P. Ashmole.

Troglosiro sp.

SEM from ♂ and ♀ (MCZ DNA100344) from Mount Dzumac Road (22°03′S, 166°28′E) (New Caledonia), 1.xii.2000, leg. G. B. Monteith (Queensland Museum Berlesate 1020).

Karripurcellia peckorum Giribet, 2003

SEM from ♂ and ♀ paratypes (MCZ 55739) from Warren Ntl Pk, near Pemberton (Western Australia, Australia), 5.vii.1980, leg. S. Peck and J. Peck.

Other material examined. Holotype ♂ (WAM T47011) and remaining paratypes (WAM T47012, FMNH).

Chileogovea oedipus Roewer, 1961

SEM from ♂ (MCZ DNA100413) from near Laguna Fría (41°30′30″S, 72°37′00″W), Parque Nacional Alerce Andino, Llanquihue Province, Región de Los Lagos (Chile), 350 m, 21.xii.2000, leg. Miller, Álvarez & Coddington.

Suzukielus sauteri (Roewer, 1916)

SEM from ♂ (Ccol) from Mount Takao, Tokyo Pref., Honshu (Japan), 9.vi.1986, leg. A. Kosaku.

Other material examined. Type series (ZMB 11490–11494).

Paramiopsalis ramulosus Juberthie, 1962

SEM from ♂ (DBAUB) from Moscoso, Pontevedra (Galicia, Spain), 24.xii.1974.

Other material examined. ♂♂ and ♀♀ from the same locality (DBAUB, MCZ).

Parasiro coiffaiti Juberthie, 1956

SEM from ♂ (MCZ) from Santa Fé de Montseny, Barcelona (Catalonia, Spain), 22.v.1993, leg. M. Rambla. SEM from ♀ (MCZ) from Riells, Prov. Barcelona (Spain), 1.iv.1935, leg. D. Ventallò.

Other material examined. Type series (MNHN 16, 1956).

Parasiro corsicus (Simon, 1872)

SEM from ♂ syntype (MNHN 16, 1956) from Porto Vecchio, Corsica (France), 22.vi.1956.

Other material examined. Remainder of type series (MNHN 16, 1956) and ♂♂ and ♀♀ from an unknown locality (ZMUC).

Parasiro minor Juberthie, 1958

SEM from ♂ (MHNG) from Mt. Pisano (Italy), 18.xii.1953, leg. Franzini.

Other material examined. ♂♂ and ♀♀ from the same collection (MHNG).

Odontosiro lusitanicus Juberthie, 1961

Material not examined.

Siro duricorius (Joseph, 1868)

SEM from (ZMB 11488) from Mt Zecjak (Croatia), June 1910, leg. R. Mesel & S. V. Anz Milben.

Other material examined. ♂♂ and ♀♀ from the same collection (ZMB 11488).

Siro serbicus Hadži, 1973

SEM from ♂ and ♀ (MCZ DNA100500) from Kucaj Mt. (Serbia), leg. I. Karaman.

Siro rubens Latreille, 1804

SEM from ♂ (DBAUB), collecting data not specified.

Other material examined. ♂♂ and ♀♀ from Mount Aigoual (DBAUB, MCZ).

Siro valleorum Chemini, 1990

SEM from ♂ (MCZ DNA100461) from Colzate (BG), c/o Baite Sedernello, Lombardia (Italy), 2.viii.2001, leg. M. Valle, Ferrario, Pantini, & Pellizzoli.

Other material examined. ♂♂ and ♀♀ from the same collection (MCZ DNA100461).

Tranteeva paradoxa Kratochvíl, 1958

Material not examined.

Siro exilis Hoffman, 1963

SEM from ♂ (FMNH #68–28) from Bickle Knob, Randolf Co., West Virginia (USA), 19.vi.1968, leg. S. Peck.

Other material examined. ♂♂ paratypes (AMNH); ♂♂ and ♀♀ (FMNH).

Siro sonoma Shear, 1980

SEM from ♂ (MCZ DNA100508) from Monte Rio (38°26′37″N, 122°59′19″W), Sonoma Co., California (USA), 20.xii.2001, leg. G. Giribet, D. Ubick & T. Briggs.

Other material examined. Paratypes (AMNH and CAS).

Siro acaroides (Ewing, 1923)

SEM from ♂ (FMNH #57–18) from Pistol River, Curry Co., Oregon (USA), 23.v.1957, leg. H. S. Dybas.

Other material examined. ♂♂ and ♀♀ (AMNH, CAS, FMNH).

Siro kamiakensis (Newell, 1943)

SEM from ♂ (FMNH #57–20) from Mt Spokane, Spokane Co., Washington (USA), 22.vi.1968, leg. H. S. Dybas.

Other material examined. ♂♂ and ♀♀ (AMNH, CAS, FMNH).

Metasiro americanus (Davis, 1933)

SEM from ♂ (FMNH #81–554) from Torreya State Park, Liberty Co., Florida (USA), 11–13.vi.1981, leg. S. Peck.

Other material examined. ♂♂ and ♀♀ paratypes (AMNH); ♂♂ and ♀♀ (AMNH, CAS, FMNH).

Marwe coarctata Shear, 1985

♀ paratype and juvenile paratypes (AMNH) from Cobra Cavern, Tena River Region, Tsavo East National Park (Kenya), 9.iii.1974, leg. J. C. Hillman. (SEM not available).

Appendix 2. Morphological characters used in the phylogenetic analyses and character discussion

GB, character number from the matrix presented by Giribet and Boyer (2002); G, character number from the matrix by Giribet (2003).

(*1*) *Eyes*: (0) absent; (1) present. (GB 1).

(*2*) *Ozophore position*: (0) type 1; (1) type 2; (2) type 3; (3) dorsal, facing 45º (GB 2; G 1) (Figs 10–11).

(*3*) *Ozophore type*: (0) plugged; (1) infolded; (2) terminal ozopore with circular opening; (3) labial; (4) disc-shaped.

A plugged ozophore is characterised by having the terminal part of the ozophore covered by smooth cuticle, with the ozopore opening in an anteroventral position, as exemplified by *Metasiro americanus* (Davis, 1933) (Fig. 11*d*). This type of ozophore is found in all members of the Sironidae, with the exception of *Suzukielus*, as well as in the Neogoveidae and Troglosironidae. Ozophores in *Stylocellus* Hansen and Sørensen, 1904 (Figs 11*g–h*) have a terminal ozopore opening formed by an infolding of two cuticular ridges. A type of ozophore with a terminal circular ozopore is found in *Suzukielus* (Fig. 11*k*) and in the members of Pettalidae (Figs 11*i–j*). *Ogovea* and *Marwe* have autapomorphic ozophores in the shape of a closed mouth (Fig. 11*f*) and a flattened disc with rounded edges (Shear 1985: fig. 2), respectively (Figs 10–11).

(*4*) *Spiral ornamentation of the ozophore*: (0) absent; (1) present.

The ozophores of certain members of the Sironidae, and the members of the genera *Troglosiro* and *Paragovia*, have a special ornamentation forming a clock-wise spiral around the ozophore when observed from the terminal region, as exemplified by *Siro exilis* Hoffman, 1963 (Fig. 10*c*) (Figs 10–11).

(*5*) *Widest part of cheliceral distal article*: (0) near base; (1) near articulation with mobile digit.

In previous studies, the adjective ‘attenuate’ was employed to characterise the special type of chelicerae of certain neogoveids and pettalids (GB 3; G 3). This coding was an attempt to reflect a former characterisation of ‘robust’ *v.* ‘attenuate’ chelicera. Here we prefer to code the quantifiable trait referring to the relative position of the maximum width in the second cheliceral segment. This maximum width is found near the articulation with the mobile digit in all the sironids (including *Suzukielus*, but not *Metasiro*), *Marwe*, and *Stylocellus globosus* Schwendinger & Giribet, 2004. Some ‘aberrant’ chelicerae of species adapted to cave environments tend to differ from the ‘typical’ cheliceral shape. The former attenuate type is now included in state ‘0’ (Figs 12–13).

(*6*) *Distal segment of chelicerae ornamentation*: (0) absent; (1) present (GB 4).

The distal segment of the chelicerae is smooth in most cyphophthalmids, but it is granulated (partially or almost completely) in all stylocellids (Giribet 2002). A similar type of scale-like ornamentation has been observed in several European sironids including *Iberosiro*, *Parasiro*, *Odontosiro*, and the *Siro duricorius*-group (Figs 12–13).

(*7*) *Dentition of the mobile digit of the chelicerae*: (0) uniform; (1) two types of dentition; (2) bilobed with smaller lobe distal.

Previous studies of cyphophthalmids focused on the differences between the pettalid type of cheliceral dentition, with a mobile digit characterised by two separate types of dentition, as exemplified by *Karripurcellia* (Fig. 15*i*). The remaining species were grouped in a single category; however, other special types of dentition are evident when chelicerae are viewed using SEM. One new state is the presence of bicuspidate teeth in the mobile digit, together with an alternation of large and small nodular teeth in the fixed digit of the American neogoveids, as exemplified by *Metagovea* (Fig. 15*c*). This character state is also observed in *Metasiro* (Fig. 15*d*) and *Troglosiro* (Fig. 15*e*) (Figs 14–15).

(*8*) *Basal article of chelicerae with dorsal crest*: (0) absent; (1) present (GB 7, G 5).

A dorsal crest (‘dorsal ridge’ of Hansen and Sørensen (1904)), adjacent to an indentation at the point of articulation with the edge of the scutum, is present in varying degrees in all cyphophthalmids. We scored it as ‘present’ when the angle formed by the margin of the chelicera on either side of the crest approaches 90º or less. In previous studies (Giribet and Boyer 2002), *Suzukielus* was coded as having a dorsal crest, but under this new definition it receives a ‘0’ coding. Most sironids lack a dorsal crest, with the exception of *Siro sonoma*, *Parasiro*, and *Odontosiro* (Figs 12–13).

(*9*) *Basal article of chelicerae with a ventral process*: (0) absent; (1) present (GB 8).

Ventral processes are more or less present in the chelicerae of all cyphophthalmids in the region where the cuticular ornamentation changes from smooth to granulated. Here, we refer to a ‘ventral process’ as a conspicuous protuberance near the insertion of the basal cheliceral segment, as seen in *Huitaca ventralis* (Fig. 13*b*). Our coding here is more restrictive than in our previous studies and only *Stylocellus ramblae* Giribet, 2002, Neogoveidae and the represented pettalids, *Troglosiro* and *Metasiro*, are scored as having the ventral process (Figs 12–13).

(*10*) *Basal article of chelicerae with a second ventral process*: (0) absent; (1) present. (GB 9) (Fig. 13*h*).

(*11*) *Palp trocanther with ventral process*: (0) absent; (1) present. (GB 10, G 7) (Figs 16–17).

(*12*) *Ornamentation of second palp article*: (0) absent; (1) present along ventral margin; (2) completely ornamented.

Most cyphophthalmids have ornamented second palp articles, particularly along the ventral margin where the granules appear conical. In *Stylocellus* and *Ogovea* (Figs 17*f–h*), the ornamentation is complete over at least the first three palp articles, whereas in other cyphophthalmids, such as *Parasiro minor* (Fig. 16*l*), the ornamentation is absent, except along the ventral margin. The ventral margins of the North American *Siro*, *Paramiopsalis ramulosus, Iberosiro distylos,* and *Parasiro coiffaiti* completely lack ornamentation (Figs 16–17).

(*13*) *Solea in tarsus I*: (0) absent; (1) present (GB 12, G 9) (Figs 18–21).

(*14*) *Leg II ornamentation*: (0) all segments smooth; (1) metatarsus and tarsus smooth; (2) metatarsus partially ornamented and tarsus smooth; (3) metatarsus ornamented and tarsus smooth; (4) metatarsus and dorso-basal part of the tarsus ornamented; (5) metatarsus ornamented and tarsus almost entirely ornamented.

In addition to the character states described previously (GB 13, G10), leg II may lack ornamentation on all articles, as found in *Marwe coarctata* (Figs 18–19).

Claws of walking legs (Figs 22–29). Cyphophthalmi have single claws on their appendages, with those of the walking legs sometimes modified by lateral projections. These have been described previously as ‘*dents ventrales*’ (e.g. Juberthie 1970), ‘lateral pegs’, ‘ventral teeth’, or ‘lateral teeth’. SEM examination has revealed that all these modifications appear to be lateral on the claw, originating from the flattened spade-like margin (e.g. Fig. 27*b*), which is typical of most cyphophthalmid claws. The type of modification may vary according to particular legs, so we have coded each leg independently. For example, *Suzukielus sauteri* has modifications in all claws (Figs 23*k*, 25*k*, 27*j*, 29*k*), *Metasiro americanus* has a smooth claw IV (Fig. 29*d*), and *Paragovia sironoides* has only modifications in claw II (Fig. 25*a*). Other combinations exist.

Giribet and Boyer (2002: their character 14) coded a 'row of ventral teeth' as present in claw II of several neogoveid species plus *Troglosiro* and *Metasiro*, and did not consider these teeth homologous to the lateral pegs of, for example, *Parasiro*. Here, we use the criteria described above to consider both modifications as homologous. The special type of teeth observed in the neogoveids is considered as a dependent character (character 17).

(*15*) *Claw of leg I with modifications*: (0) absent; (1) present.

(*16*) *Claw of leg II with modifications*: (0) absent; (1) present.

(*17*) *Claw of leg II with special row of teeth forming a comb*: (0) absent; (1) present.

The modifications of the claw of leg II are sometimes in this special state, characterised by multiple, adjacent, tooth-like projections in one side of the claw, creating a comb-like appearance (Figs 25*a–e*). *Parasiro minor* (Fig. 24*l*), *Parasiro corsicus* (Fig. 24*k*), *Metasiro americanus* (Fig. 25*d*), *Troglosiro* (Fig. 25*e*), and the Neogoveidae (Figs 25*a–c*) exhibit comb-like teeth on claw II. This character only applies to those species with modifications in claw II (character 17).

(*18*) *Claw of leg III with modifications*: (0) absent; (1) present.

(*19*) *Claw of leg IV with modifications*: (0) absent; (1) present.

(*20*) *Male tarsus IV*: (0) entire; (1) bisegmented (GB 15, G 11) (Figs 30–31).

(*21*) *Adenostyle*: (0) lamelliform; (1) ending in a tuft of setae; (2) fimbriate; (3) triangular and heavily sclerotised; (4) plumose; (5) digitiform; (6) bilobed tip (GB 16, G 12).

The adenostyle of most cyphophthalmids is lamelliform (e.g. Fig. 32*a*), however, in *Stylocellus* it terminates in a tuft of setae (Fig. 33*g*). Here, we have coded a series of autapomorphic states describing the adenostyles of *Metasiro* (fimbriate; Fig. 33*d*), *Ogovea* (triangular and heavily sclerotised; Fig. 33*f*), *Paramiopsalis* (plumose; Fig. 32*i*), *Paragovia* (digitiform; Fig. 33*a*), and *Iberosiro* (with a bilobed tip ending; Fig. 6*d*). Giribet and Boyer (2002) coded *Paragovia sironoides* Hansen, 1921 and *Ogovea* as having lamelliform adenostyles, and *Metasiro americanus* as having an adenostyle ending in a tuft of setae, but here we are more restrictive in the codings (Figs 32–33).

(*22*) *Adenostyle in the most-basal region of the tarsus*: (0) absent; (1) present.

The adenostyle of most cyphophthalmids emerges from the fourth tarsus of males near its middle (e.g. Fig. 30*a*). However, in several neogoveids (Figs 31*a–c*), it emerges adjacent to the articulation with the metatarsus. The elevated position of certain adenostyles, as in *Parasiro corsicus* (Fig. 30*k*) or *Siro rubens* (Fig. 30*e*) causes the adenostyle to appear to rise out of the most basal part of the tarsus. We coded the adenostyle position as 'most-basal' when the proximal edge of the adenostyle emerges at a distance from the metatarsus less than the width of the adenostyle. Using this criterion, the adenostyle of *Paragovia sironoides* was considered most-basal, although in previous studies (GB 17) it has been scored otherwise (Figs 30–31).

(*23*) *Ornamentation of tarsi III and IV*: (0) smooth; (1) ornamented.

The third and fourth tarsi of the majority of cyphophthalmids are smooth; those of *Stylocellus*, *Ogovea cameroonensis, Paragovia sironoides*, and *Odontosiro* are granulated (Figs 30–31).

(*24*) *Proximal end of coxae I meeting along the midline*: (0) absent; (1) present.

The proximal ends of coxae I in males meet at the midline, for example *Siro valleorum* (Fig. 34*f*), in *Troglosiro,* and all sironids except *Suzukielus sauteri* (Roewer, 1916) (Fig. 35*j*) and *Metasiro americanus* (Fig. 35*d*). In all other taxa, the coxae I endites are separated by an open space or by the palpal endites, as in *Chileogovea oedipus* Roewer, 1961 (Fig. 35*i*) (Figs 34–35).

(*25*) *Second coxae*: (0) free; (1) fused to coxae of leg III (GB 11).

(*26*) *Proximal end of male coxae III meeting along the midline*: (0) absent; (1) present.

The proximal end of coxae III in males can meet forming a midline suture, as in *Parasiro coiffaiti* (Fig. 34*j*), or fail to meet, as in *Metasiro americanus* (Fig. 35*d*). In the latter case, the suture formed by coxae III–IV joins the suture formed by coxae II–III. Coxae III of the included pettalids, *Troglosiro,* and sironids meet at the midline, with the exception of *Paramiopsalis, Iberosiro, Metasiro* and the North American *Siro* (except for *Siro kamiakensis*); data not available for *Odontosiro* (Figs 34–35).

(*27*) Coxae *II and III endites with processes running along their suture*: (0) absent; (1) present.

The endites of male coxae II and III sometimes extend in parallel along their suture, as in *Siro duricorius* (Fig. 34*g*). This causes the coxae III endites to appear U- or V-shaped in most cyphophthalmids, with the exceptions of *Stylocellus globosus* (Fig. 35*g*), *Parasiro* (Figs 34*j–l*), *Siro valleorum* (Fig. 34*f*), and the North American *Siro* (Figs 34*a–d*). *Marwe* is coded as inapplicable because it does not have endites (Shear 1985) (Figs 34–35).

(*28*) *Sternum*: (0) absent; (1) present.

The sternum of Opiliones and other arachnids has been discussed by Giribet *et al*. (2002: character 17) (see also Hansen and Sørensen 1904; Shultz 1998), who coded it as present in stylocellids but absent in *Siro* and *Parasiro*. For the current matrix, a sternal plate has only been observed in *Stylocellus* (Fig. 35*g*), *Ogovea* (Fig. 35*f*) and *Paragovia* (Fig. 35*a*) (Figs 34–35).

(*29*) *Gonostome of male in anterior position*: (0) absent; (1) present.

The gonostome in Neogoveidae males has been shifted to an anterior position relative to the rest of the Cyphophthalmi, as exemplified by *Metagovea philipi* Goodnight & Goodnight, 1980 (Fig. 35*c*). This alteration causes the proximal ends of coxae IV to no longer meet at the midline (Figs 34–35).

(*30*) *Shape of the gonostome:* (0) semicircular-trapezoidal; (1) sub-hexagonal.

In most cyphophthalmids, the gonostome is semicircular or trapezoidal with its widest part being at its posterior end where the first abdominal sternite runs perpendicular to the longitudinal axis of the animal. In the neogoveids (Figs 35*a–c*), as well as in *Metasiro americanus* (Fig. 35*d*), the gonostome has a more or less pentagonal or hexagonal shape, with the abdominal sternite forming the posterior wall of the gonostome not constituting the widest aperture of the gonostome (Figs 34–35).

(*31*) *Anterior projections of male coxae III endite*: (0) no projections; (1) projections in gonostome wall; (2) projections adjacent to coxal pore; (3) projections along suture of coxae IV.

Horn-like projections rise out of male coxae IV endites in most cyphophthalmids from a variety of positions. The majority of these projections arise on the anterior margin of the gonostome wall, as exemplified in *Siro acaroides* (Fig. 34*a*). However, in the *Siro duricorius*-group, *Siro rubens*, and *Tranteeva*, the projections are adjacent to the pore formed in the coxae III–IV suture (Figs 34*e*, *g–h*). In *Iberosiro* the projections take an intermediate position along the coxae IV midline suture, and in *Marwe*, *Karripurcellia* (Fig. 35*h*), and *Stylocellus* (Fig. 35*g*), the projections appear to be completely absent (Figs 34–35).

(*32*) *Endites of coxae IV running adjacent to midline suture for a length longer than gonostome*: (0) absent; (1) present.

The gonostome of Pettalidae is notable for its small size and has been scored as a 'small gonostome' in previous studies (GB 20, G 13) when the suture between coxae IV is longer than the gonostome. Several groups, such as *Siro exilis* (Fig. 34*c*) satisfy this criterion, but clearly have gonostomes of a different type. The character state in the pettalids (Figs 35*h–i*) and *Ogovea* (Fig. 35*f*) can alternatively be characterised by the margins of coxal IV endites running parallel to the coxae IV suture for a length greater than that of the gonostome. Species with an anterior gonostome (character 29) are inapplicable because coxae IV do not meet in the midline (Figs 34–35).

(*33*) *Spiracle shape*: (0) circular; (1) open circle; (2) 'C' shaped (GB 21, G 14).

Based on stereomicroscopy *Metasiro* and *Suzukielus* were coded as an open circle by Giribet and Boyer (2002: character 21), but SEM examination shows that they have circular spiracles (Fig. 37*d*, *k*) (Figs 36–37).

(*34*) *Male sternal glands*: (0) absent; (1) present (GB 22).

(*35*) ** Sternal apophysis of male*: (0) absent; (1) present (GB 23).

(*36*) ** V-shape modification of sternites 6–8*: (0) absent; (1) present (G 15).

(*37*) *Sternite 8, 9, and tergite IX*: (0) all free ; (1) sternites 8 and 9 medially fused; (2) sternite 9 and tergite IX fused, but sternite 8 free; (3) all fused into corona analis; (4) sternites 8 and 9 completely fused, tergite IX free.

These characters have been well described in previous studies (GB 24, G 16), however, sternites 8 and 9 are completely fused in *Metasiro americanus* (Fig. 39*d*), and we have added this as a fifth state (Figs 5*a*; Fig. 38–39).

(*38*) *Relative position of sternite 9 and tergite IX*: (0) stylocelloid type; (1) pettalid type (GB 25) (Figs 38–39).

(*39*) *Longitudinal carina in male anal plate*: (0) absent; (1) present (G 18).

A longitudinal keel is found on the anal plate of males of most sironids (Figs 38*b–i*), but *Iberosiro* (Fig. 5*a*)*, Parasiro* (Figs 38*j–l*)*, Odontosiro, Siro acaroides* (Fig. 38*a*), and *Metasiro americanus* (Fig. 39*d*) lack such a modification. However, *Metasiro* and *Siro acaroides* have a distinct lack of granulation running longitudinally on the anal plate; we code this as an independent character (Figs 38–39).

(*40*) *Lack of ornamentation in midline of male anal plate*: (0) absent; (1) present.

Many cyphophthalmids that have a longitudinal carina on the anal plate also lack ornamentation on this modification (Fig. 38*a–d*, *g*, *h*; Fig. 39*d*). Nevertheless, the carinas of *Stylocellus globosus, Paramiopsalis, Siro rubens, Siro valleorum,* and *Suzukielus* appear fully ornamented, which indicates independence of both characters.

(*41*) *Male abdominal exocrine glands (anal glands)*: (0) absent; (1) present (GB 29, G 24) (Figs 38–39).

(*42*) *Opening of male abdominal exocrine glands (anal glands)*: (0) in tergite VIII; (1) in tergite IX; (2) in both tergites VIII and IX.

SEM analysis has revealed that pores of anal glands can appear independently in tergite IX, as in *Chileogovea oedipus* (Fig. 39*j*), in tergite VIII, as in *Siro kamiakensis* (Fig. 38*b*), or in both tergites, as in *Suzukielus sauteri* (Fig. 39*k*). Along with *Stylocellus globosus* (Fig. 39*g*), most sironids have anal gland pores on tergite VIII, with the exceptions of *Iberosiro, Parasiro, Odontosiro,* and *Metasiro americanus*. Three species in our study have anal glands with pores in tergite IX: *Chileogovea oedipus, Suzukielus sauteri*, and *Metasiro americanus* (Fig. 39*d*) (Figs 38–39).

(*43*) *Posterior elongation of opisthosoma in female*: (0) absent; (1) present.

The opisthosoma of female *Siro rubens* and *Siro valleorum* is extended into a terminal tube-like elongation (Juberthie 1970: fig. 1; Chemini 1989). Although most dramatic in females, this modification is exhibited to a lesser extent in the males of *Siro valleorum*.

(*44*) *Ventral setae of penis*: (0) absent; (1) present (GB 31).

(*45*) *Movable fingers of penis*: (0) absent; (1) present.

The penises of all sironids are characterised by a pair of dorsal hook-like movable fingers adjacent to the gonopore. Movable fingers are present in members of the Sironidae, where they have been found in all individuals examined except for *Siro kamiakensis* (Shear 1980) and *Metasiro americanus* (Juberthie 1960), and are also present in several pettalids.

(*46*) *Ovipositor with sense organs*: (0) absent; (1) present (GB 32).

*Characters 35 and 36 are uninformative, but are presented here for consistency with our previous matrices and descriptive purposes.

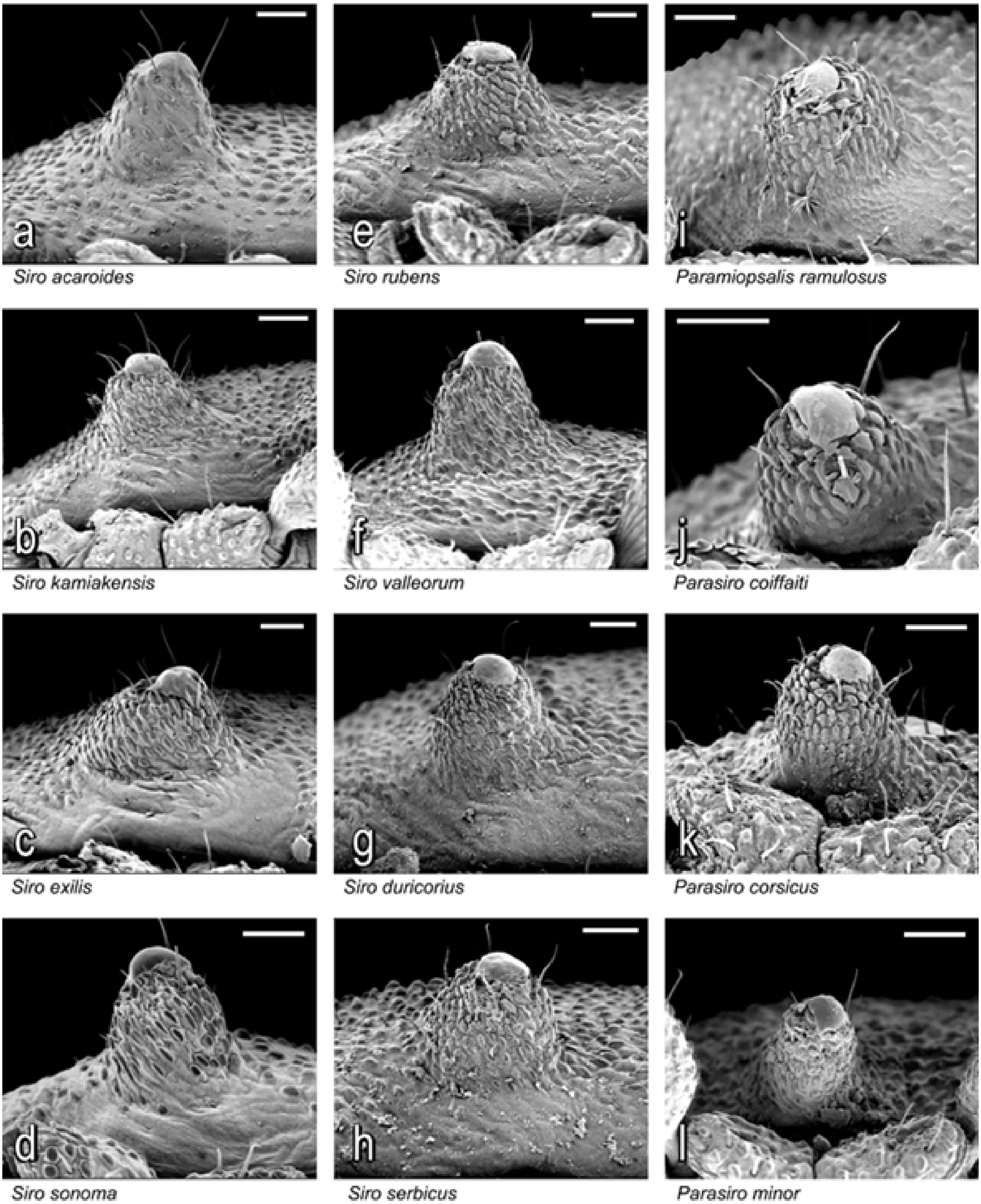
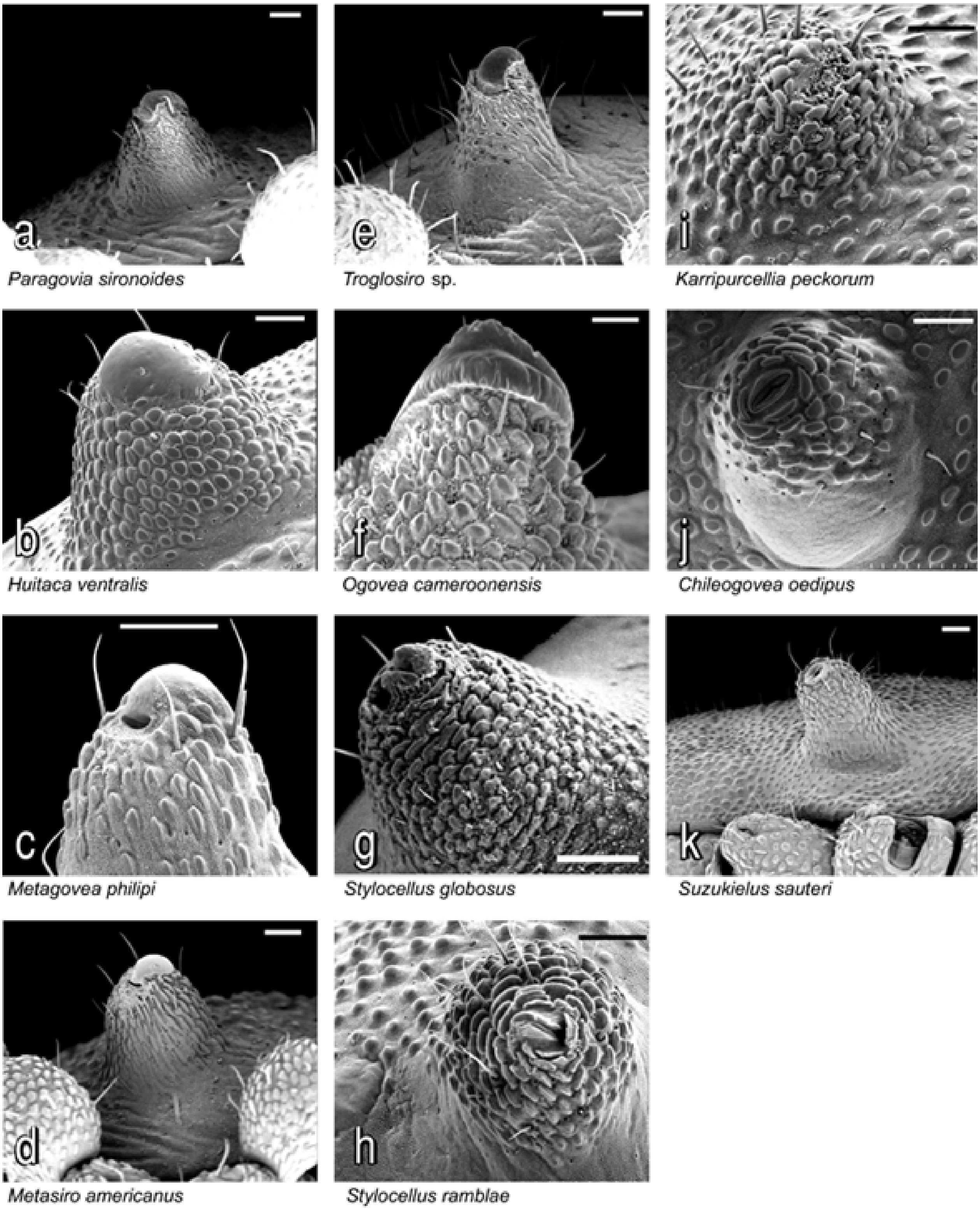
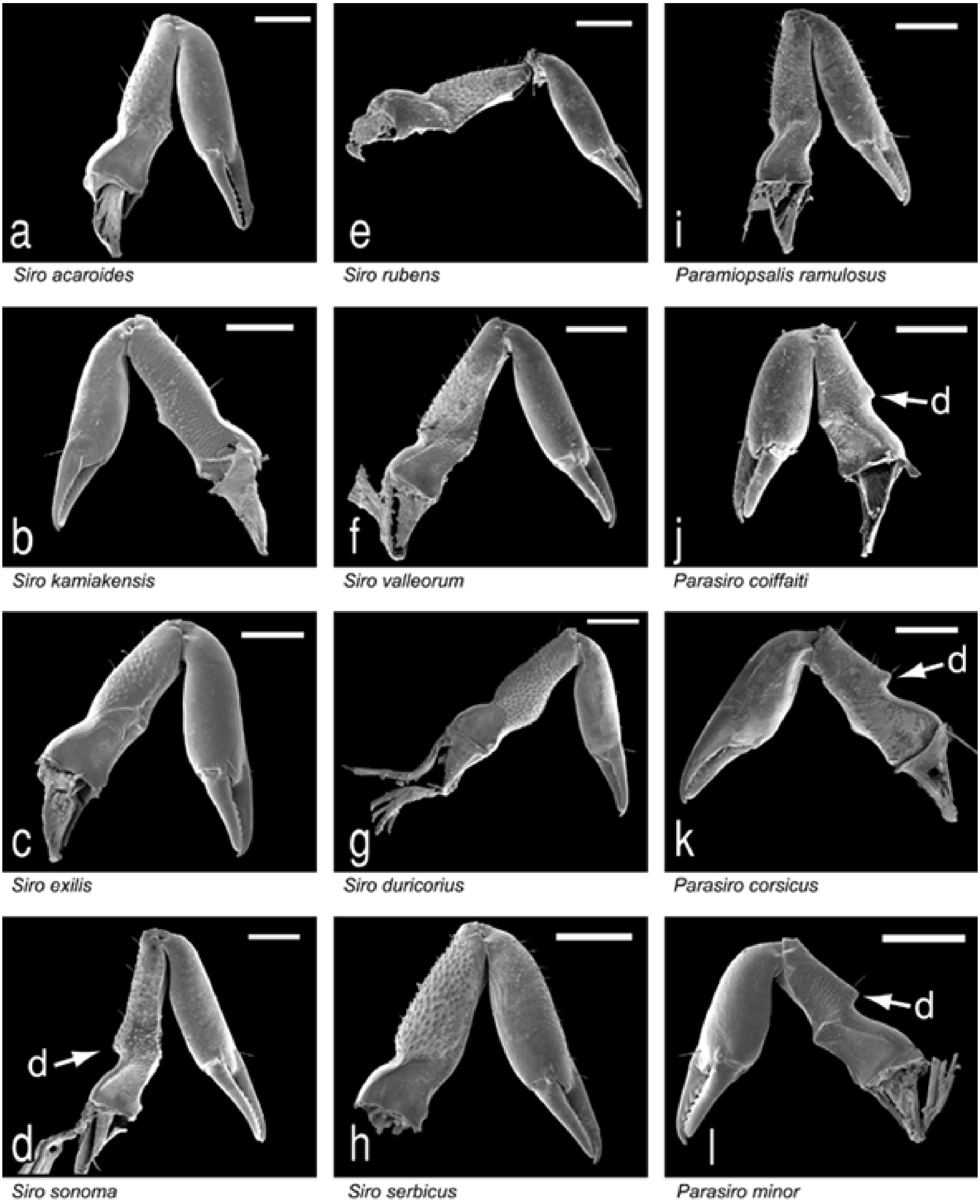


Fig. 10. Ozophores for sironid species, left corresponds to anterior on the animals. *a*, *Siro acaroides*; *b*, *Siro kamiakensis*; *c*, *Siro exilis*; *d*, *Siro sonoma*; *e*, *Siro rubens*; *f*, *Siro valleorum*; *g*, *Siro duricorius*; *h*, *Siro serbicus*; *i*, *Paramiopsalis ramulosus*; *j*, *Parasiro coiffaiti*; *k*, *Parasiro corsicus*; *l*, *Parasiro minor*. Scale bar = 50 µm.



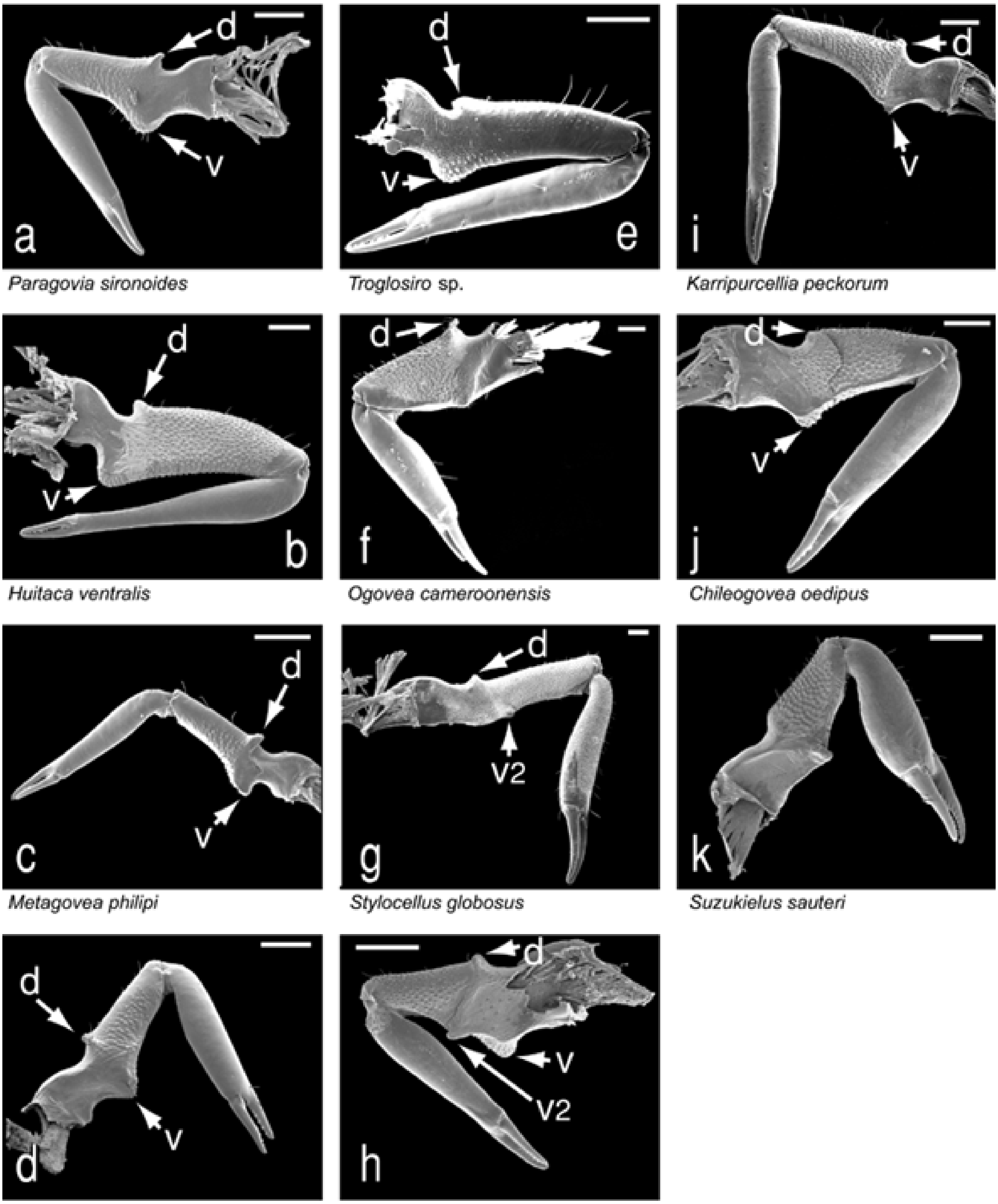
Paragovia sironoides
Troglosiro sp.
Karripurcellia peckorum
Huitaca ventralis
Ogovea cameroonensis
Chileogovea oedipus
Metagovea philipi
Stylocellus globosus
Suzukielus sauteri
Metasiro americanus
Stylocellus ramblae

Fig. 11. Ozophores for selected outgroup taxa, left corresponds to anterior on the animals. *a*, *Paragovia sironoides*; *b*, *Huitaca ventralis*; *c*, *Metagovea philipi*; *d*, *Metasiro americanus*; *e*, *Troglosiro* sp.; *f*, *Ogovea cameroonensis*; *g*, *Stylocellus globosus*; *h*, *Stylocellus ramblae*; *i*, *Karripurcellia peckorum*; *j*, *Chileogovea oedipus*; *k*, *Suzukielus sauteri*. Scale bar = 50 µm.



Siro acaroides
Siro rubens
Paramiopsalis ramulosus
Siro kamiakensis
Siro valleorum
Parasiro coiffaiti
Siro exilis
Siro duricorius
Parasiro corsicus
Siro sonoma
Siro serbicus
Parasiro minor

Fig. 12. Chelicerae for sironid species (lettering as in Fig. 10), lateral view. d, Dorsal crest. Scale bar = 200 µm.



Paragovia sironoides

Troglosiro sp.

Karripurcellia peckorum

Huitaca ventralis

Ogovea cameroonensis

Chileogovea oedipus

Metagovea philipi

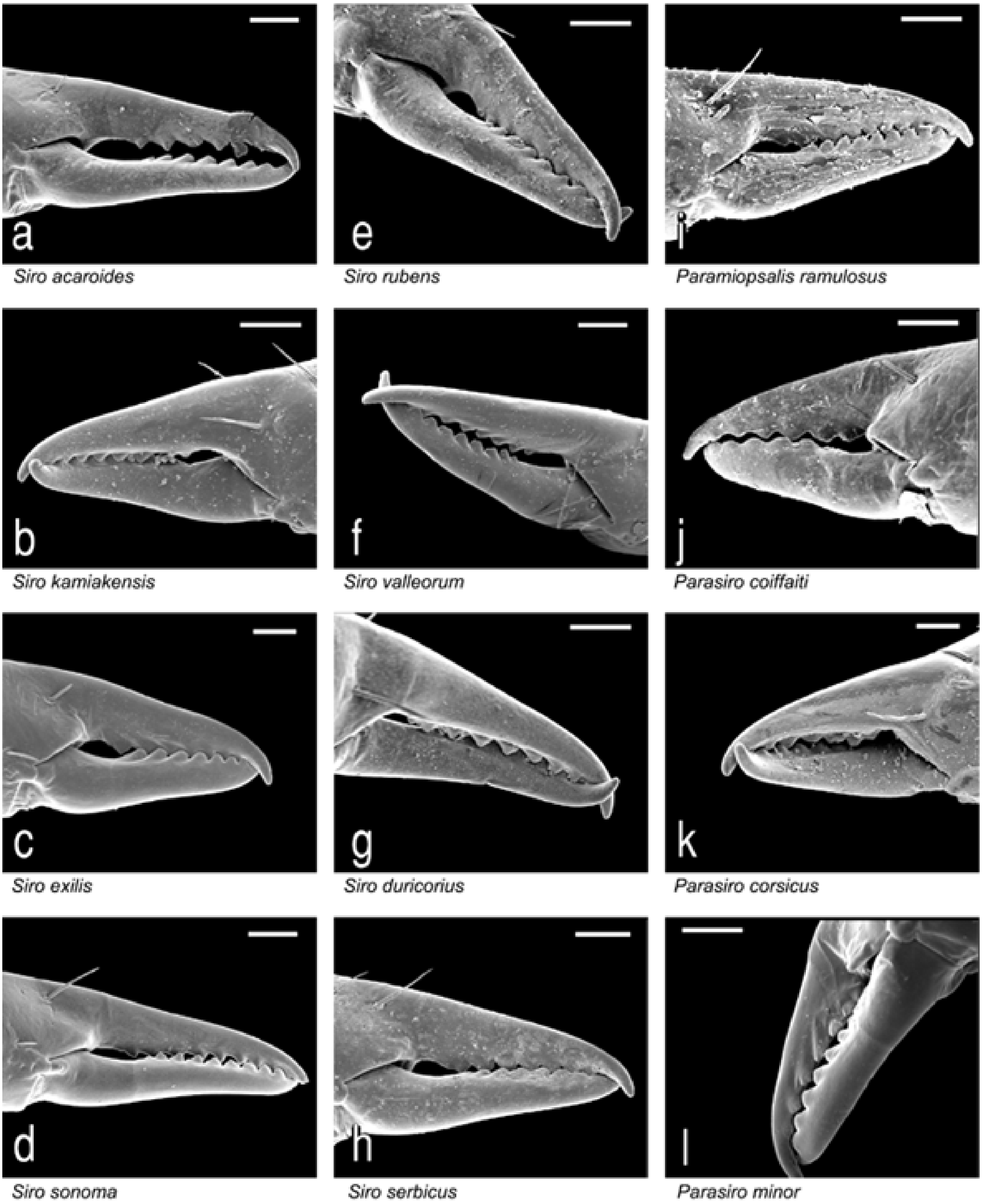
Stylocellus globosus

Suzukielus sauteri

Metasiro americanus

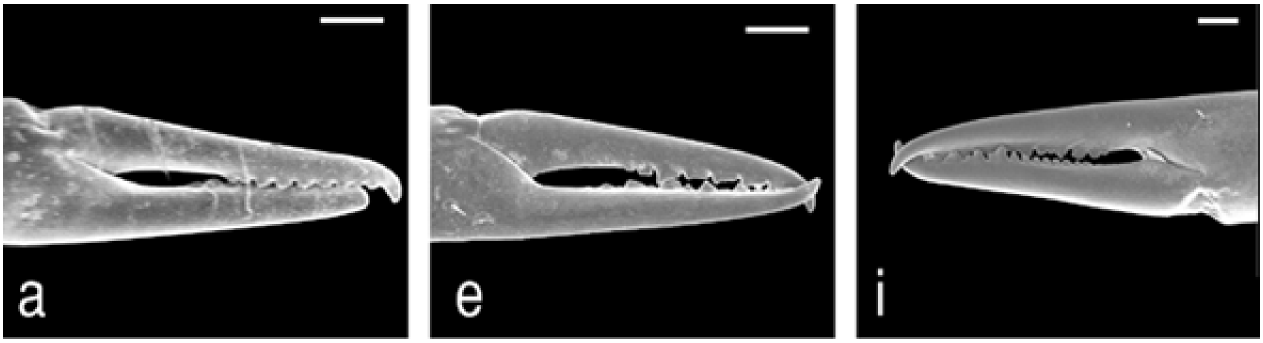
Stylocellus ramblae

Fig. 13. Chelicerae for selected outgroup species (lettering as in Fig. 11), lateral view. d, Dorsal crest; v, ventral process; v2, second ventral process. Scale bar = 200 µm.

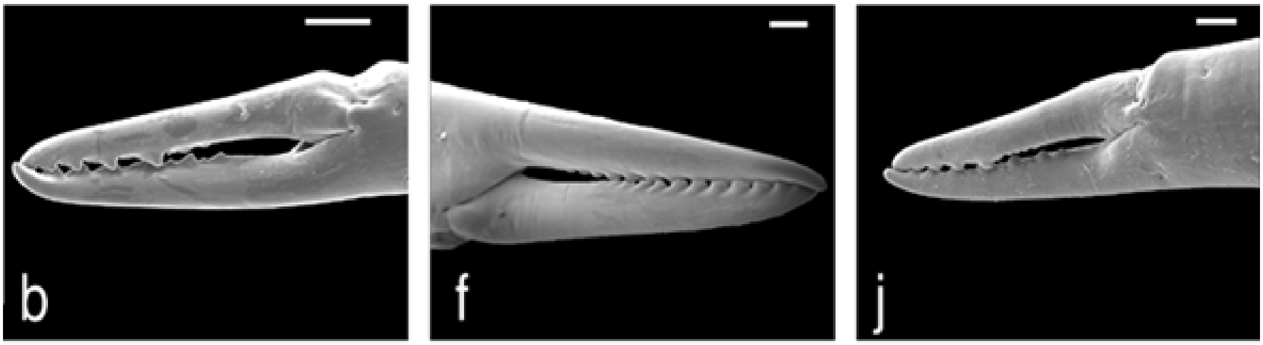


Siro acaroides
Siro rubens
Paramiopsalis ramulosus
Siro kamiakensis
Siro valleorum
Parasiro coiffaiti
Siro exilis
Siro duricorius
Parasiro corsicus
Siro sonoma
Siro serbicus
Parasiro minor

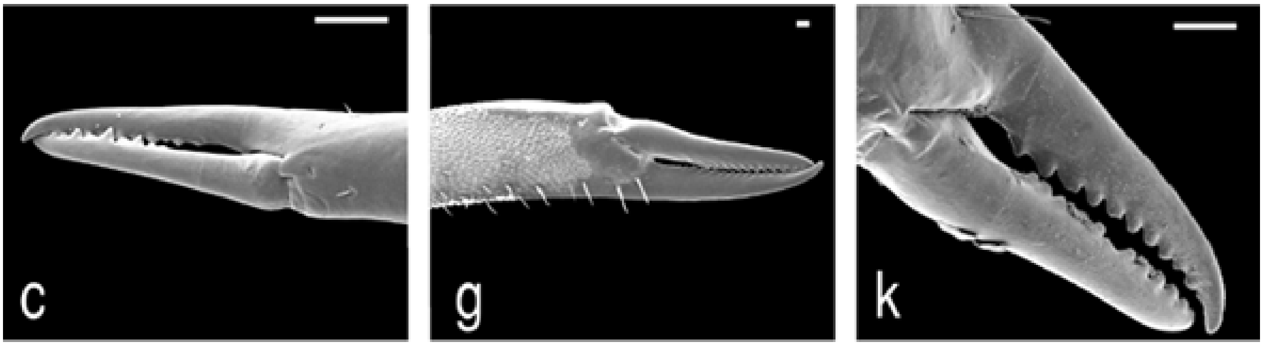
Fig. 14. Cheliceral dentition for sironid species (lettering as in Fig. 10). Scale bar = 50 µm.



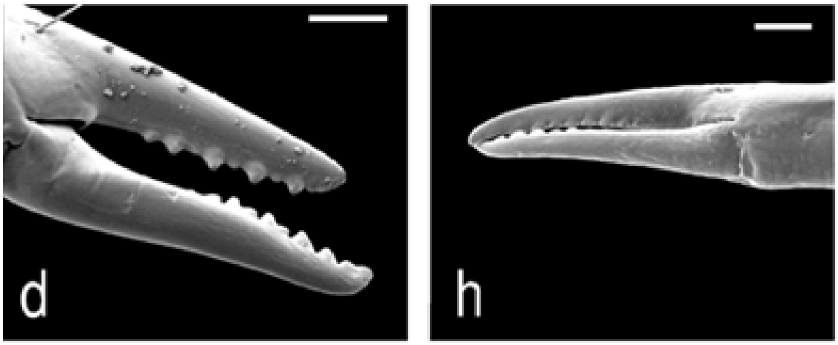
Paragovia sironoides *Troglosiro* sp. *Karripurcellia peckorum*



Huitaca ventralis *Ogovea cameroonensis* *Chileogovea oedipus*

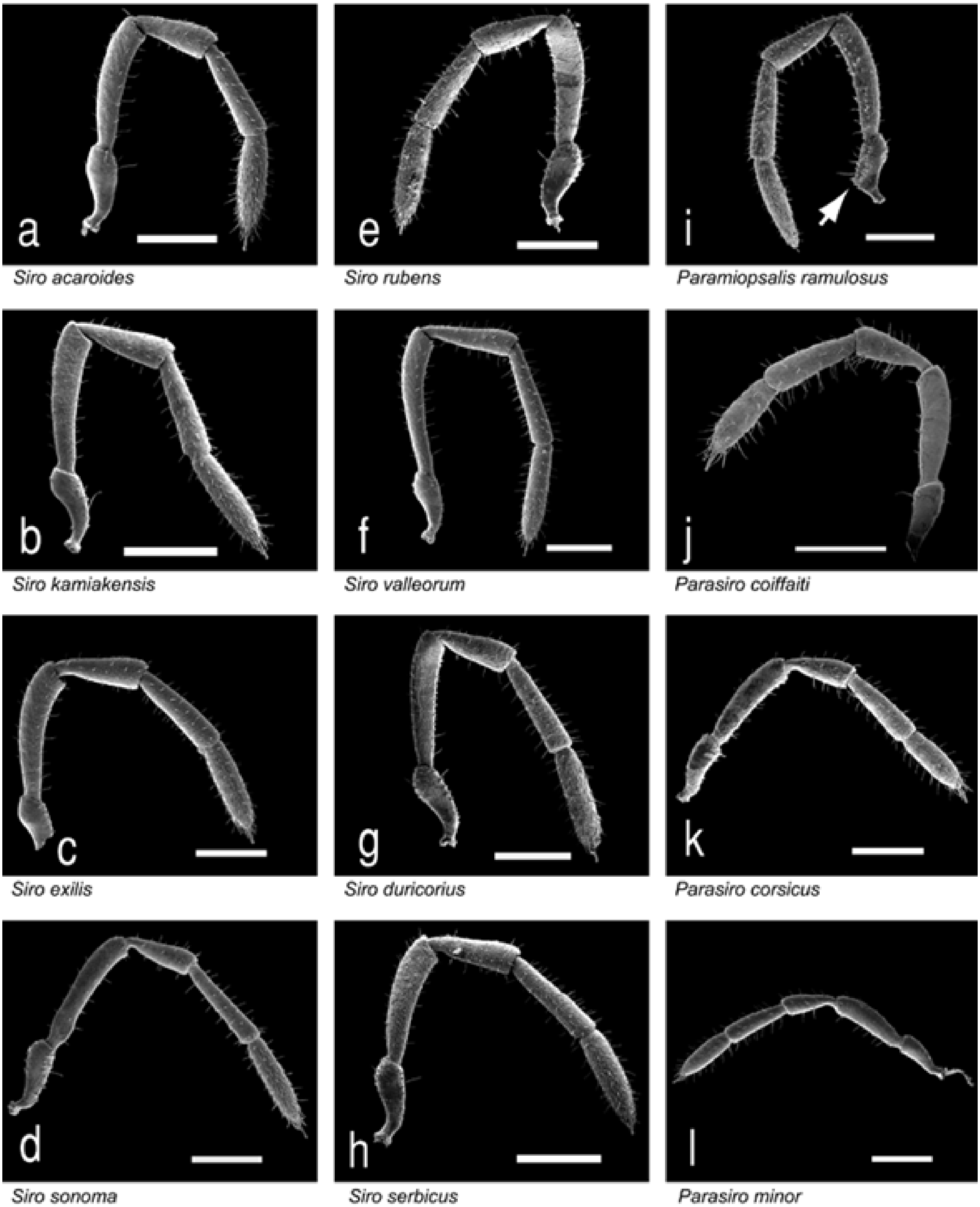


Metagovea philipi *Stylocellus globosus* *Suzukielus sauteri*



Metasiro americanus *Stylocellus ramblae*

Fig. 15. Cheliceral dentition for selected outgroup species (lettering as in Fig. 11). Scale bars = 50 µm.



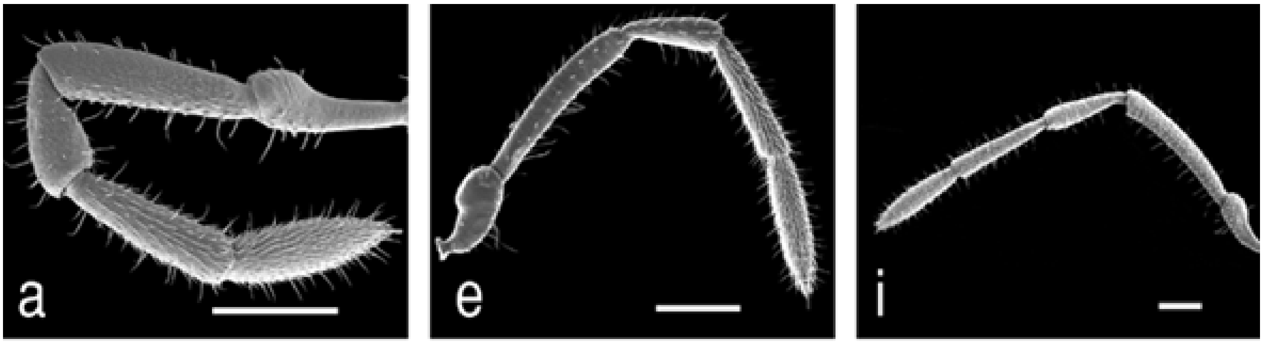
Siro acaroides *Siro rubens* *Paramiopsalis ramulosus*

Siro kamiakensis *Siro valleorum* *Parasiro coiffaiti*

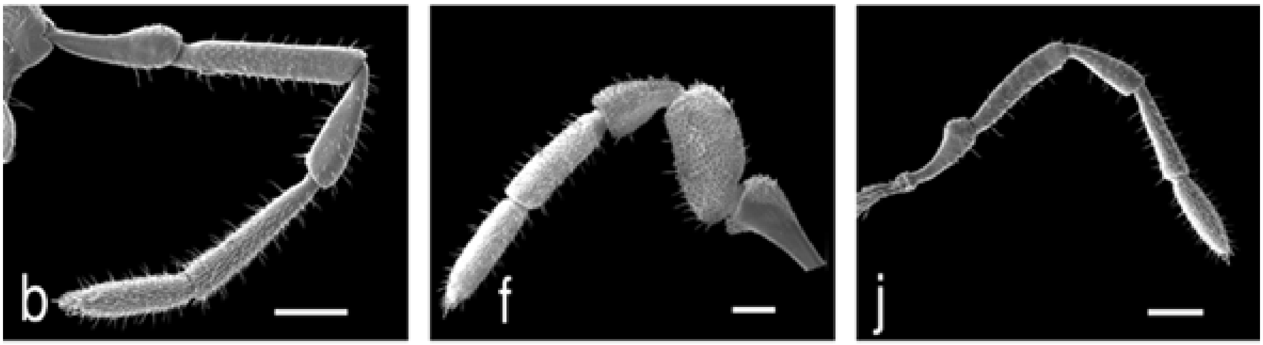
Siro exilis *Siro duricorius* *Parasiro corsicus*

Siro sonoma *Siro serbicus* *Parasiro minor*

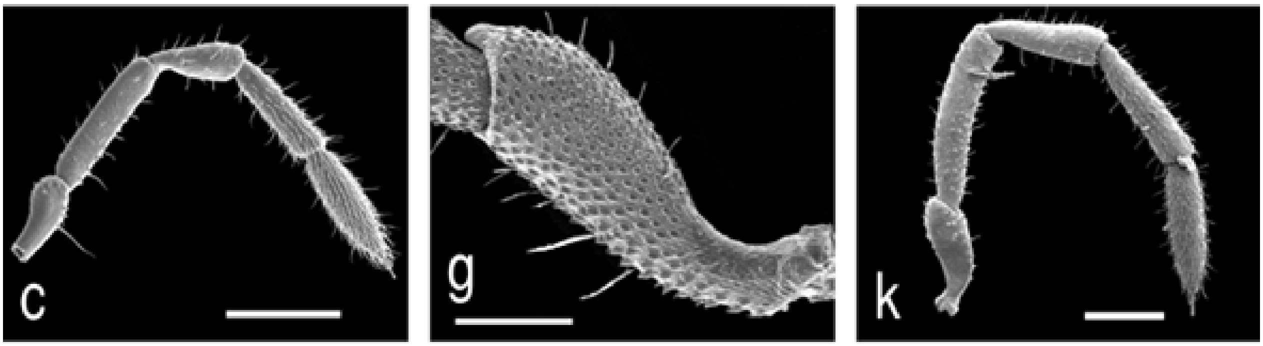
Fig. 16. Palps for sironid species (lettering as in Fig. 10), lateral view. Arrow indicates ventral process of palp trochanter. Scale bar = 200 µm.



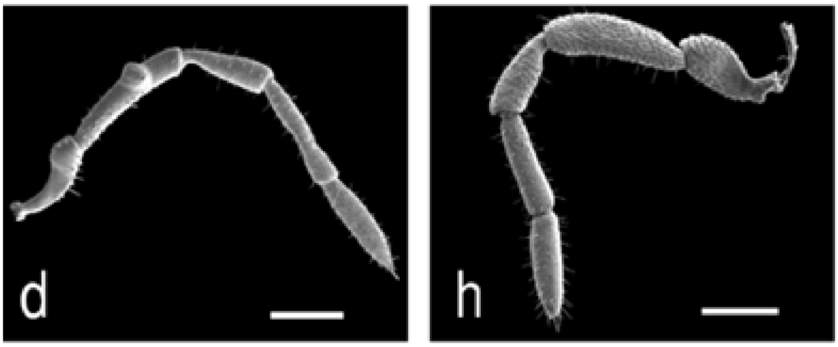
Paragovia sironoides *Troglosiro* sp. *Karripurcellia peckorum*



Huitaca ventralis *Ogovea cameroonensis* *Chileogovea oedipus*

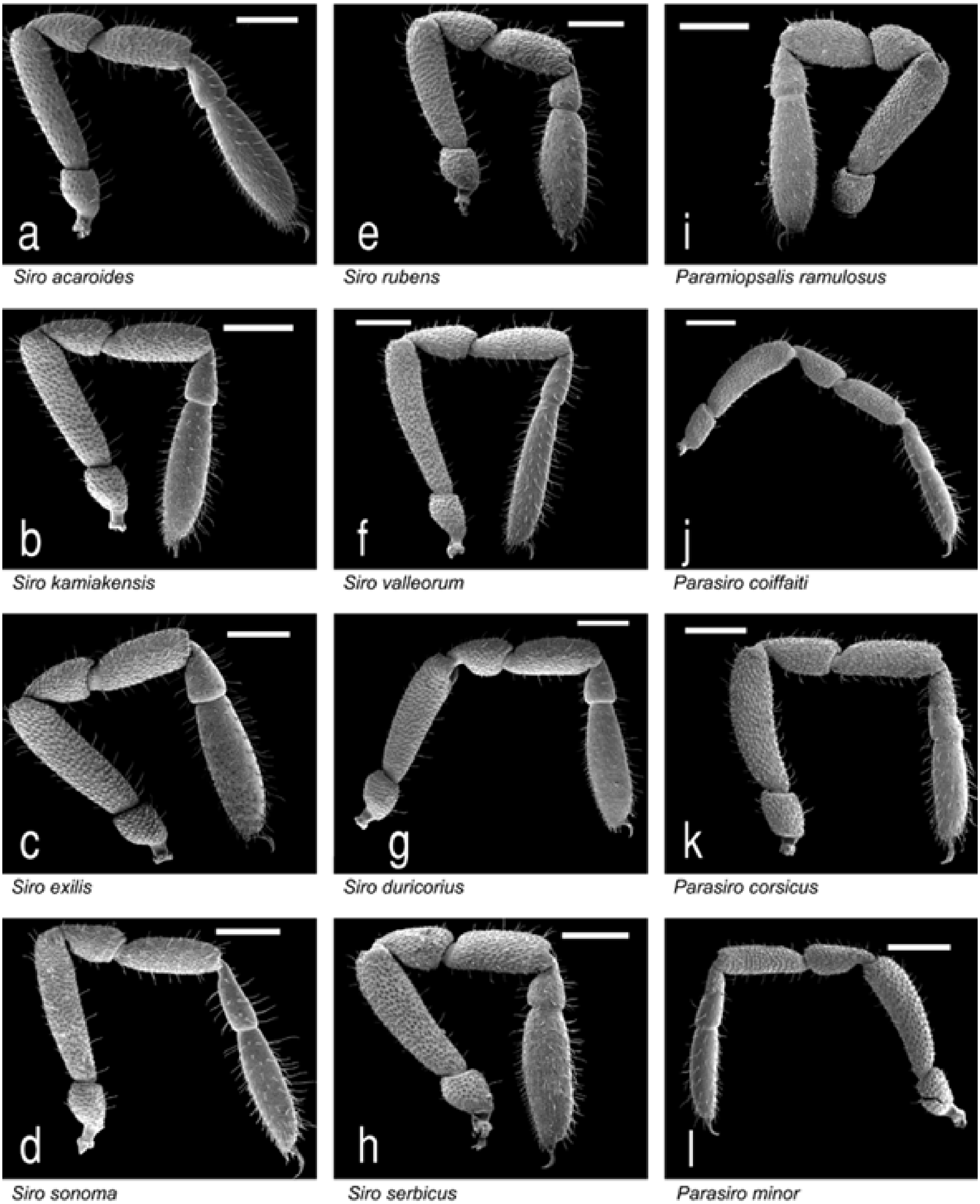


Metagovea philipi *Stylocellus globosus* *Suzukielus sauteri*



Metasiro americanus *Stylocellus ramblae*

Fig. 17. Palps for selected outgroup species (lettering as in Fig. 11), lateral view. Scale bar = 200 µm.



Siro acaroides *Siro rubens* *Paramiopsalis ramulosus*

Siro kamiakensis *Siro valleorum* *Parasiro coiffaiti*

Siro exilis *Siro duricorius* *Parasiro corsicus*

Siro sonoma *Siro serbicus* *Parasiro minor*

Fig. 18. Legs I for sironid species (lettering as in Fig. 10), lateral view. Scale bar = 200 µm.

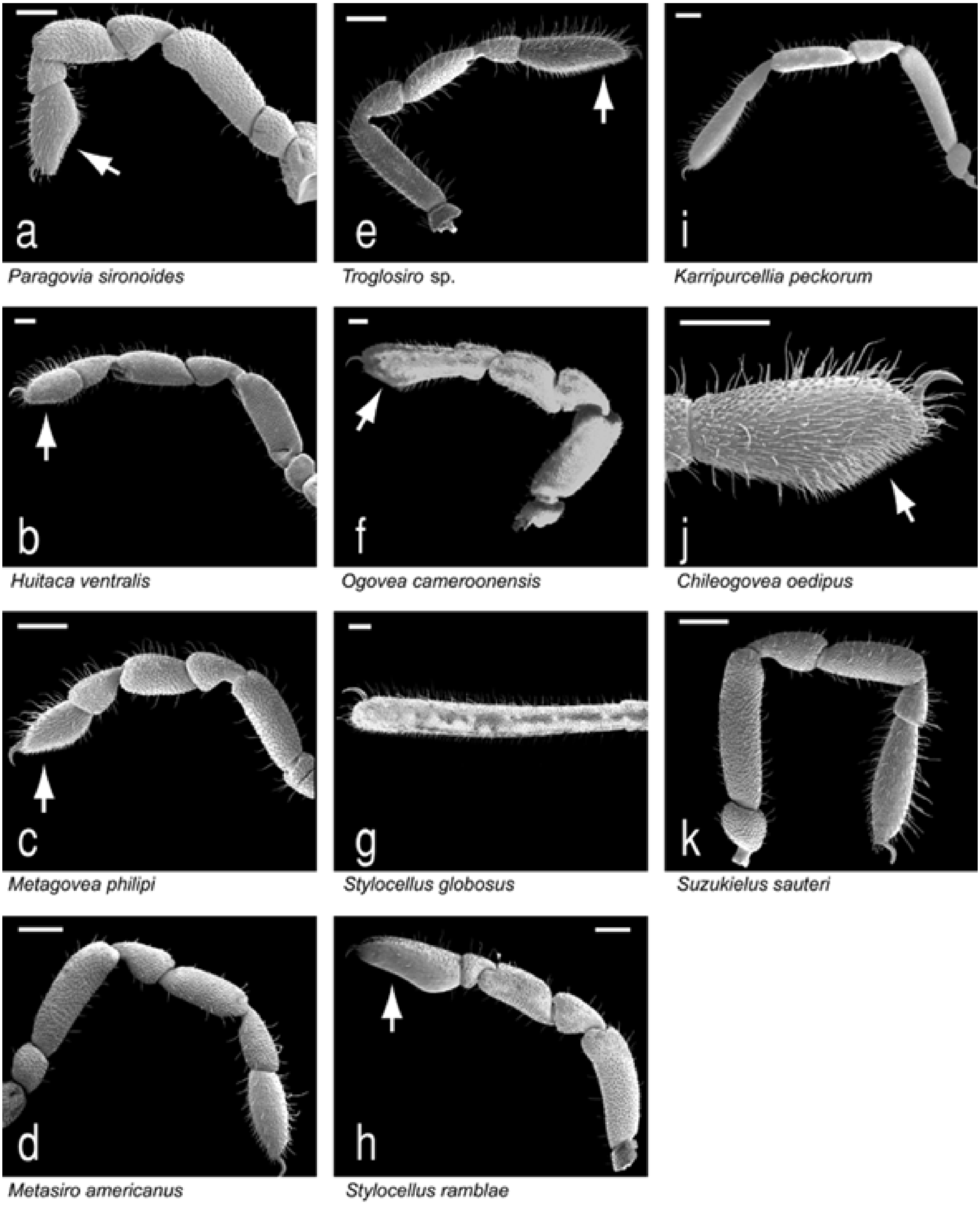
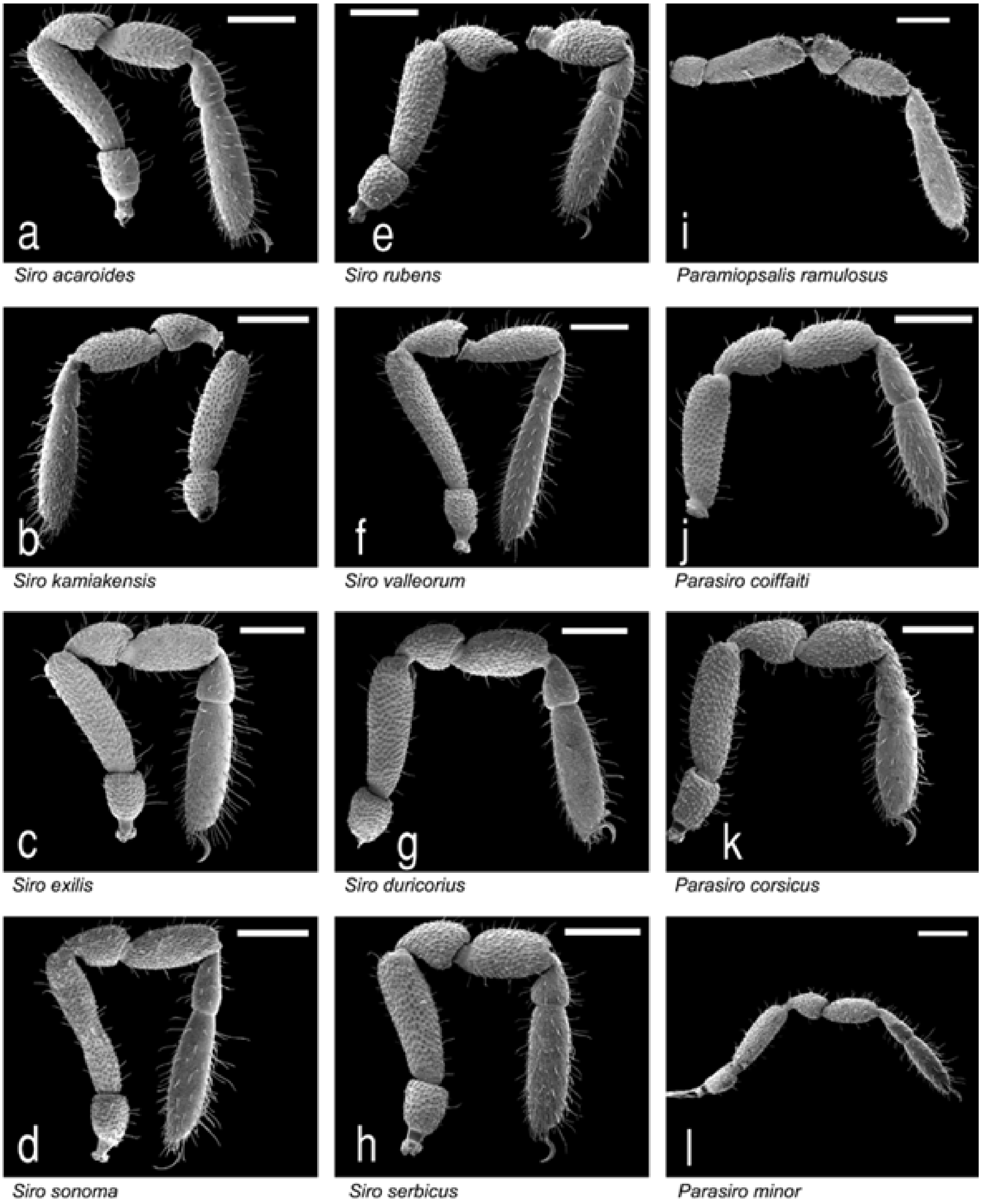


Fig. 19. Legs I for selected outgroup species (lettering as in Fig. 11), lateral view. Arrows indicate soleae. Scale bar = 200 µm.



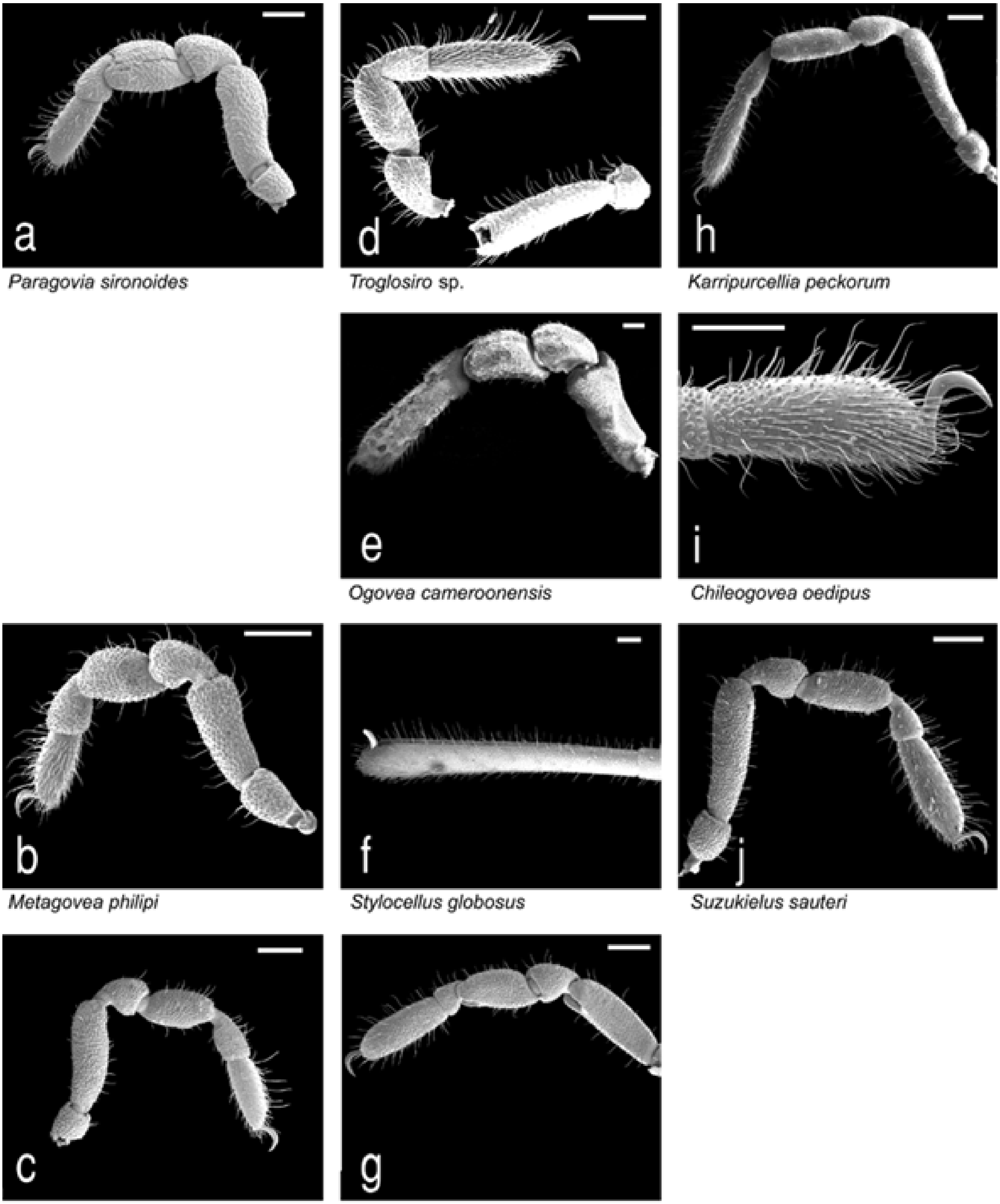
Siro acaroides *Siro rubens* *Paramiopsalis ramulosus*

Siro kamiakensis *Siro valleorum* *Parasiro coiffaiti*

Siro exilis *Siro duricorius* *Parasiro corsicus*

Siro sonoma *Siro serbicus* *Parasiro minor*

Fig. 20. Legs II for sironid species (lettering as in Fig. 10), lateral view. Scale bar = 200 µm.



Paragovia sironoides

Troglosiro sp.

Karripurcellia peckorum

Ogovea cameroonensis

Chileogovea oedipus

Metagovea philipi

Stylocellus globosus

Suzukielus sauteri

Metasiro americanus

Stylocellus ramblae

Fig. 21. Legs II for selected outgroup species, lateral view. *a*, *Paragovia sironoides*; *b*, *Metagovea philipi*; *c*, *Metasiro americanus*; *d*, *Troglosiro* sp.; *e*, *Ogovea cameroonensis*; *f*, *Stylocellus globosus*; *g*, *Stylocellus ramblae*; *h*, *Karripurcellia peckorum*; *i*, *Chileogovea oedipus*; *j*, *Suzukielus sauteri*. Scale bar = 200 µm.

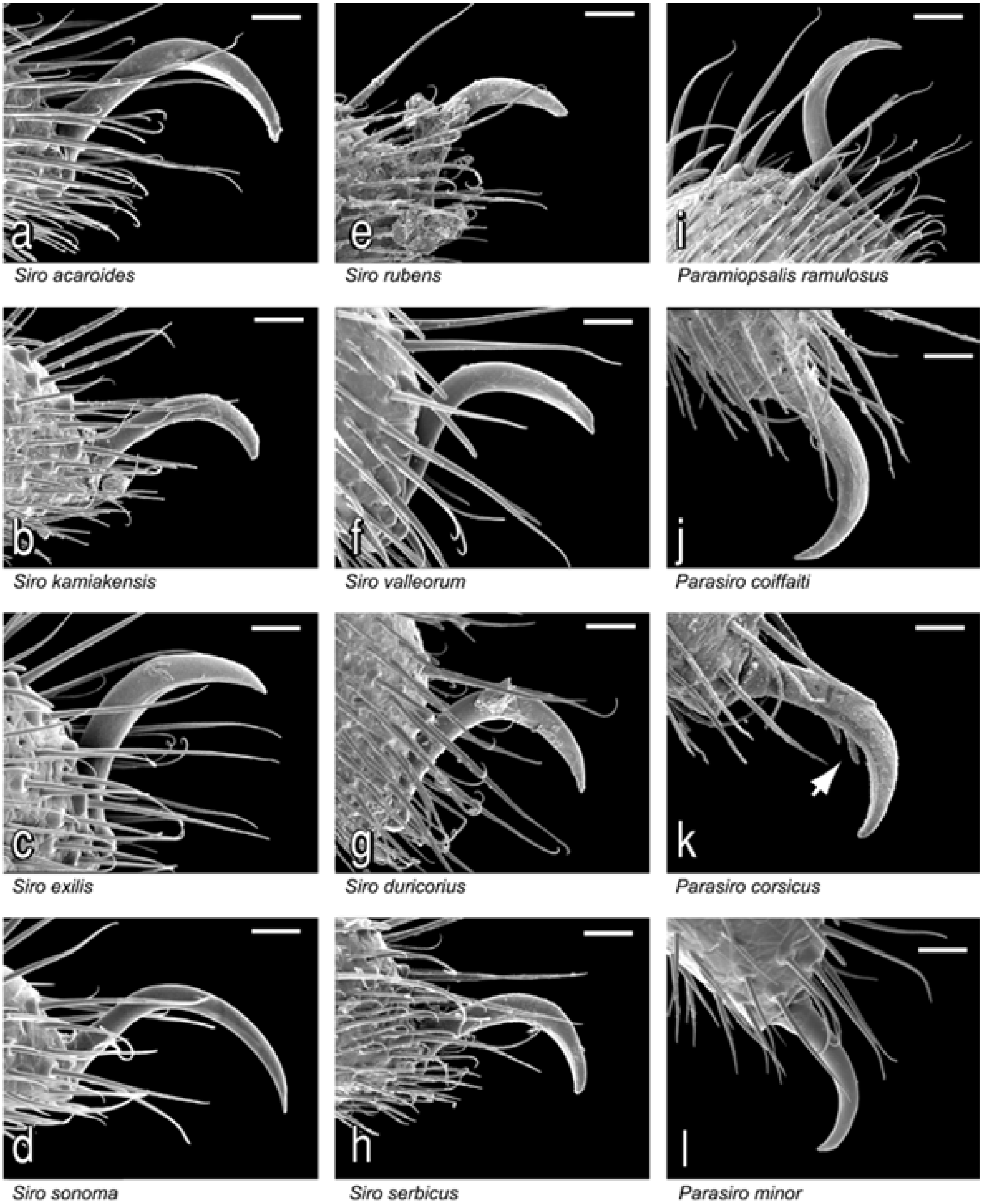
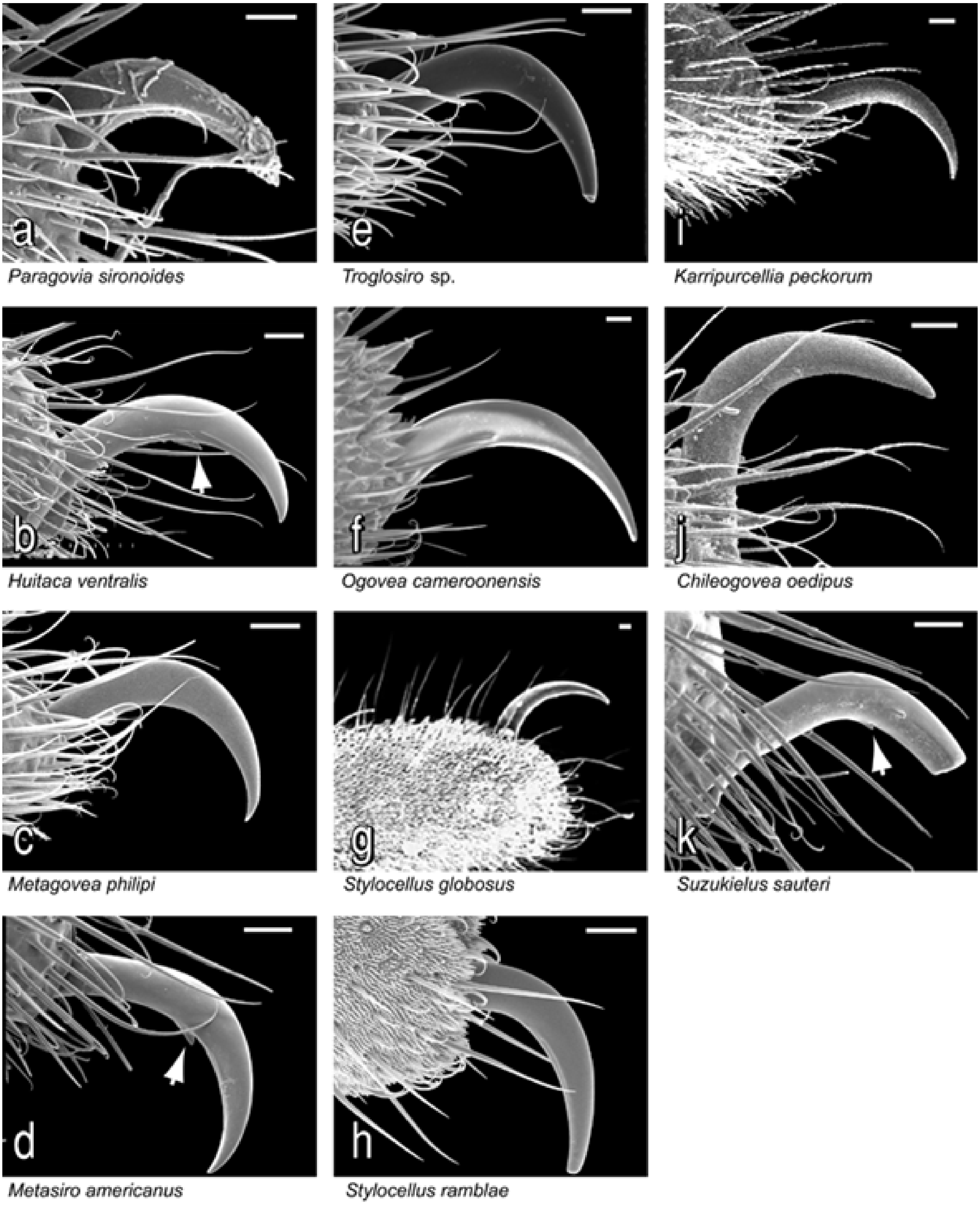


Fig. 22. Claws of leg I for sironid species (lettering as in Fig. 10), lateral view. Arrow indicates lateral modification. Scale bar = 20 µm.



Paragovia sironoides

Troglosiro sp.

Karripurcellia peckorum

Huitaca ventralis

Ogovea cameroonensis

Chileogovea oedipus

Metagovea philipi

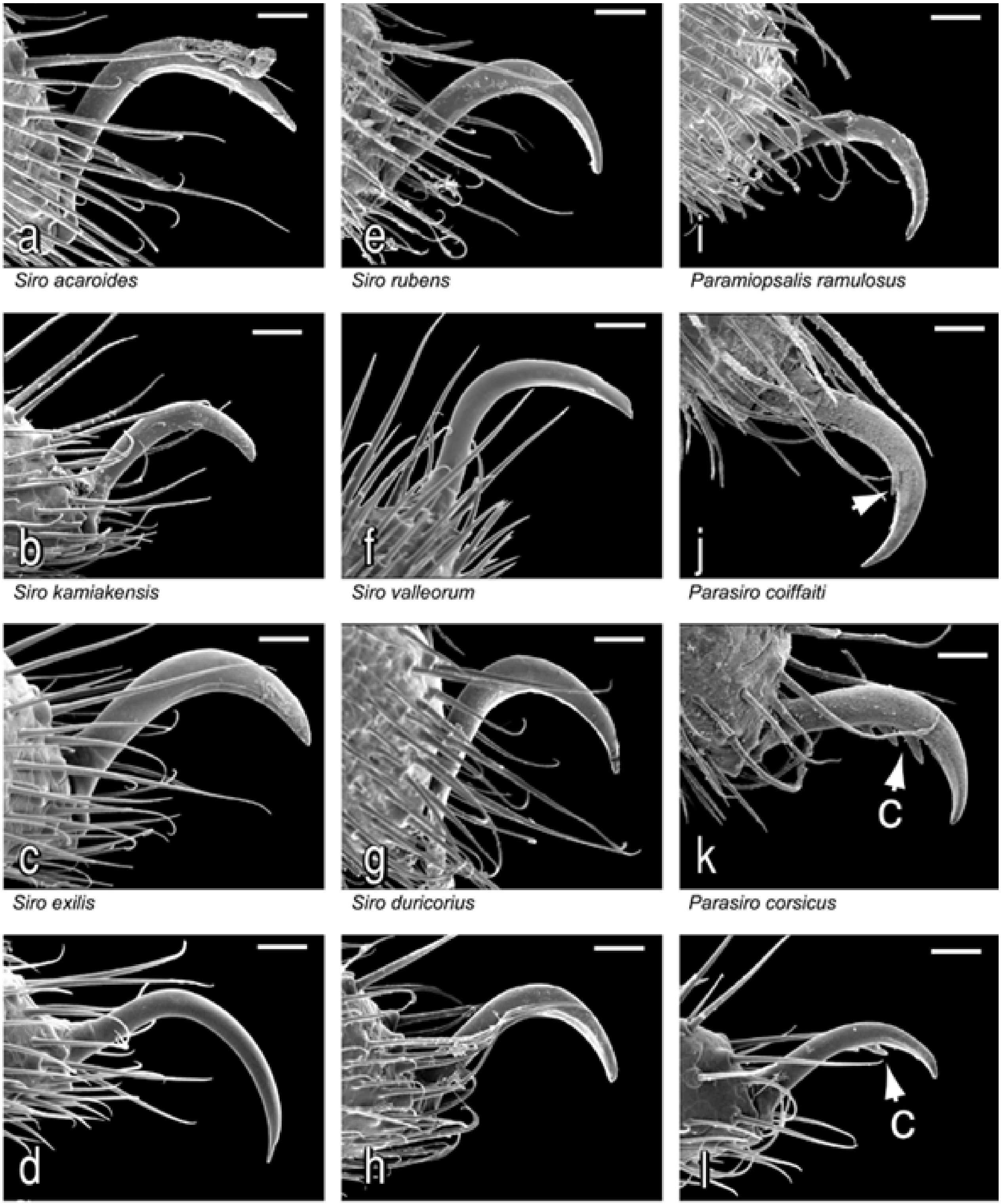
Stylocellus globosus

Suzukielus sauteri

Metasiro americanus

Stylocellus ramblae

Fig. 23. Claws of leg I for selected outgroup species (lettering as in Fig. 11), lateral view. Arrows indicate lateral modification. Scale bar = 20 μm.



Siro acaroides

Siro kamiakensis

Siro exilis

Siro sonoma

Siro rubens

Siro valleorum

Siro duricorius

Siro serbicus

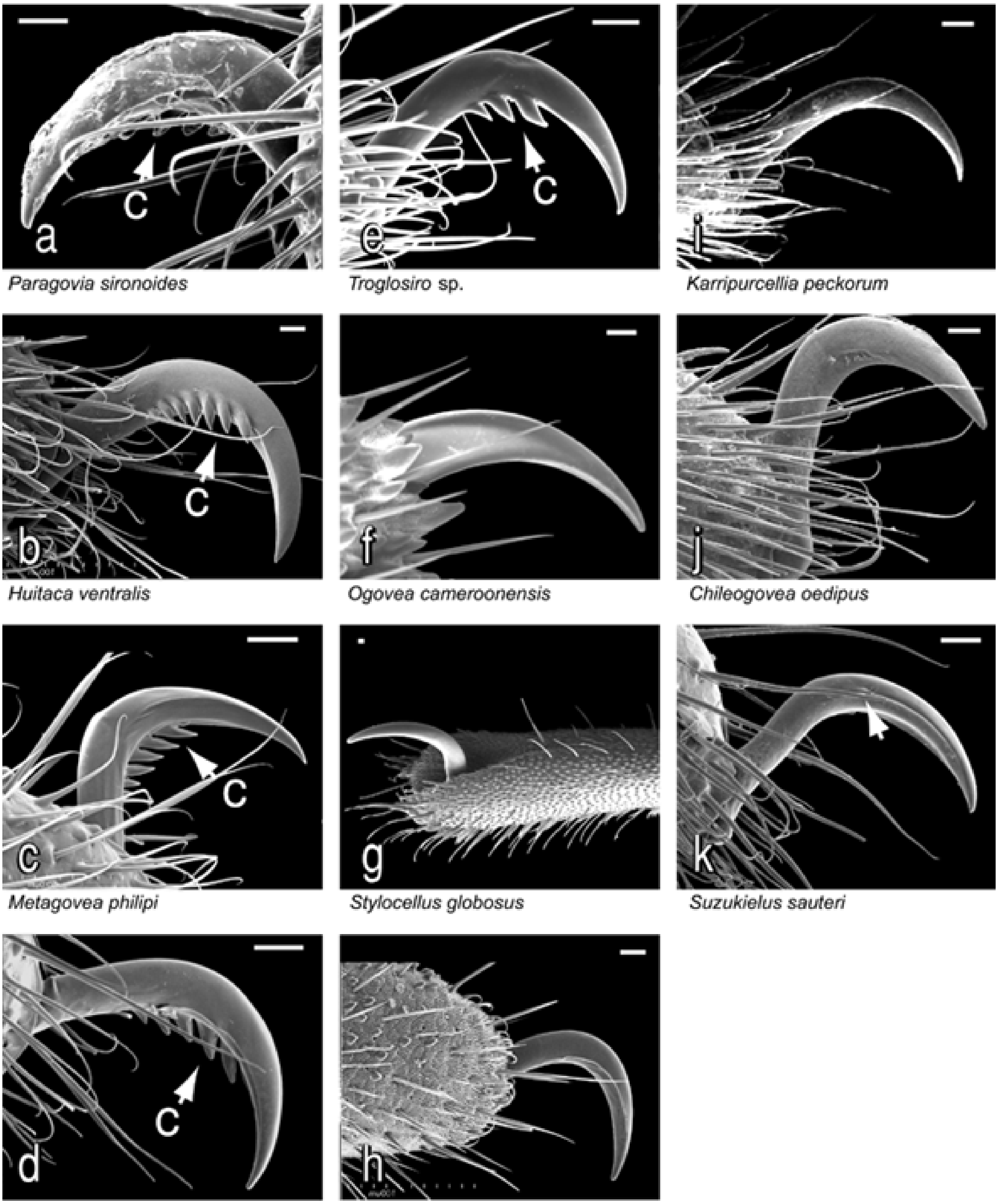
Paramiopsalis ramulosus

Parasiro coiffaiti

Parasiro corsicus

Parasiro minor

Fig. 24. Claws of leg II for sironid species (lettering as in Fig. 10), lateral view. Arrows indicate lateral modification. c, comb-like modification. Scale bar = 20 µm.



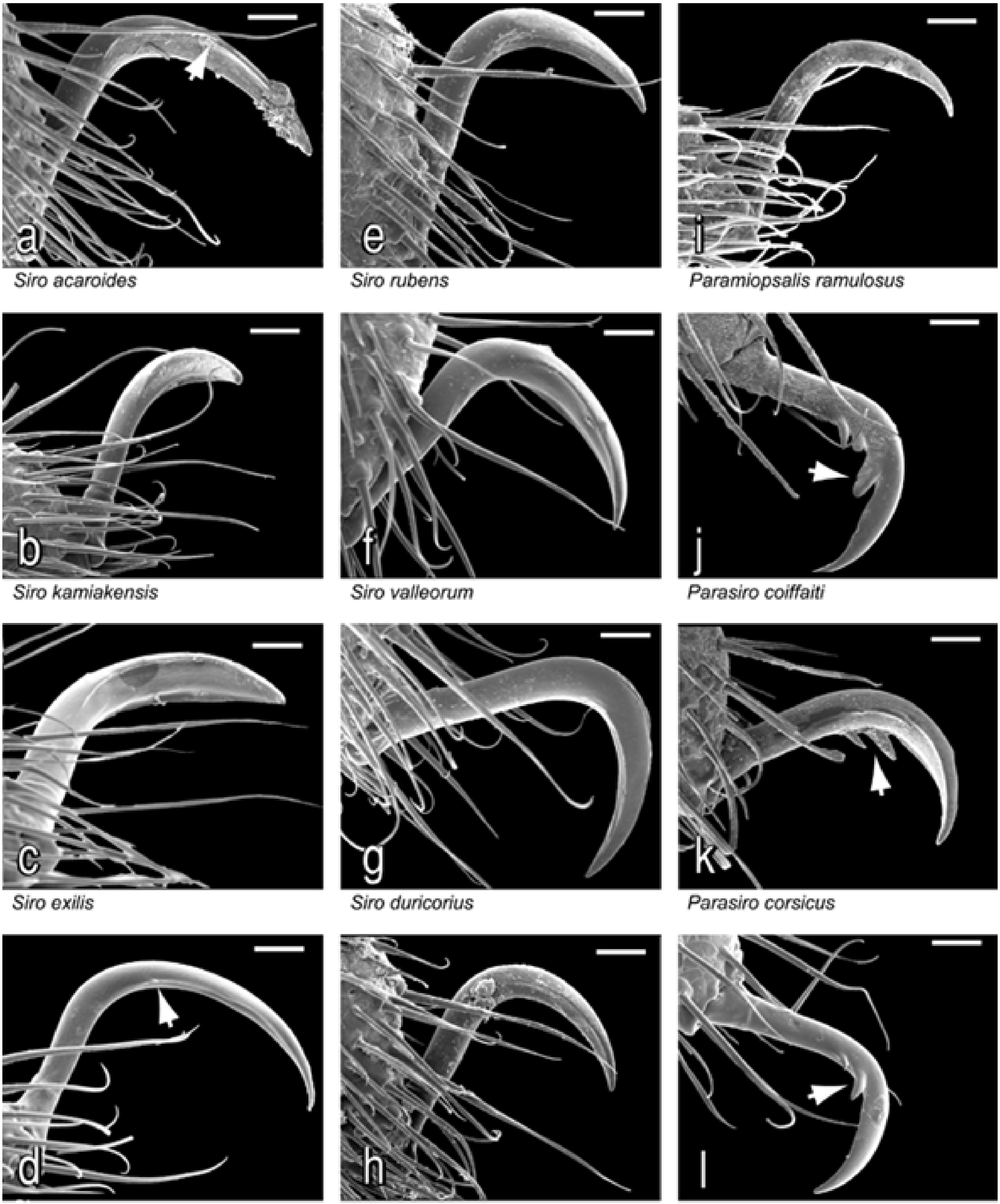
Paragovia sironoides *Troglosiro* sp. *Karripurcellia peckorum*

Huitaca ventralis *Ogovea cameroonensis* *Chileogovea oedipus*

Metagovea philipi *Stylocellus globosus* *Suzukielus sauteri*

Metasiro americanus *Stylocellus ramblae*

Fig. 25. Claws of leg II for selected outgroup species (lettering as in Fig. 11), lateral view. Arrows indicate lateral modification. c, Comb-like modification. Scale bar = 20 µm.



Siro acaroides

Siro kamiakensis

Siro exilis

Siro sonoma

Siro rubens

Siro valleorum

Siro duricorius

Siro serbicus

Paramiopsalis ramulosus

Parasiro coiffaiti

Parasiro corsicus

Parasiro minor

Fig. 26. Claws of leg III for sironid species, lateral view (lettering as in Fig. 10). Arrows indicate lateral modification. Scale bar = 20 μm.

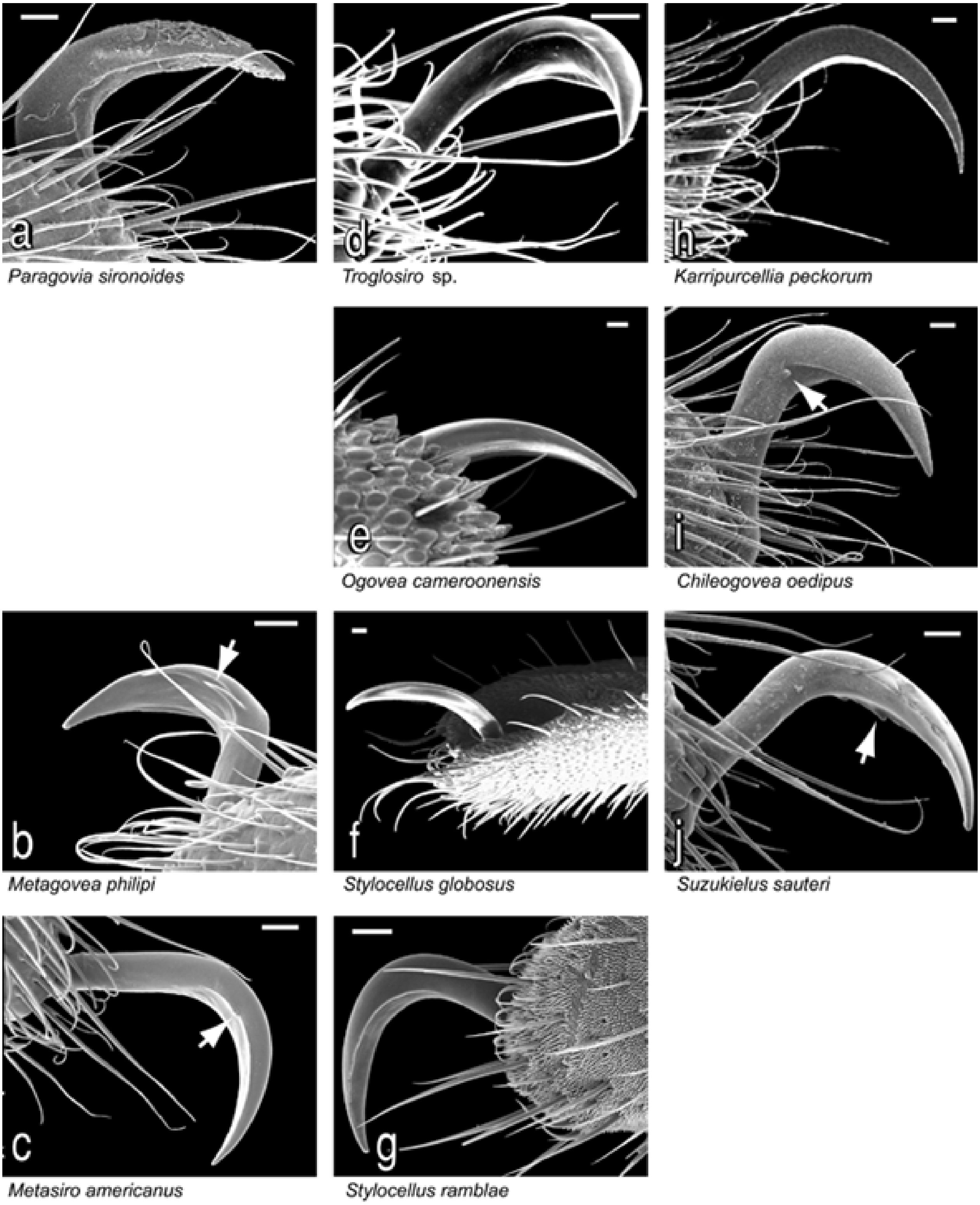
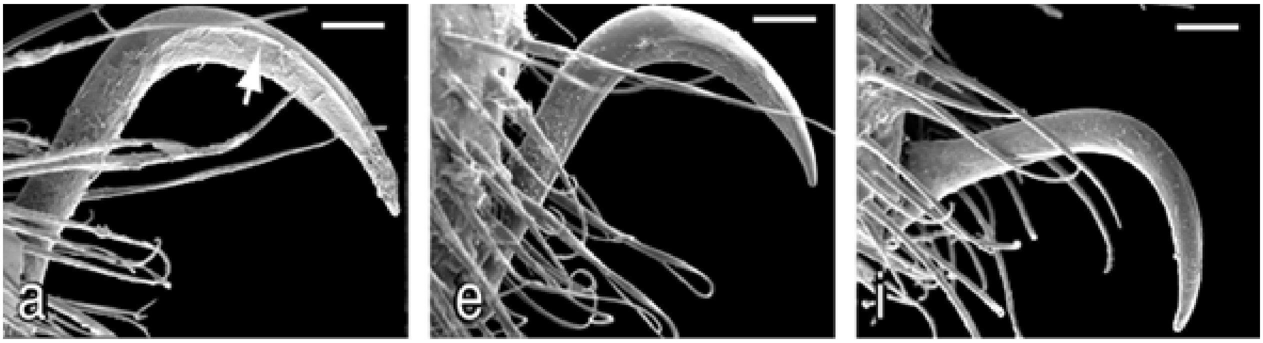
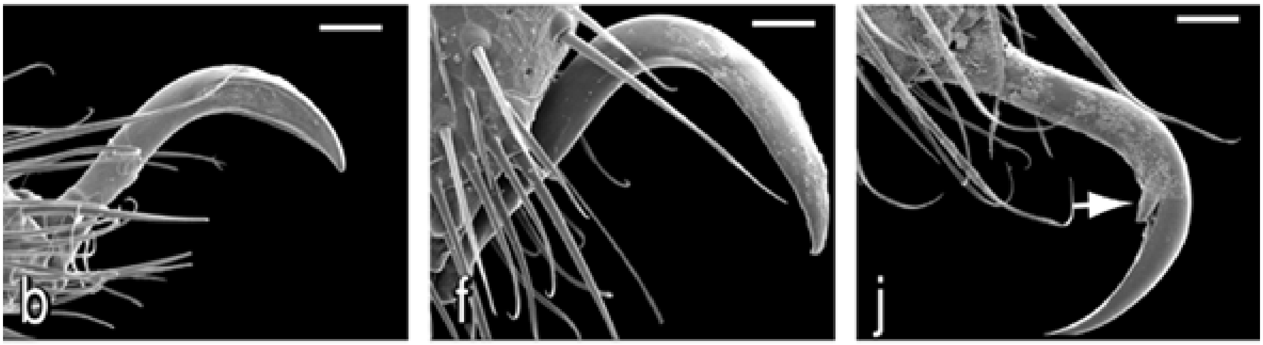


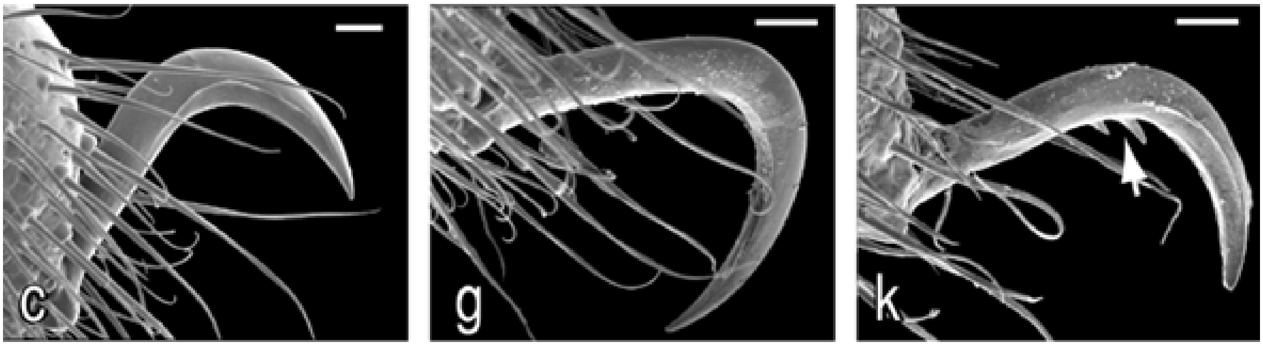
Fig. 27. Claws of leg III for selected outgroup species, lateral view. *a*, *Paragovia sironoides*; *b*, *Metagovea philipi*; *c*, *Metasiro americanus*; *d*, *Troglosiro* sp.; *e*, *Ogovea cameroonensis*; *f*, *Stylocellus globosus*; *g*, *Stylocellus ramblae*; *h*, *Karripurcellia peckorum*; *i*, *Chileogovea oedipus*; *j*, *Suzukielus sauteri*. Arrows indicate lateral modification. Scale bar = 20 µm.



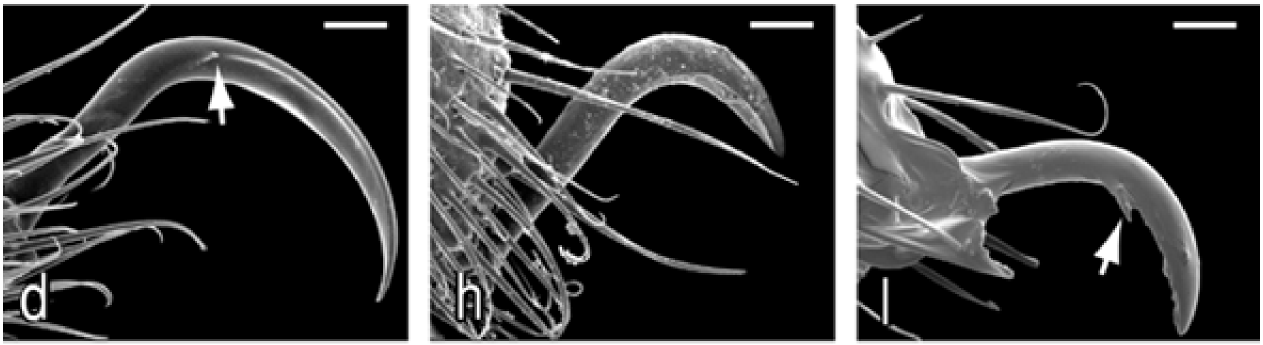
Siro acaroides *Siro rubens* *Paramiopsalis ramulosus*



Siro kamiakensis *Siro valleorum* *Parasiro coiffaiti*

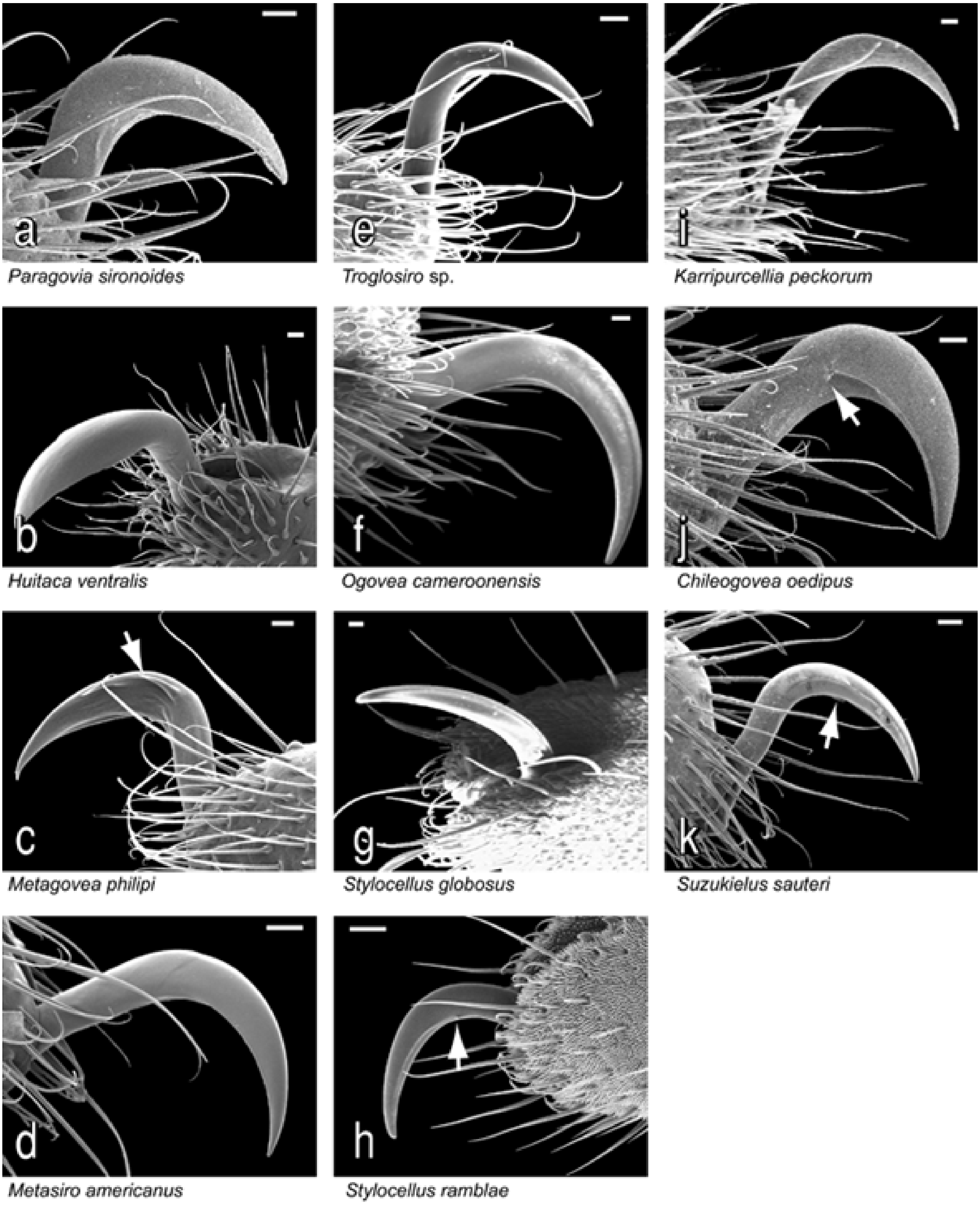


Siro exilis *Siro duricorius* *Parasiro corsicus*



Siro sonoma *Siro serbicus* *Parasiro minor*

Fig. 28. Claws of leg IV for sironid species (lettering as in Fig. 10), lateral view. Arrows indicate lateral modification. Scale bar = 20 µm.



Paragovia sironoides
Troglosiro sp.
Karripurcellia peckorum
Huitaca ventralis
Ogovea cameroonensis
Chileogovea oedipus
Metagovea philipi
Stylocellus globosus
Suzukielus sauteri
Metasiro americanus
Stylocellus ramblae

Fig. 29. Claws of leg IV for selected outgroup species (lettering as in Fig. 11), lateral view. Arrows indicate lateral modification. Scale bar = 20 µm.

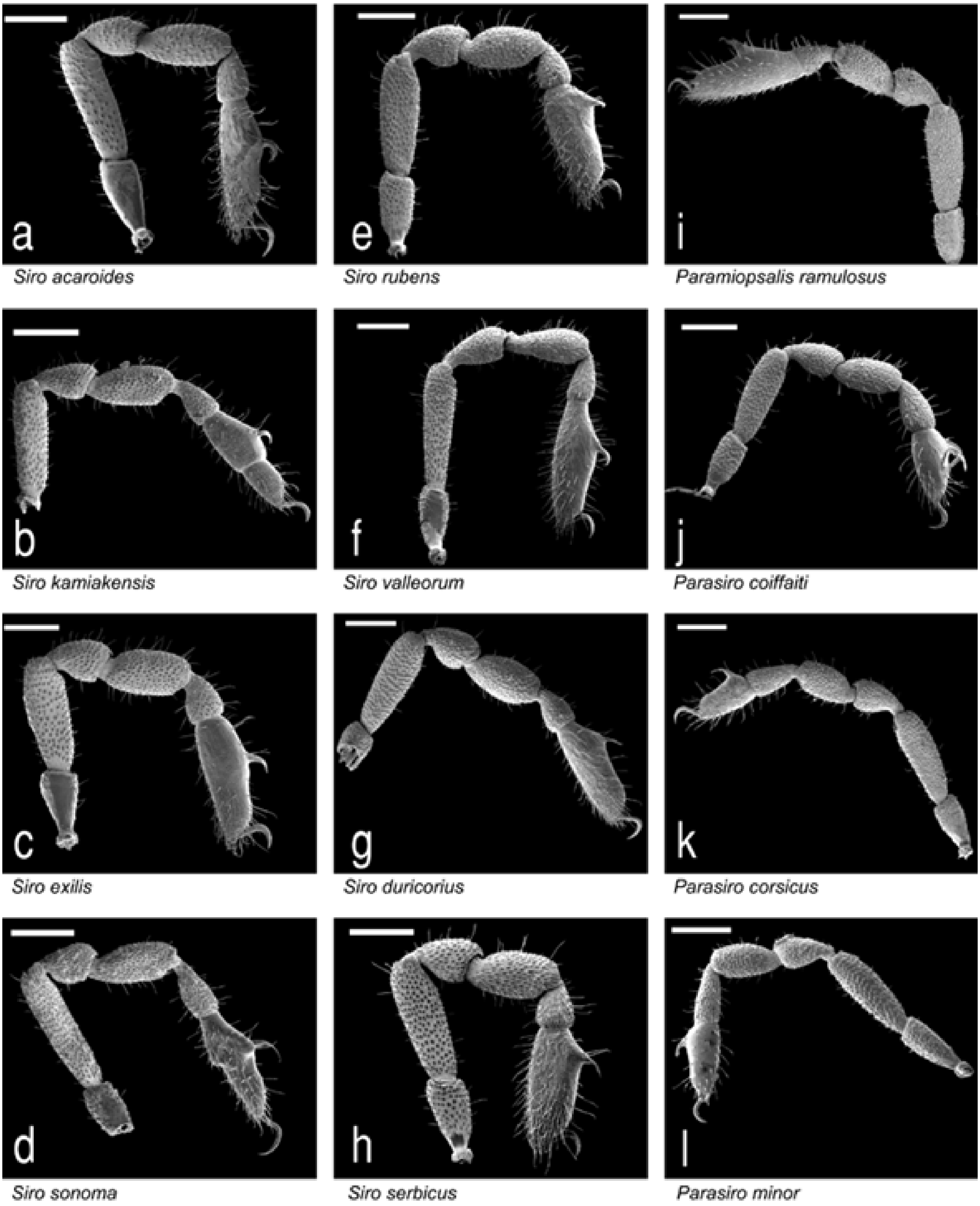
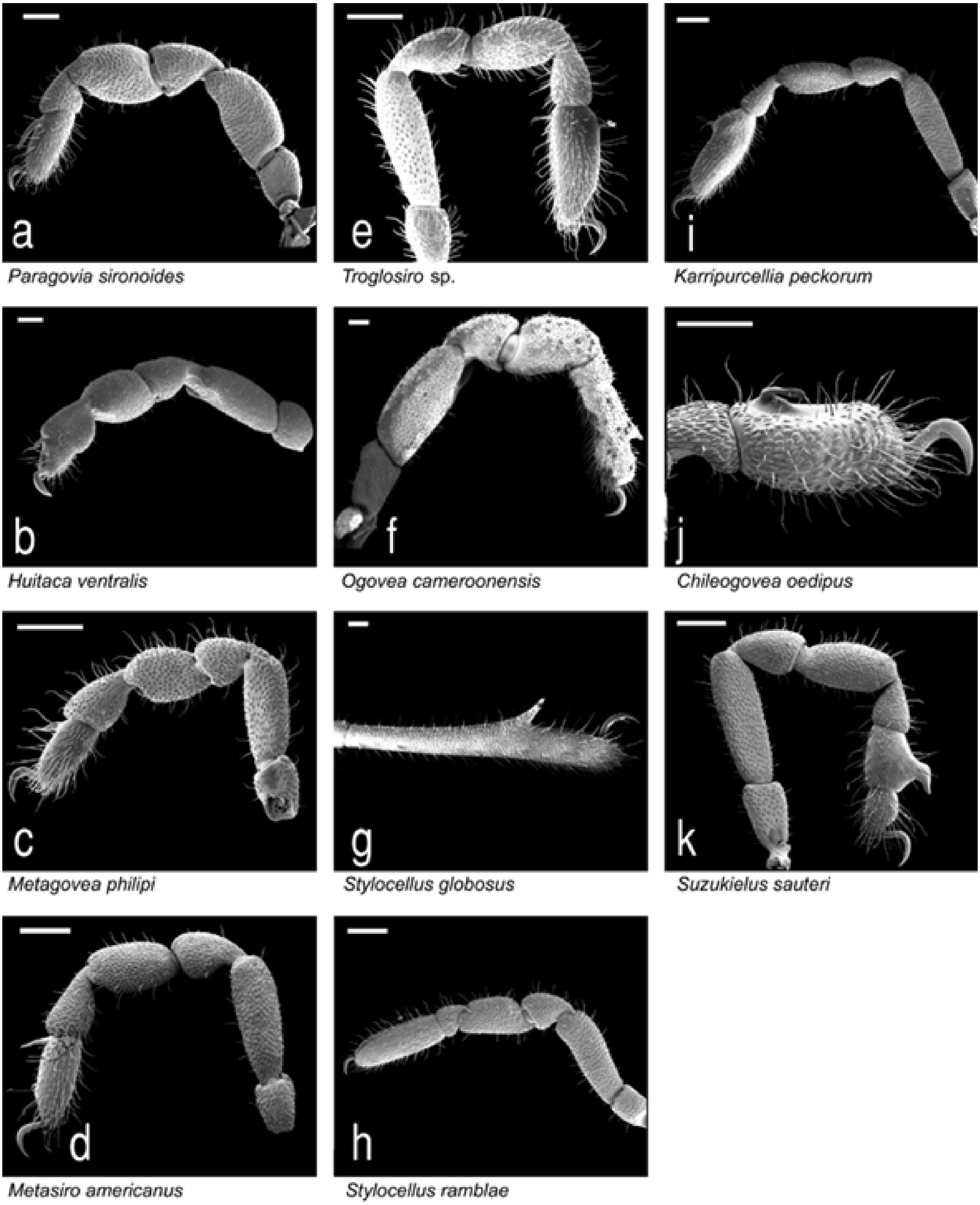


Fig. 30. Male legs IV for sironid species (lettering as in Fig. 10), lateral view. Scale bar = 200 µm.



Paragovia sironoides
Troglosiro sp.
Karripurcellia peckorum
Huitaca ventralis
Ogovea cameroonensis
Chileogovea oedipus
Metagovea philipi
Stylocellus globosus
Suzukielus sauteri
Metasiro americanus
Stylocellus ramblae

Fig. 31. Male legs IV for selected outgroup species (lettering as in Fig. 11), lateral view. Scale bar = 200 µm.

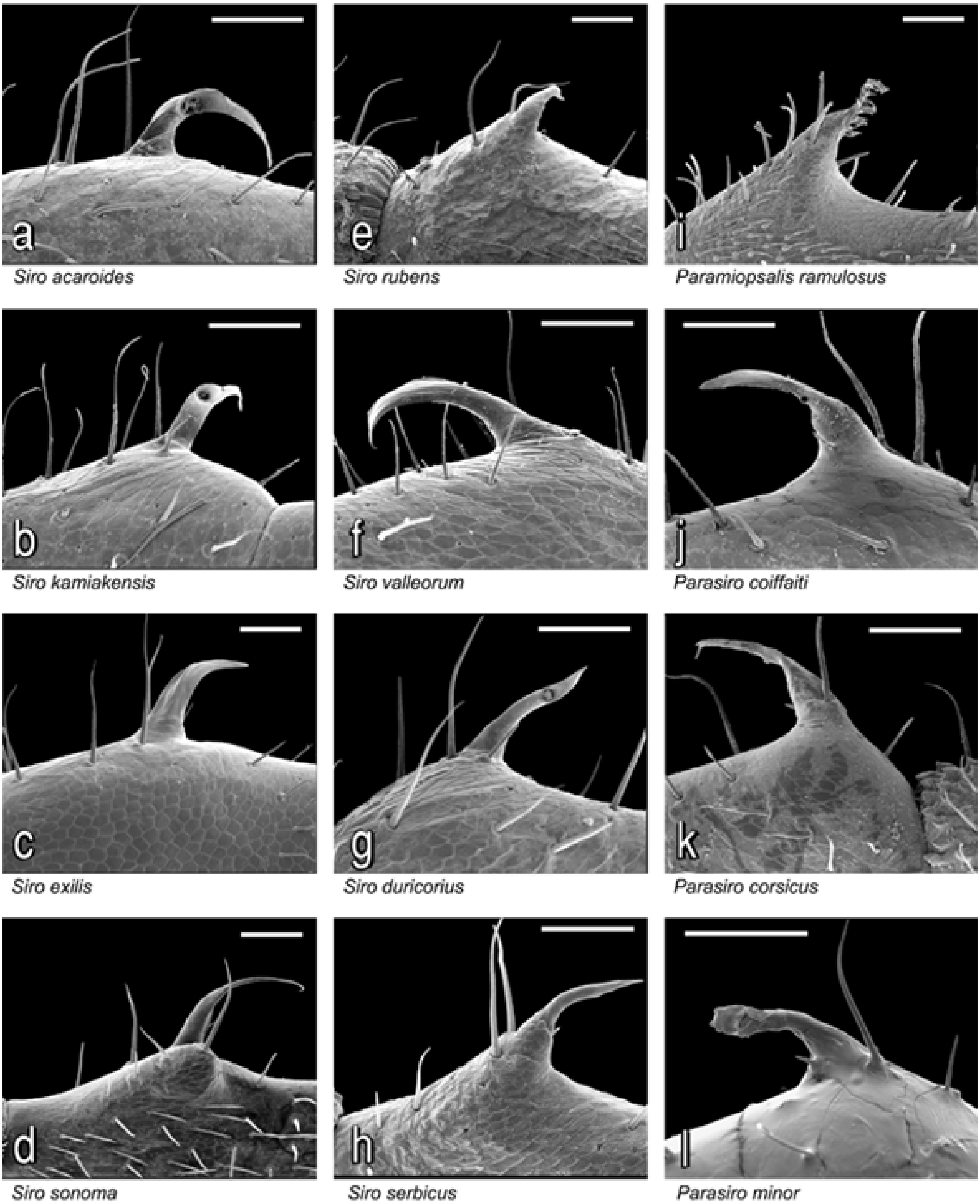
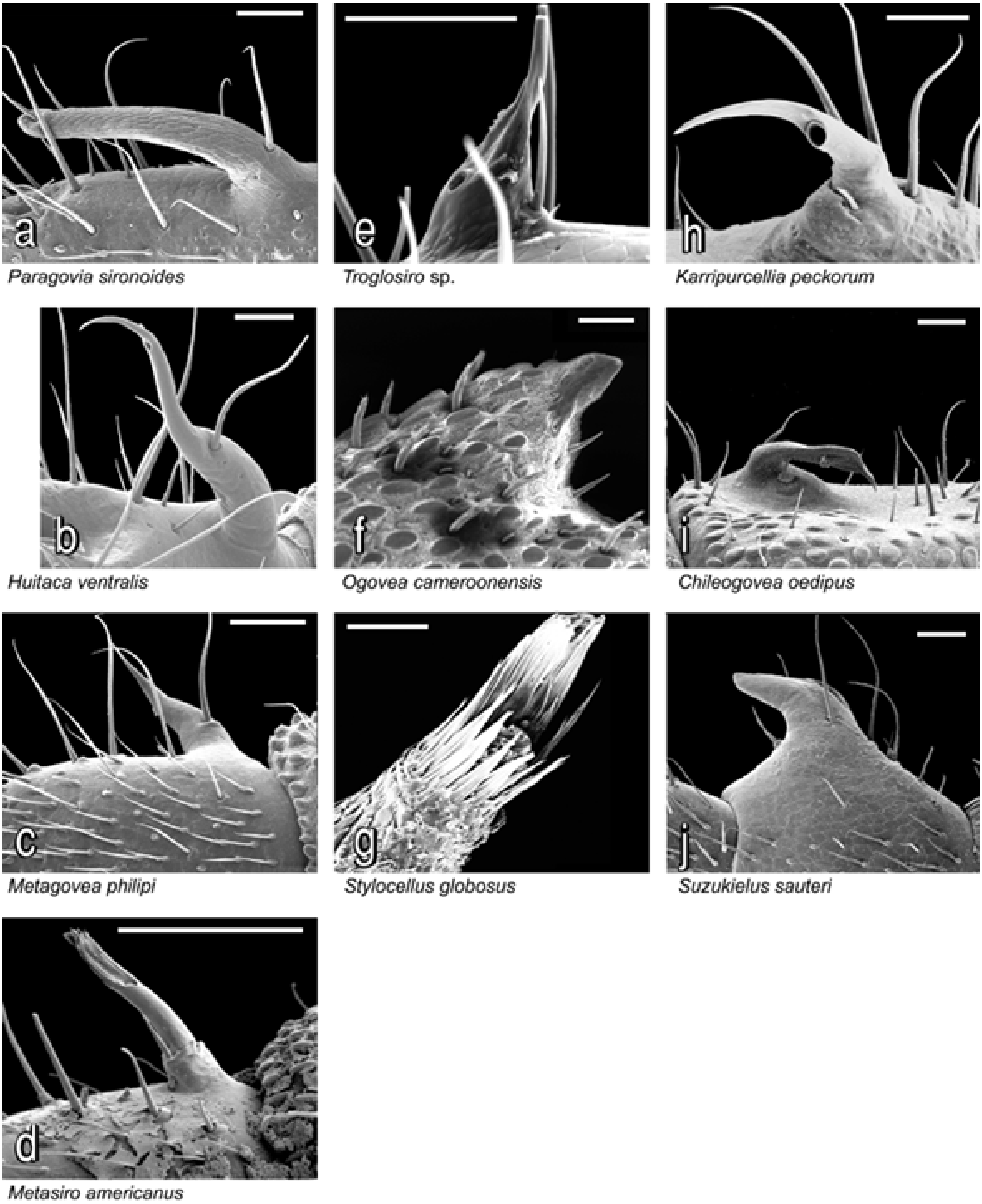
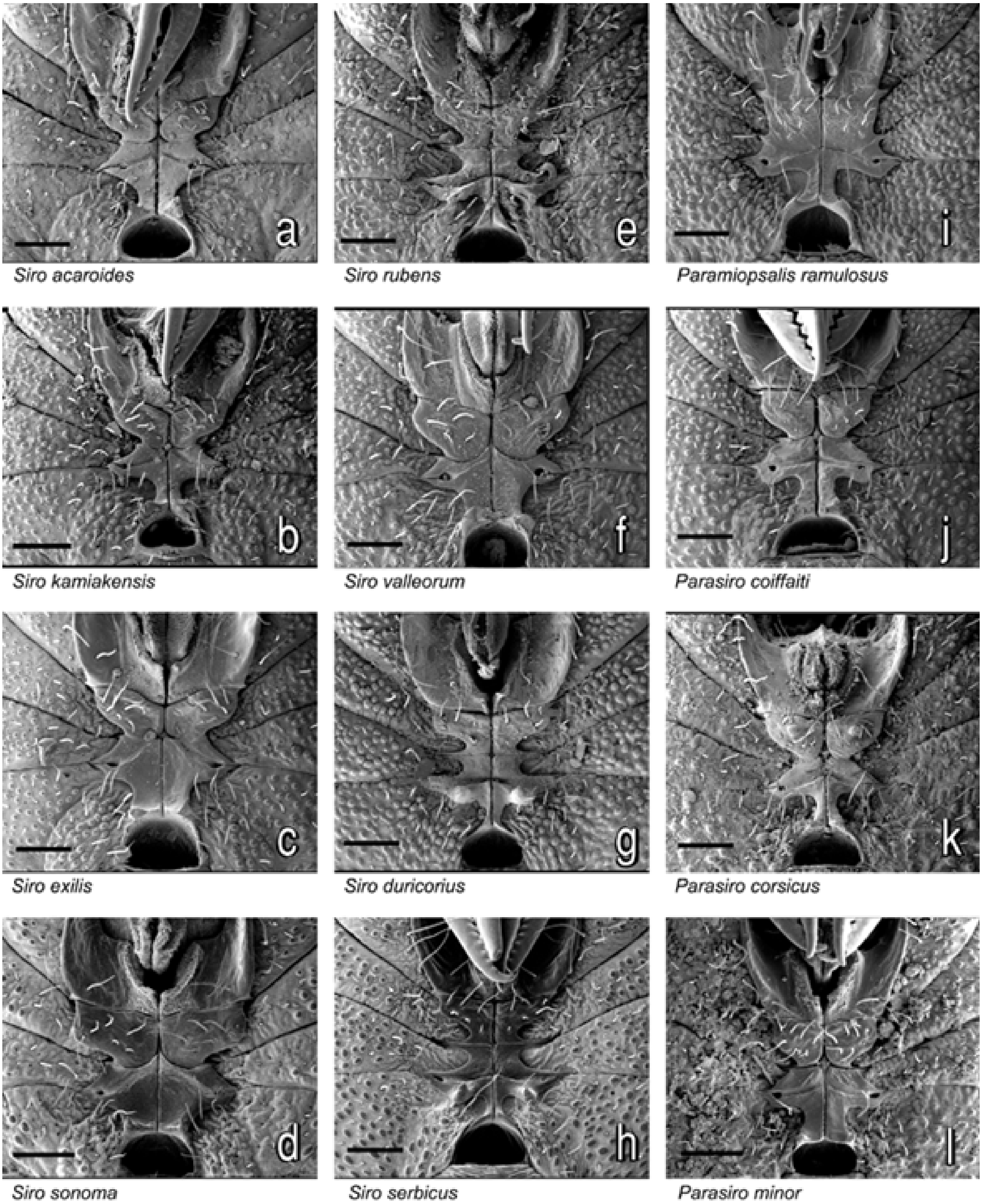


Fig. 32. Adenostyles for sironid species (lettering as in Fig. 10). Scale bar = 50 µm.



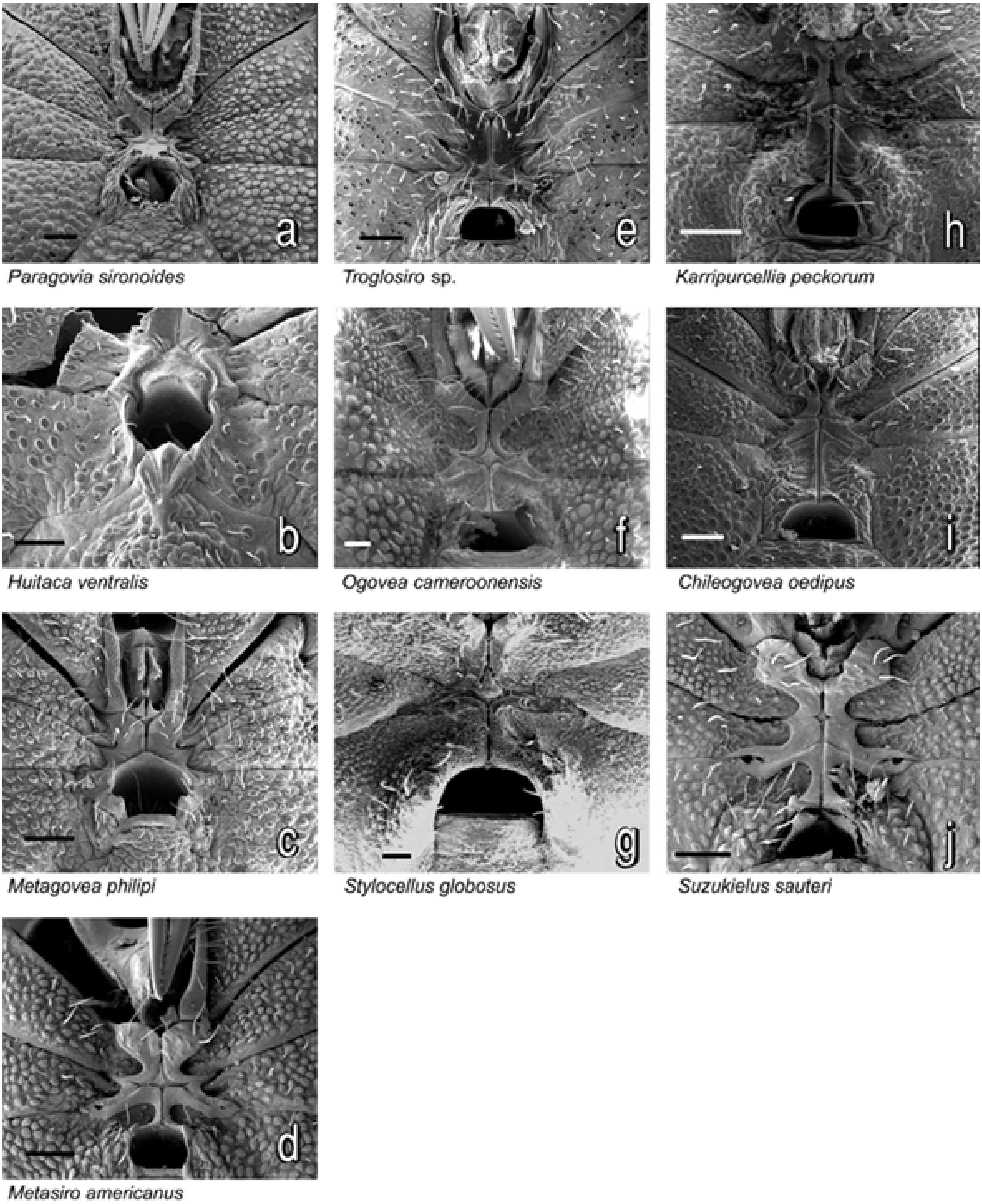
Paragovia sironoides
Troglosiro sp.
Karripurcellia peckorum
Huitaca ventralis
Ogovea cameroonensis
Chileogovea oedipus
Metagovea philipi
Stylocellus globosus
Suzukielus sauteri
Metasiro americanus

Fig. 33. Adenostyles for selected outgroup species. *a*, *Paragovia sironoides*; *b*, *Huitaca ventralis*; *c*, *Metagovea philipi*; *d*, *Metasiro americanus*; *e*, *Troglosiro* sp.; *f*, *Ogovea cameroonensis*; *g*, *Stylocellus globosus*; *h*, *Karripurcellia peckorum*; *i*, *Chileogovea oedipus*; *j*, *Suzukielus sauteri*. Scale bar = 50 µm.



Siro acaroides
Siro rubens
Paramiopsalis ramulosus
Siro kamiakensis
Siro valleorum
Parasiro coiffaiti
Siro exilis
Siro duricorius
Parasiro corsicus
Siro sonoma
Siro serbicus
Parasiro minor

Fig. 34. Male sternal regions of sironid species (lettering as in Fig. 10). Scale bar = 100 µm.



Paragovia sironoides

Troglosiro sp.

Karripurcellia peckorum

Huitaca ventralis

Ogovea cameroonensis

Chileogovea oedipus

Metagovea philipi

Stylocellus globosus

Suzukielus sauteri

Metasiro americanus

Fig. 35. Male sternal regions of selected outgroup species. *a*, *Paragovia sironoides*; *b*, *Huitaca ventralis*; *c*, *Metagovea philipi*; *d*, *Metasiro americanus*; *e*, *Troglosiro* sp.; *f*, *Ogovea cameroonensis*; *g*, *Stylocellus globosus*; *h*, *Karripurcellia peckorum*; *i*, *Chileogovea oedipus*; *j*, *Suzukielus sauteri*. Scale bar = 100 µm.

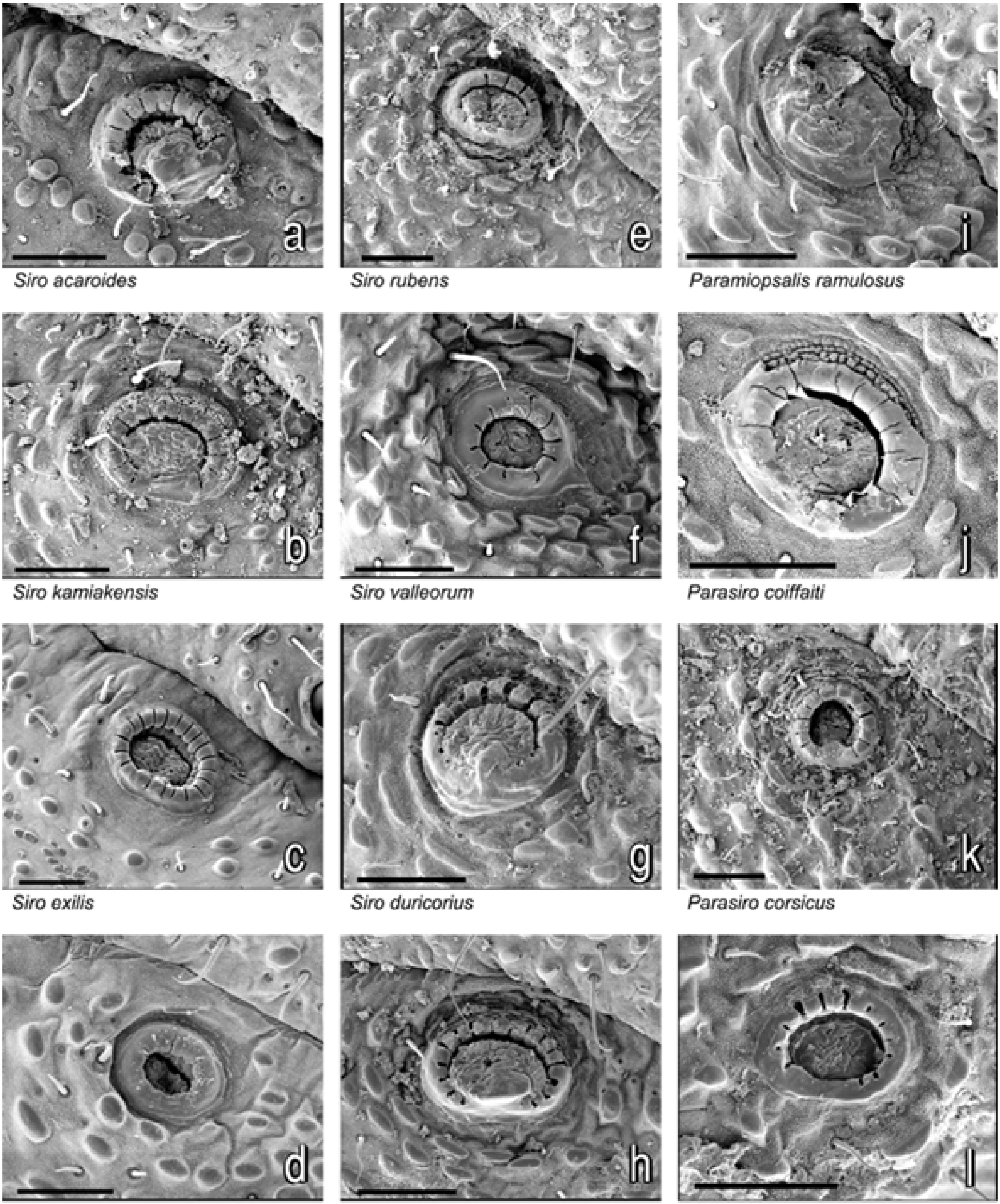
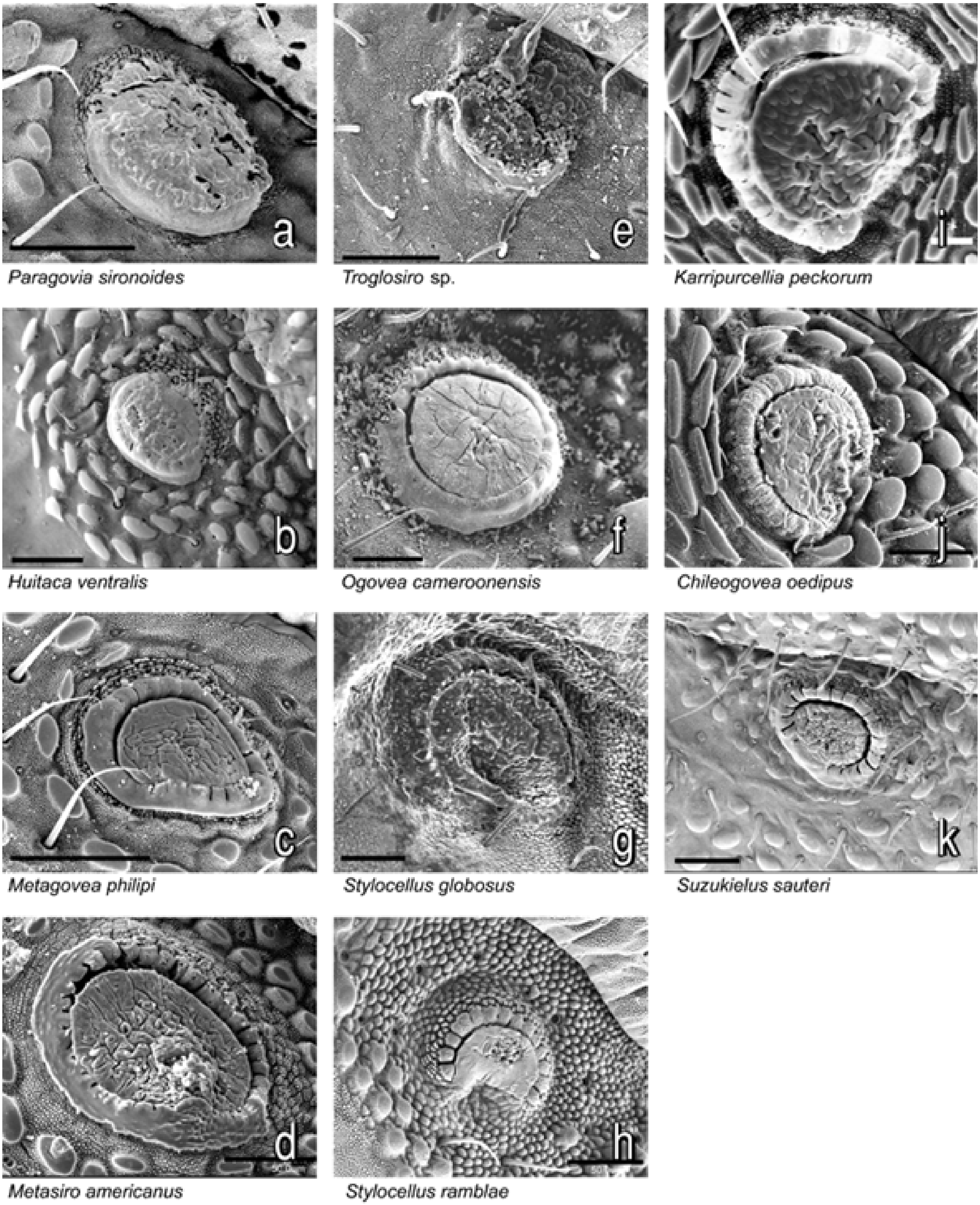
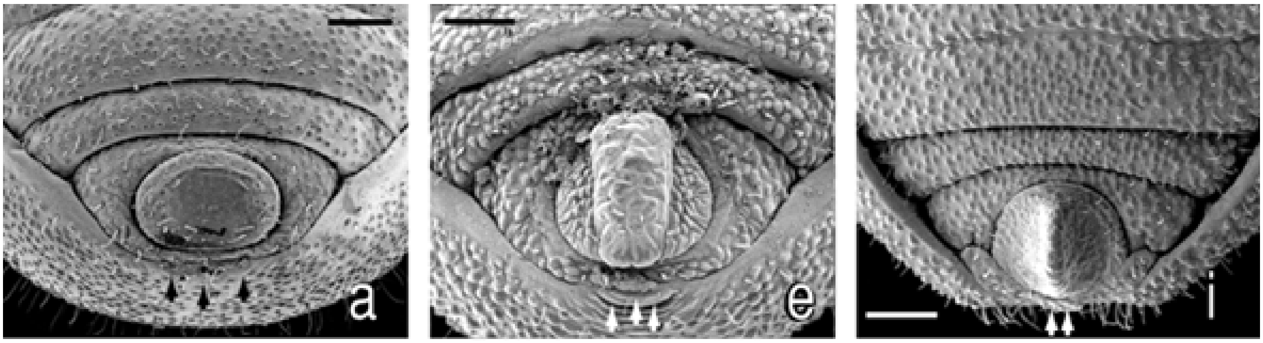


Fig. 36. Spiracles of sironid species (lettering as in Fig. 10), up corresponds to anterior of the animals. Scale bar = 50 µm.

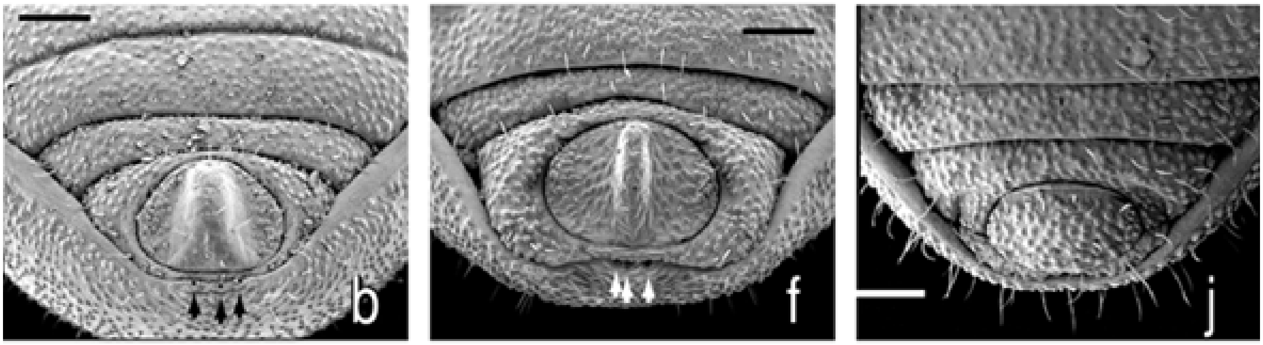


Paragovia sironoides
Troglosiro sp.
Karripurcellia peckorum
Huitaca ventralis
Ogovea cameroonensis
Chileogovea oedipus
Metagovea philipi
Stylocellus globosus
Suzukielus sauteri
Metasiro americanus
Stylocellus ramblae

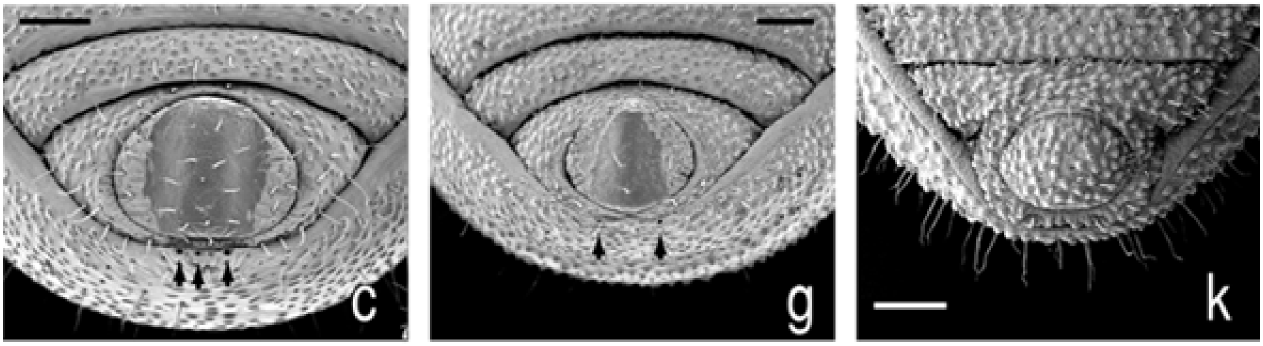
Fig. 37. Spiracles of selected outgroup species (lettering as in Fig. 11), up corresponds to anterior on the animals. Scale bar = 50 µm.



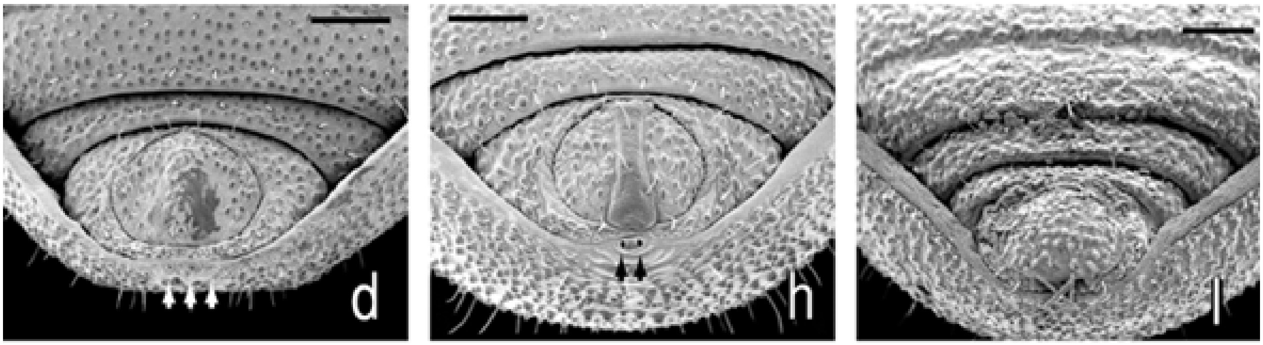
Siro acaroides *Siro rubens* *Paramiopsalis ramulosus*



Siro kamiakensis *Siro valleorum* *Parasiro coiffaiti*

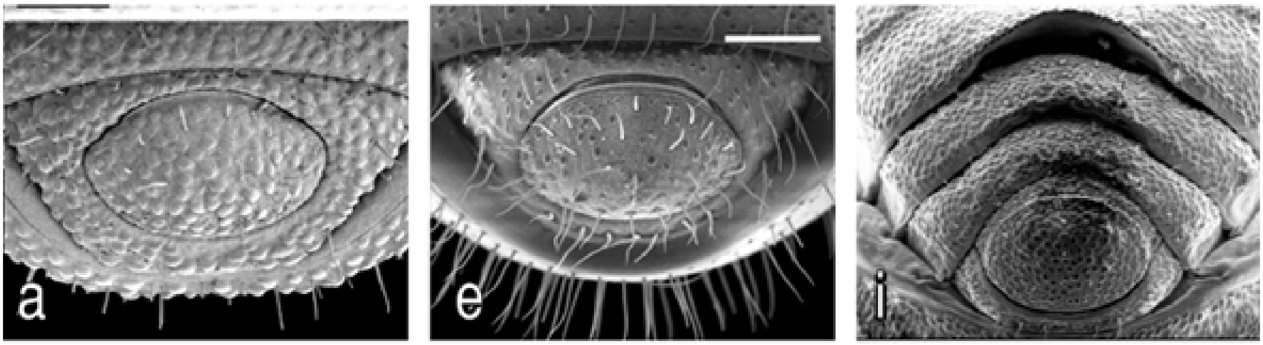


Siro exilis *Siro duricorius* *Parasiro corsicus*

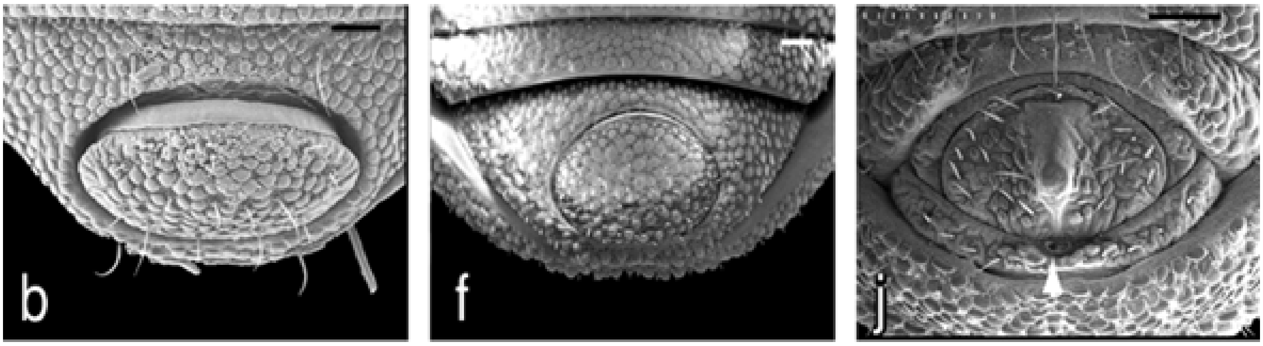


Siro sonoma *Siro serbicus* *Parasiro minor*

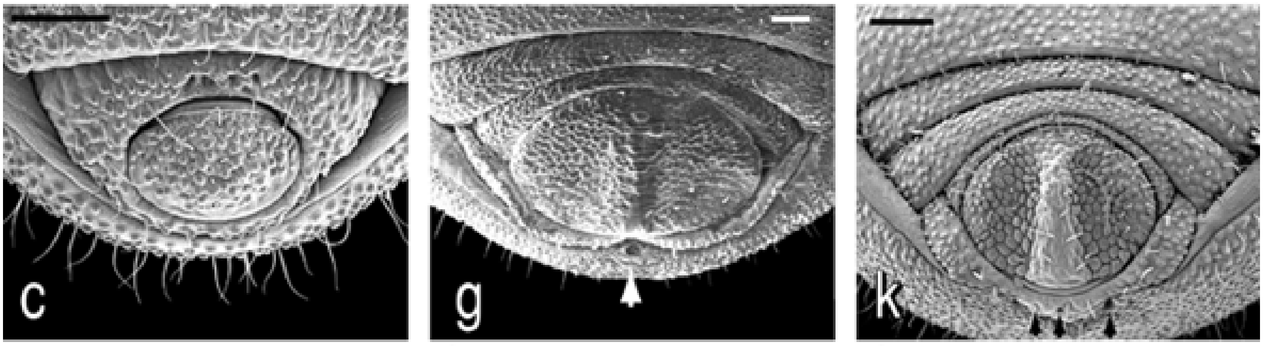
Fig. 38. Male anal regions of sironid species (lettering as in Fig. 10). Arrows indicate pores of abdominal exocrine glands (anal glands). Scale bar = 100 μm.



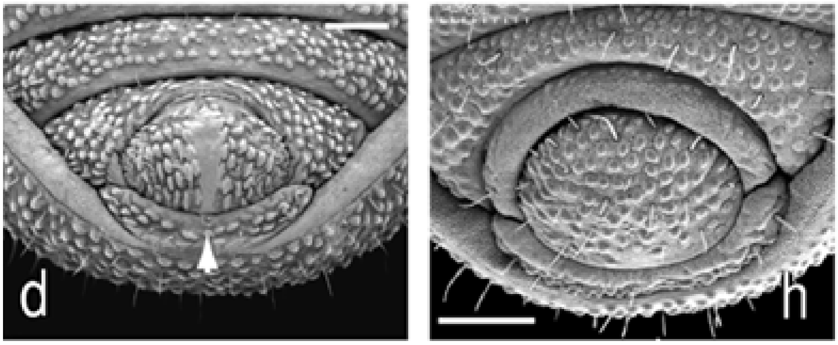
Paragovia sironoides *Troglosiro* sp. *Karripurcellia peckorum*



Huitaca ventralis *Ogovea cameroonensis* *Chileogovea oedipus*



Metagovea philipi *Stylocellus globosus* *Suzukielus sauteri*



Metasiro americanus *Stylocellus ramblae*

Fig. 39. Male anal regions of selected outgroup species (lettering as in Fig. 11). Arrows indicate pores of abdominal exocrine glands (anal glands). Scale bar = 100 µm.