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Original paper

North American sironids (Opiliones, Cyphophthalmi) and composition of the family Sironidae with a description of two new species

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Summary. A revised composition of the family Sironidae is given. Two North American genera, namely *Holosiro* Ewing, 1923 and *Neosiro* Newell, 1943, are resurrected, one new genus, *Arhesiro* gen. nov., a subgenus, *Tillamooksiro* sbg. nov., and two new species, *Holosiro ewingi* sp. n. and *Neosiro* (*T.*) *martensi* sp. n. are described. Diagnostic characters of Cyphophthalmi families are presented and discussed.

Keywords: *Arhesiro*, family composition, *Holosiro,* morpho-anatomy, *Neosiro*, Neartic, new genus, new species, new subgenus, North America, Sironidae, *Tillamooksiro*, western Palearctic.

INTRODUCTION

According to present knowledge, the cyphophthalmid family Sironidae is distributed in the western Palearctic (Europe and Asia Minor) and in the Nearctic (genus *Suzukielus* Juberthie, 1970 from Japan does not belong to this family). It is present in areas which have had a permanent land phase during the last ca. 300 Ma, or that had been in close contact with such areas. Roughly, the distribution (diversification and spreading) of this family is connected with the formation of Pangaea (its tropical belt), the breakup of Pangaea, Neo-tethys and Atlantic Ocean openings and their extensions. Family diversification took place on the Laurasian paleocontinent (its western and central part), northern Gondwana and archipelagos broken off from them. Today's picture of the family distribution is strongly influenced by Pleistocene events, when sironids became extinct in wide areas of northern Europe and North America.

The current picture of the family distribution shows a clear separation into two very distant centers. These are the wider areas of southern Europe with Asia Minor (the core of the family diversity) and the western part of North America. In North America, the family is presented only with the genus *Siro* Latreille, 1796, which is also present in the European fauna (Karaman et al. 2022). It is unusual that faunistically highly different and spatially very distant areas contain phylogenetically closely related faunal elements, as suggested by the fact that they belong to the same genus.

In North America, the genus *Siro* is presented by 10 species that have been described to date (Giribet and Shear 2010; Giribet et al. 2017). However, molecular studies indicate a greater diversification than is suggested by current taxonomy

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(Giribet et al. 2017). The first two discovered North American sironid species were initially described in separate genera: *Holosiro* Ewing, 1923 and *Neosiro* Newell, 1943. Both genera were synonymized with the European genus *Siro* by Newel (1947) and Shear (1980), respectively. These changes were done with good reason, because both genera were defined by inappropriate characters, wrong observations or single species apomorphies.

Based on a recent study of European *Siro* species (Karaman et al. 2022), some North American sironids and published results of previous studies, in the present work I define diagnostic characters of the genus *Siro* and related North American representatives that I single out from this genus. A definition of diagnostic characters and a revised composition of the family Sironidae are also given.

Thanks to material that was kindly provided by Professor Jochen Martens, I give a description of two new species. This paper is dedicated to Professor Jochen Martens and his 80th anniversary. His studies on Opiliones have always been an inspiration and encouragement to my work. The standards he introduced into Opiliones taxonomy raised the field to much higher levels, which have still not been achieved for the vast majority of arthropod groups.

MATERIALS AND METHODS

Dissection of specimens and slide mounting were done as described in Karaman (2009). The separated body parts were prepared by dehydration through a graded alcohol series before being cleaned in a sonicator. Dried samples mounted on stubs were prepared in a Baltec SCD005 sputter coater. Scanning electron microscopy (SEM) photographs were recorded with a JEOL-JSM-64601v SEM microscope under high vacuum. Microscopic photographs were done on a Zeiss Axio Imager A1. Drawings based on phoptographs were made in Adobe Illustrator CS2 on a Genius graphics tablet.

TAXONOMICAL PART

Family Sironidae

As a group, Cyphophthalmi reached its phenotypic evolutionary stasis very early. They are probably the first specialized substrate living (endogean) group of Opiliones and certainly in that sense the most successful. This fact is often overlooked when talking about cyphophthalmid biology, which emphasizes leaf litter as their primary habitat (de Bivort et al. 2012). Adaptation to life in soil and rock crevices, small holes, cracks and other narrow spaces in the substrate defined their morphology, nanism and unique acariform appearance among opilions. One of the features that emphasizes preadaptation of terricole ancestors into endogean forms of Cyphophthalmi is a change in the orientation of the forelegs (conspicuous at the coxae) from lateral to forward[1]. Such a change, along with a reduction of body dimensions was a necessary adaptation to move through the narrow spaces of the substrate (especially important for seasonal vertical migrations). Living in such conditions does not emphasize significant evolutionary changes, but conservatism, which is obvious in their case. In that sense, troglomorphic species among Cyphophthalmi are a rare exception and a phenomenon manifested by elongated extremities as a form of pre-adaptation to climbers in large underground spaces. However, given the relatively short lifespan of such biotopes (in geological terms) and their temporal and spatial discontinuity, such specialized forms of Cyphophthalmi represent evolutionary dead ends and are isolated phenomena.

Related to the early origin of Cyphophthalmi, the Cyphopalpatores concept (Martens et al. 1981) is the most realistic. It is a concept that assumes the common origin of suborders Cyphophthalmi and Palpatores (here as sister groups) in relation to a third suborder Laniatores, which is morphologically the most diversified and the most numerous group of Opiliones. This concept automatically excludes the possibility of assuming an acariform appearance for early ancestors of Opiliones. In an alternative concept where Phalangida (Laniatores + Palpatores) and Cyphophthalmi are sister groups (as in Giribet et al. 1999, 2002), such an assumption is possible.

The conservatism of particular characters of Cyphophthalmi, including the composition of their secretions (Raspotnig et al. 2012), presents a major problem and challenge in species delimitation and even more so in defining taxonomic ranks. Subjective taxonomic categories such as genus or family must, with their composition, reflect as objectively as possible the real phyletic relationships between the species included. That should be supported by appropriate characters, which is not easy in this group. One such character set refers to the ventral prosomal complex (coxosternal region) and myliosoma (Fig. 1) which are probably the most important characters in defining higher taxonomic categories such as family and genus, showing clear phylogenetic signals.

Wide coxal lobes I and II are characteristic for the family Sironidae. Coxal lobes II are 2.5 to 3.5 times wider as long, with almost straight or slightly arched frontal margins (Fig. 2). Coxal endites I kept continuity. *Parasiro* Hansen & Sørensen, 1904 is similar, based on these characters (Fig. 2F), but differs in the profile of coxal lobes I and II. In all other families, coxal lobes I are more or less narrowed and retracted.

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[1] Independently similar changes occurred in the opilionid family Trogulidae as a reflection of their tight relationship with the snails on which they prey (the need to get in through a narrow aperture and shell cavity).

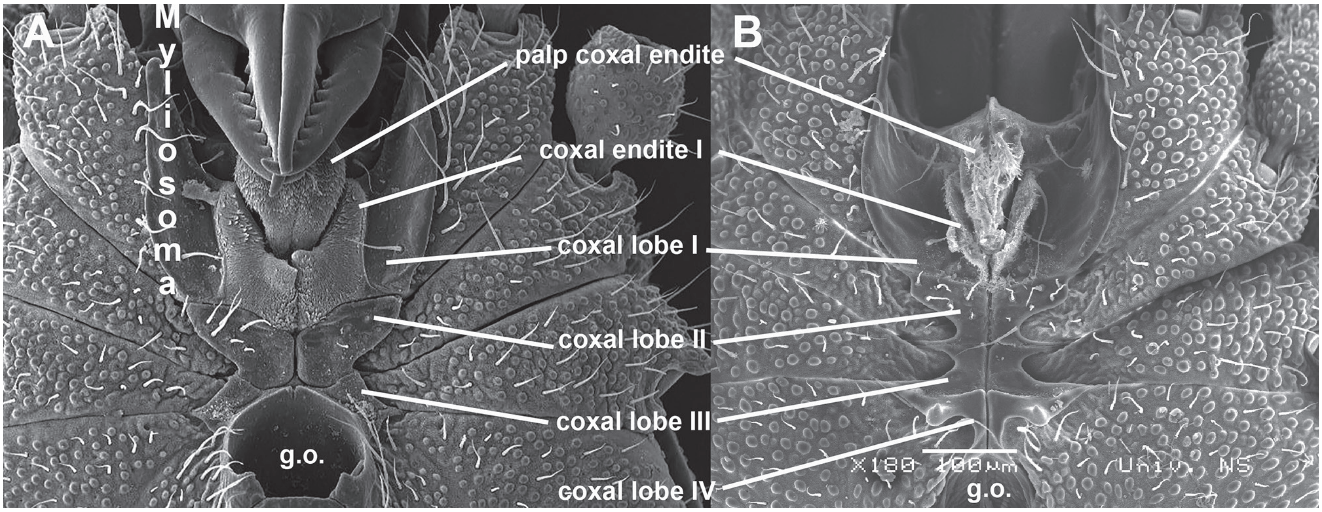

Fig. 1. Coxosternal region (prosomal complex) with myliosoma. **A**, *Neosiro exilis* comb. n. female; **B**, *Cyphopthalmus serbicus* male (g.o.-genital opening).

In Pettalidae (southern Gondwana distribution), coxal lobes II are less than two times wider as long, bowl shaped (Fig. 3). Frontal margins drawn medially, frame the detached basal part of coxal endites I.

In Stylocellidae (South East Asia distribution) coxal lobes II are elongated and in the form of a goblet (Figs 4B-D). Basic styllocelids are somewhat wider than long or as wide as long, while others are longer than wide. Frontal margins indented medially, deeply in most. The basal part of the coxal endites I is detached from the medial ones.

Among the representatives of Ogoveoidea families (Troglosironidae, Ogoveidae and Neogoveidae) the basic type of prosomal complex is with coxal lobes II of cup form, 1.5-2 times wider as long; coxal endites I with detached basal part from the lateral one; pronounced tendency to shorten coxal lobes III and IV in males. *Metasiro* Juberthie, 1960 (south eastern USA) which are basal representatives of the family Neogoveidae (Benavides et al. 2019) show such shapes in the coxosternal region (Fig. 7A in Clouse and Wheeler 2014).

In Troglosironidae (New Caledonia) coxal lobes II are two times wider as long; of cup form (Fig. 5B). In some species there is a more or less divergent medial part of the frontal margin (as in Fig. 14. in Sharma and Giribet 2009). A similar structure is characteristic of the species *Ankarartra franzi* Shear & Gruber 1996 (Madagascar) (Fig. 5A) (possibly at the base of the family Troglosironidae or superfamily Ogoveoidea?). However, it is clearly different by narrower coxal lobes II, which are with lateral protrusions of their frontal margins into the space of the coxal lobes I.

In *Ogovea* (family Ogoveidae) (equatorial West Africa) (Fig. 5 in Giribet and Prieto 2003) coxal lobes II are broad in their anterior part, 1.5 times wider as long; frontally divergent at right angle. Lateral protrusions are present on their frontal margins. The similar structure of coxal lobes II characterizes the genus *Parogovia* (family Neogoveidae) from equatorial West Arica (see Benavides et al. 2019). Spatial closeness (all species are from the same region of Cameroon, Equatorial Guinea and Gabon) and the similarity of coxosternal structures, indicate the possible phyletic closeness of the species of these two genera.

Among Neogoveidae (Neotropics and West Africa) the structure of the prosomal complex differs considerably among genera (see in Benavides et al. 2019) (Figs 5C-D). It is a consequence of significant anatomical changes that have occurred among family members. With the exception of the basal genus *Metasiro*, the tendency to shorten male coxal lobes III and IV in males is noticeable (Karaman 2013), which is a direct consequence of the relocation of male abdominal exocrine glands (most probably nuptial glands, secreting nuptial gift) from an anal region position (anal glands) to the frontal opisthosomal sternites (sternal glands). The change is most likely accompanied by the displacement of the couple's positions during the act of spermatophore transfer. This change causes the male gonopore to move anteriorly (the position of the female gonostome) to a distance from the frontal margin of the coxal lobes II that corresponds to its own width or even length. The correlation of spermatopositor elongation that accompanies the relocation of the male gonopore is also striking. The same tendency, though to a lesser extent, characterizes members of the family Troglosironidae and Ogoveidae, which points to the conclusion that in these related groups this change happened independently. Comparing the prosomal complex structures of different neogoveid genera and phylogenetic relations given in Benavides et al. (2019), their high phylogenetic signal is noticeable.

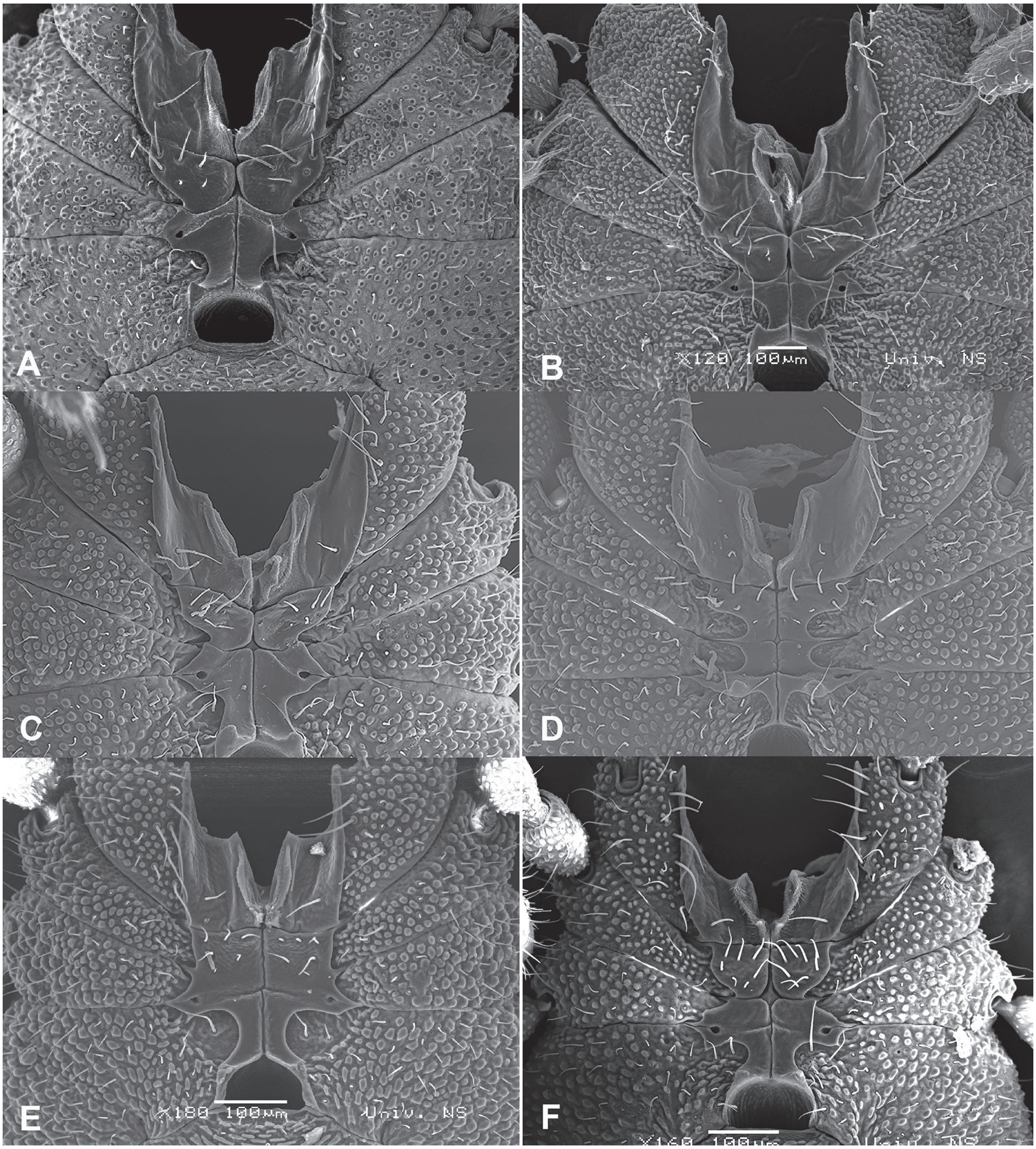

Fig. 2. Coxosternal region of males, **A**-**E** Sironidae. **A**, *Siro rubens*; **B**, *Siro crassus*; **C**, *Neosiro exillis*; **D**, *Cyphophthalmus duricorius*; **E**, *Paramyopsalis* sp.; **F**, *Parasiro coiffaiti*.

In most Neogoveidea the detached basal part of the coxal endites I is of triangular form (at least for most of them) (Figs 5C-D). Based on the coxosternal structure, *Leggogovia pabsgarnoni* (Legg, 1990) (West Africa - Sierra Leone) seems to be closely related to the genus *Neogovea* Hinton, 1938 (South America - Guyana Shield). *Shearogovea mexasca* (Shear, 1977) (Mexico), based on the same structures, shows affinity to the genus *Microgovia* Benavides, Hormiga & Giribet, 2019 (South America - Guyana Shield and Amazonas).

Structures of the coxae of the pedipalps and the coxal endites with their peculiarities, more or less, are in correspondence with the differences in the ventral prosomal complex in these families as well.

Structures of the ventral prosomal complex and myliosoma region in the taxonomy of Cyphophthalmi must be considered to be one of the key characters in defining species, as well as higher taxonomic ranks.

Here I focus on the family Sironidae. The current com-

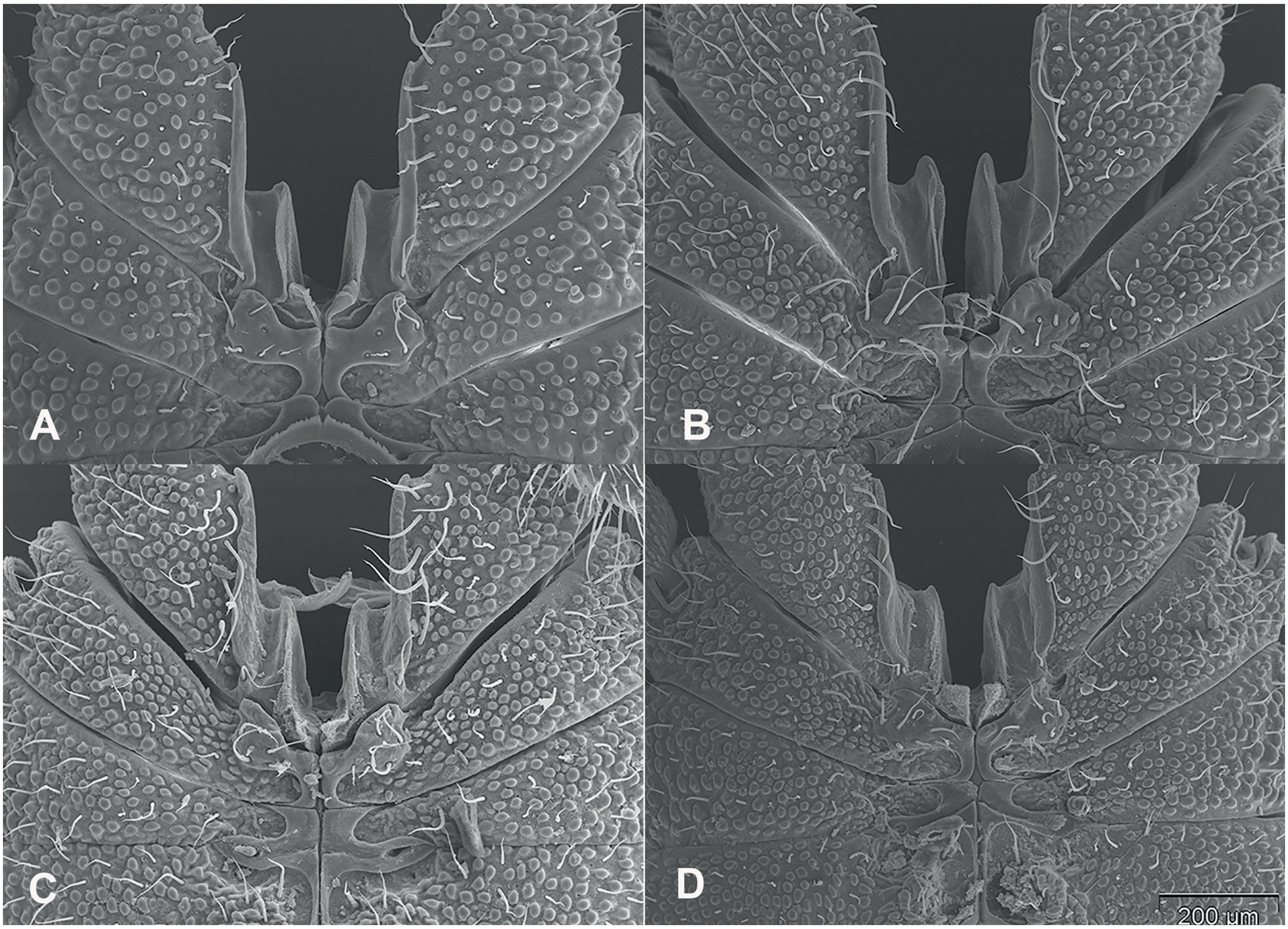

Fig. 3. Coxosternal region, Pettalidae. **A**, *Purcellia ilustrans* female; **B**, *Manangotria taolanaro* female; **C**, *Milipurcellia sierwaldae* male; **D**, *Karripurcellia peckorum* male.

position of the oldest established cyphophthalmid family is polyphyletic. Currently, the generally accepted composition of this family includes 7 genera: *Siro*, *Cyphophthalmus* Joseph, 1868, *Parasiro*, *Suzukielus*, *Odontosiro* Juberthie, 1961, *Paramiopsalis* Juberthie, 1962, and *Iberosiro* de Bivort & Giribet, 2004. Giribet et al. (2012) highlighted the questionable monophyly of the family, suggesting its paraphyletic origin.

Clear morphological differences exclude the monospecific genus ***Suzukielus*** from this family to which it is currently assigned. The structure of myliosoma and coxosternites (Fig. 4A) of the single species of this genus shows affinity to Pettalidae and to Stylocellidae as well (where its author, Roewer originally classified it - then subfamily Stylocellinae). The entire basal part of endites of coxal lobes I is deeply embedded among coxal lobes II, into a space almost square in shape. Laterally they are completely surrounded by anterior abruptly dilated coxal lobes II. In Pettalidae these extensions are laterally of a slightly three-lobed form (Fig. 3) while in *Suzukielus* they are more goblet-shaped, as in Stylocellidae (Figs 4B-D).

The genus ***Odontosiro***, the morphological characteristics of which have been presented by Juberthie (1961), shows some affinity to the Ogoveiodea and I do not consider it here as a member of the family Sironidae. It is probably a basal member of Ogoveiodea, just like the genus *Ankarartra* Shear & Gruber, 1996 from Madagascar. Genus *Ankarartra* with the shape and structure of the coxal lobes of legs I–II and myliosoma (Fig. 5A) shows similarity with Troglosironidae (New Caledonia) (Fig. 5B), and the genus *Metasiro* (Forida and S. Carolina USA) (Fig. 7A in Clouse and Wheeler 2014) which is basal in the family Neogoveidae (Giribet et al. 2012). Genus *Odontosiro* by spermatopositor structure, elongated pedipalp coxae, basal position of adenostyle on male 4th leg, and the presence of denticles on leg claws, cannot be a member of the family Sironidae. It is also questionable whether a sister group relationship to genus *Parasiro* is justified by some of the mentioned characters and plesiomorphies regarding the position of the odontophores (Juberthie 1961; Giribet et al. 2012). Insight into the shape and structure of the coxal lobes and myliosoma of *Odontosiro lusitanicus* Juberthie, 1961 could solve this dilemma.

The east African species ***Marwe coarctata*** Shear, 1985 from a cave in Kenya was included by Giribet et al. (2012) in this family, as close to the genera *Paramiopsalis* and *Iberosiro*, without adequate explanation. Although some important details are missing in the original description, I see affinity of this species to the genus *Fangensis* Rambla, 1994*, i.e.* supporting a position at the basis of the family Stylocellidae – subfamily Fangensinae (Clouse 2012). This is based on my brief observations of the holotype in limited conditions as well as on the illustrations of the original description (Shear 1985). My conclusions are based primarily on the structure of *M. coarctata* ventral prosomal complex, which is developed as typical for the genus *Fangensis*. It is characterized by elongated and very narrow coxal lobes II (so narrowed and inconspicuous that Shear (1985) did not present it in his illustration) that slightly expand anteriorly, shortened coxosternites III that do not meet medially, more terminal position of the adenostyle of male 4th leg, as well as a conspicuously constricted dorsum at VII tergite. Some of the mentioned traits appear among some representatives from other cyphophthalmid families but never in such combination.

The genus ***Parasiro*** clearly stands out in the family with a number of unique characters mostly listed by Juberthie (1958) in his diagnosis of the genus. Based on the structure of myliosoma and coxal lobes (Fig. 2F), it is closest to the family Sironidae. Results of some genetic studies (Giribet et al. 2012, 2017) suggest a position of this genus separate from the family Sironidae. According to a number of unique morphological characteristics of the genus, I do not treat it as a member of the family Sironidae. Heterogeneity of the relevant morphoanatomical characters suggests a very old diversification of the genus. It is, as far as we know, present in the areas of the western Mediterranean (Sardinia, Corsica, a NW part of Apennine peninsula and Pyrenees foothills on Mediterranean coast) (Juberthie1988; de Bivort and Giribet 2004) but also in the Caucasus (Transcaucaus), parts of Asia Minor and the Aegean, as well as SW part of Apennine

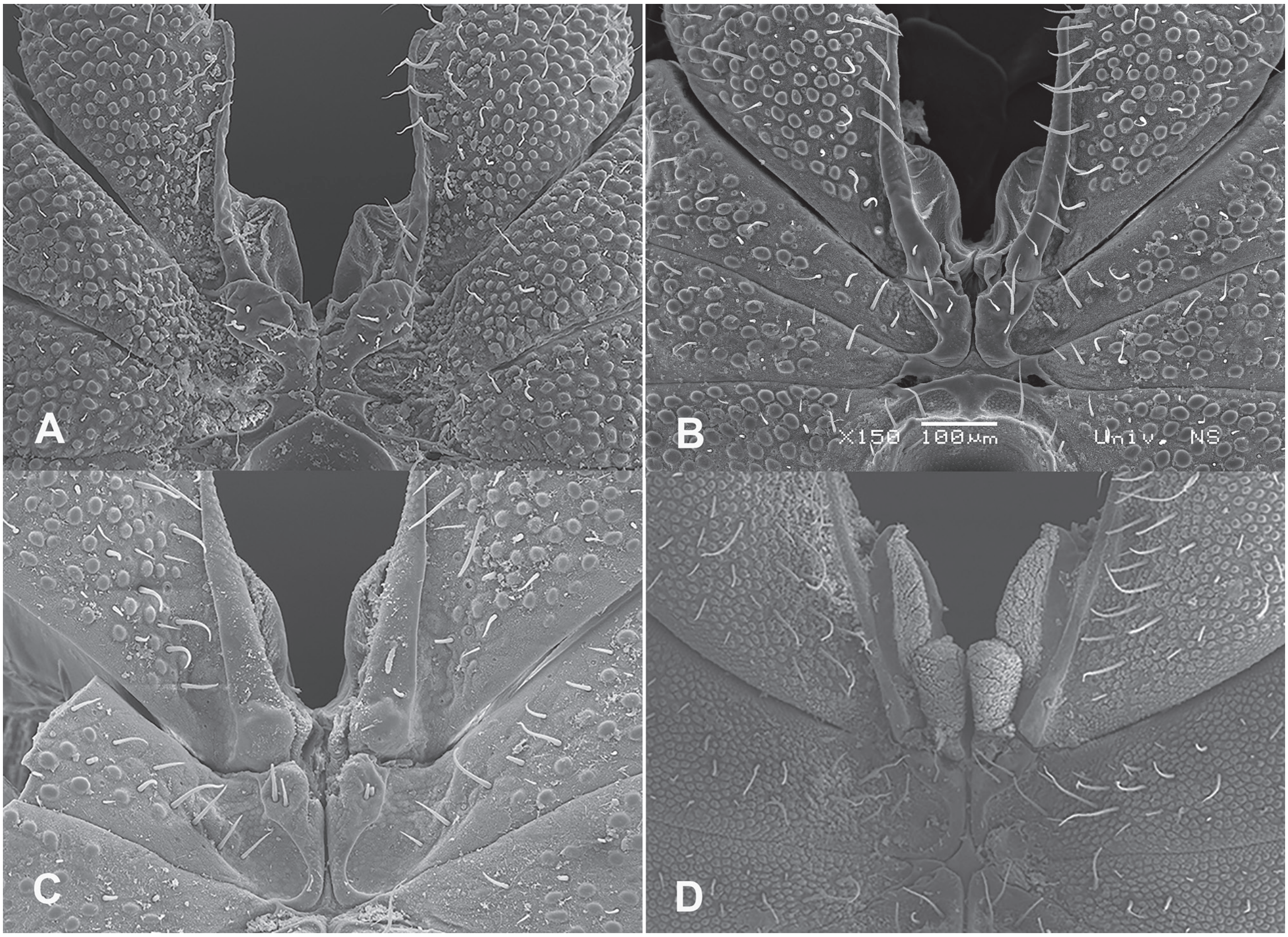

Fig. 4. Coxosternal region. **A**, *Suzukielus sauteri* female; **B**-**D**, Stylocellidae – **B**, *Meghalaya* sp. male, Trang Province, Thailand; **C**, *Leptopsalis* sp. male; **D**, *Miopsalis* sp. male.

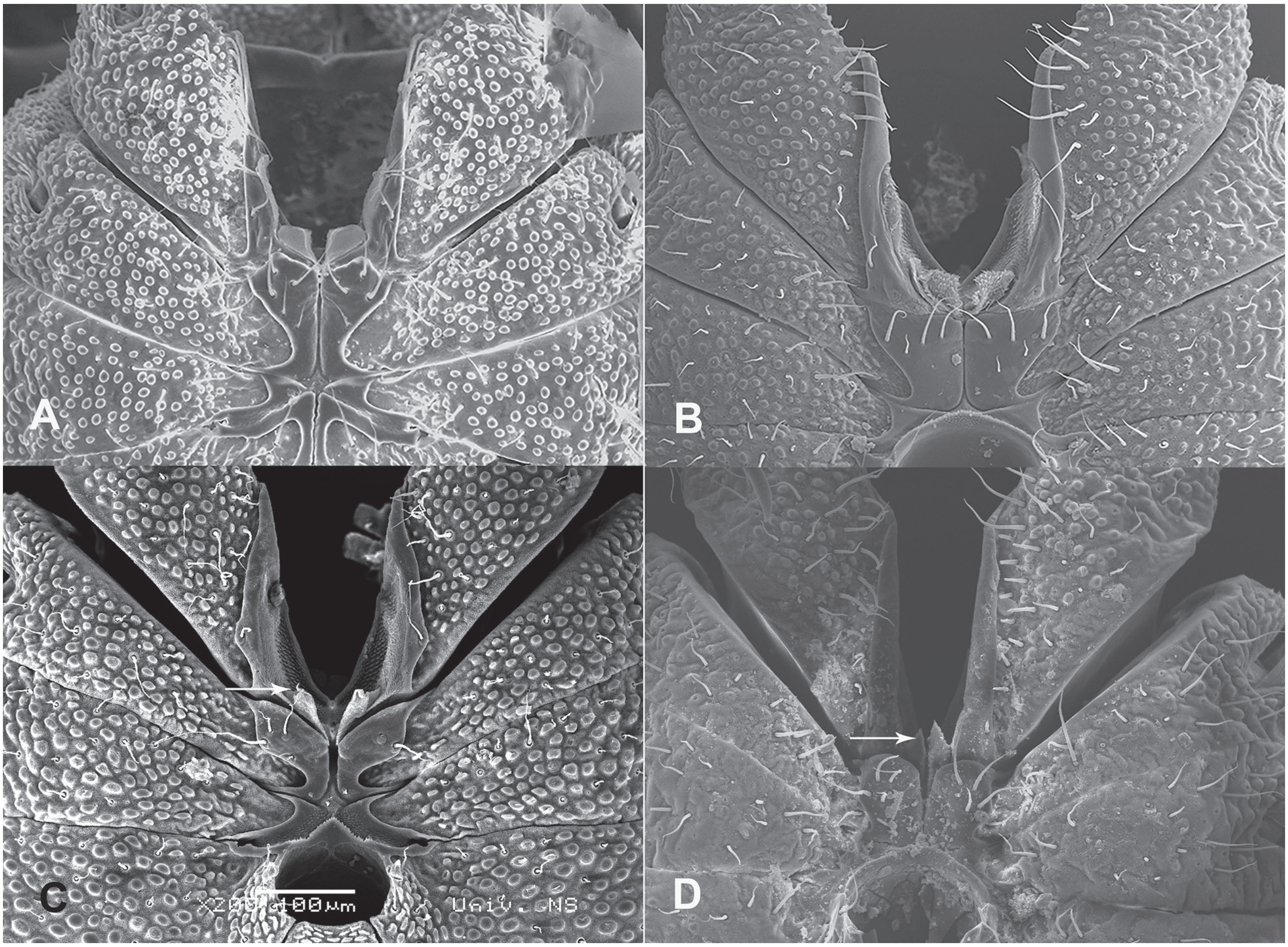

Fig. 5. Coxosternal region. **A**, *Ankakartra franzi* male, Madagascar; **B**, *Troglosiro* sp. female (Troglosironidae), New Caledonia; **C**, *Tucanogovea schusteri* male (Neogoveidae), Brasil; **D**, *Metagovea* sp. female (Neogoveidae), Colombia. Arrows indicate basal parts of the coxal endites.

peninsula (all unpublished data, work in progress). All mentioned areas share the same geological origin. Terrains of the Transcaucasia, Asia Minor and parts of Apennine peninsula were parts of the Cimmerian superterrane (also some continental fragments of the Iberian Peninsula). At the mid-Permian - Triassic this superterrane (a string of terranes) broke away from the northern margin of Gondwana (then a part of Pangea) (Ruban et. al. 2007) and accreted to the Eurasian plate. The western Cimmerian terranes and related parts of northern Gondwana are the areas of the origin of the genus *Parasiro*.

The remaining genera (*Siro*, *Cyphophthalmus*, *Paramiopsalis* and *Iberosiro*) show clear mutual affinities by a series of morphoanatomical characteristics: coxal lobes I wide, almost as wide as the width of the rest of coxae I (or at least 2/3 of their width); the plane of coxal lobes I is parallel to the plane of the ventral body surface (Figs 6A-B); coxal endites I wide, all in one, not divided in medial and proximal part; coxal lobes II wide, wider than long, their frontal edge is straight not depressed medially (Fig. 9); spermatopositor of „siro type“ (Shear 1980) with smooth diverging digiti mobiles (digiti mobiles mediales). These characteristics can be designated as diagnostic for the family Sironidae.

A problem in analyzing the position of Sironidae among Cyphophthalmi is that most of the mentioned diagnostic characters of the family are plesiomorphic. Spermatopositor structure of "siro type" (after Shear 1980) is spread among representatives of the southern hemisphere family Pettalidae too and some basic representatives of some other families (*Metasiro* - Neogoveidae), which underscores its plesiomorphic state. Ventral prosomal complex and myliosoma structure in Sironidae and *Parasiro* are more primitive among Cyphophthalmi. Their myliosoma structure represents a transitional form in the process of specialization for life in a narrow space and microphagous feeding. This is manifested by further rapprochement of coxae I and the retraction of

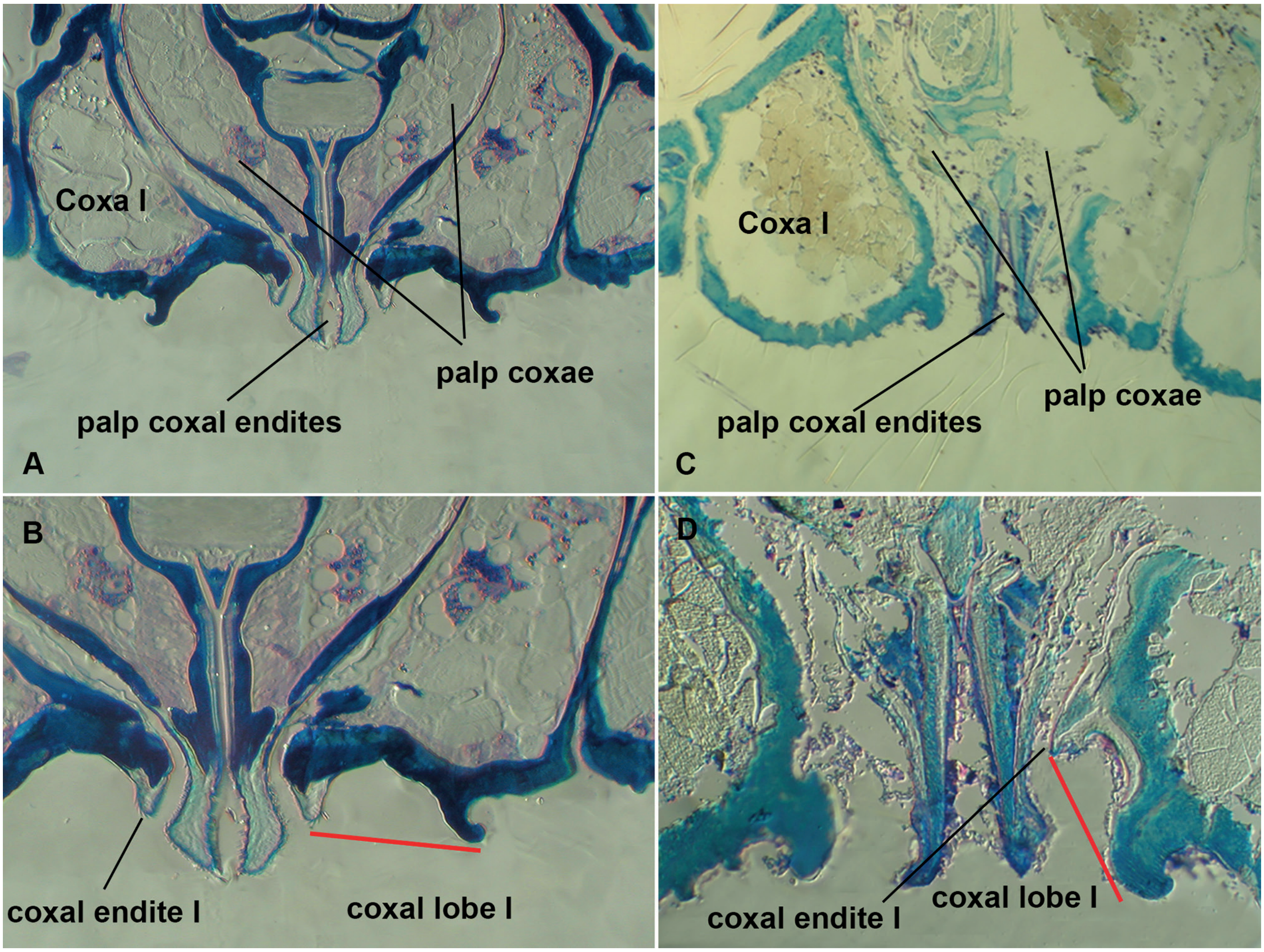

Fig. 6. Body cross section at the level of the palp coxae. **A-B**, *Cyphophthalmus duricorius*; **C-D**, Stylocellidae. Red line inclination indicates the position of coxal lobi I surface in relation to the ventral body surface.

coxal lobes I in other Cyphophthalmi, forming a structure to which the alternative name stomotheca is more appropriate (Figs 6C-D). Mentioned diagnostic characteristics put the family Sironidae with *Parasiro* in the basis of Cyphophthalmi phylogeny, which contradicts the results of numerous molecular analyses (Boyer et al. 2007; Giribet et al. 2012, 2017). In any case, the myliosoma structure in Sironidae and *Parasiro* could be treated as plesiomorphism too.

I attach more taxonomical importance to the characteristics of the ventral prosomal complex and myliosoma, primarily because they are obviously more conserved than other characters, as well as based on the assumed role of smooth surfaces of coxal lobes in the process of spermatophore production (Karaman 2005). Of course, with their simple structure and passive role, they cannot have the importance that the copulatory apparatus has in the taxonomy of other groups of Opiliones, but their specificities, however, are the result of sexual selection. I assume that the role of coxal lobes II is particularly important because their shape is specific to a group of closely related species or often even species-specific.

The shape and structure of the coxal lobes II and III clearly diagnose genera within the family Sironidae, and even the degree of relatedness among species. Based on the mentioned characteristics and some additional characters presented in previous studies, seven genera can thus be recognized in the family Sironidae: *Siro*, *Cyphophthalmus*, *Paramiopsalis*, *Iberosiro*, resurrected *Holosiro*, resurrected *Neosiro* and *Arhesiro* gen. nov. Within the genus *Holosiro* a new subgenus *Tillamooksiro* subgen. nov. is here established.

Genus *Siro* Latreille, 1796

Genus with disjunct distribution in Europe. Represented by six endemic species (Karaman et al. 2022) present from areas in France Massif Central, to Southeastern Alps and Eastern Carpathian Mountains. Genus is defined by the structure of the ventral prosomal complex, details of spermatopositor structure and the protruding anal region in females. The third character is missing in *Siro franzi* Karaman & Raspotnig, 2022, here treated as a lost character (Karaman et al. 2022), and in a fossil species from Bitterfeld amber (*Siro platypedipus* Dunlop & Giribet, 2003) whose affiliation to this genus must be verified by analysis of currently unknown coxosternal structure. The other European fossil species *Siro balticus* Dunlop & Mitov, 2011 is moved to North American genus *Neosiro* (see below). Genus *Siro* is easy to separate from the other sironids including closely related North American genera by the shape of coxal lobes II (Figs 2A-B, 9). Anterior margins of coxal lobes II are straight, mutually slightly diverging, almost at right angle to the longitudinal body axis. Coxal lobes III very short, medially protruded and inserted separating the posterior third of the coxal lobes II. Spermatopositor of the *Siro* species is characterized by short digiti mobiles, reaching up to the proximal margin of the medial lobe. Male anal plate with pronounced medial ridge and granular flat surfaces. Three anal gland pores widely separated, 1/3 of the anal plate width (1/4 in *S. crassus* and *S. ozimeci* in which the anal plate is expanded as well as the complete body).

Genus *Cyphophthalmus* Joseph, 1868

Genus represented by 32 described and many more still undescribed species. It is distributed from the northwestern part of Asia Minor (in general, north of the Izmir Ankara suture which is treated as part of the boundary between Laurasia and Gondwana (Okay et al. 2020)) in the east through the greater part of the Balkan Peninsula to the foothills of southeastern Alps on the west. A species from Cyprus (based on a juvenile specimen) seems to belong to this genus. So far it is clearly separated from the mentioned distribution area of the genus and probably has a separate origin from northern Gondwana. There is the possibility that the genus *Cyphophthalmus* expanded further west in the Mediterranean. Photographs and SEM pictures of males of *Siro rubens* presented in de Bivort and Giribet (2004, Figs 30e, 32e, 34e, 38e), Boyer and Giribet (2007, Fig. 8a), Giribet (2007, Fig. 4.4a) as well as in Giribet (2015) online "Catalog of Cyphophthalmi", are in fact illustrations of some *Cyphophthalmus* species of the Aegean lineage (Murienne et al. 2010), possibly close to species from Ionian region in Greece (*corfuanus* - *eratoe* group).

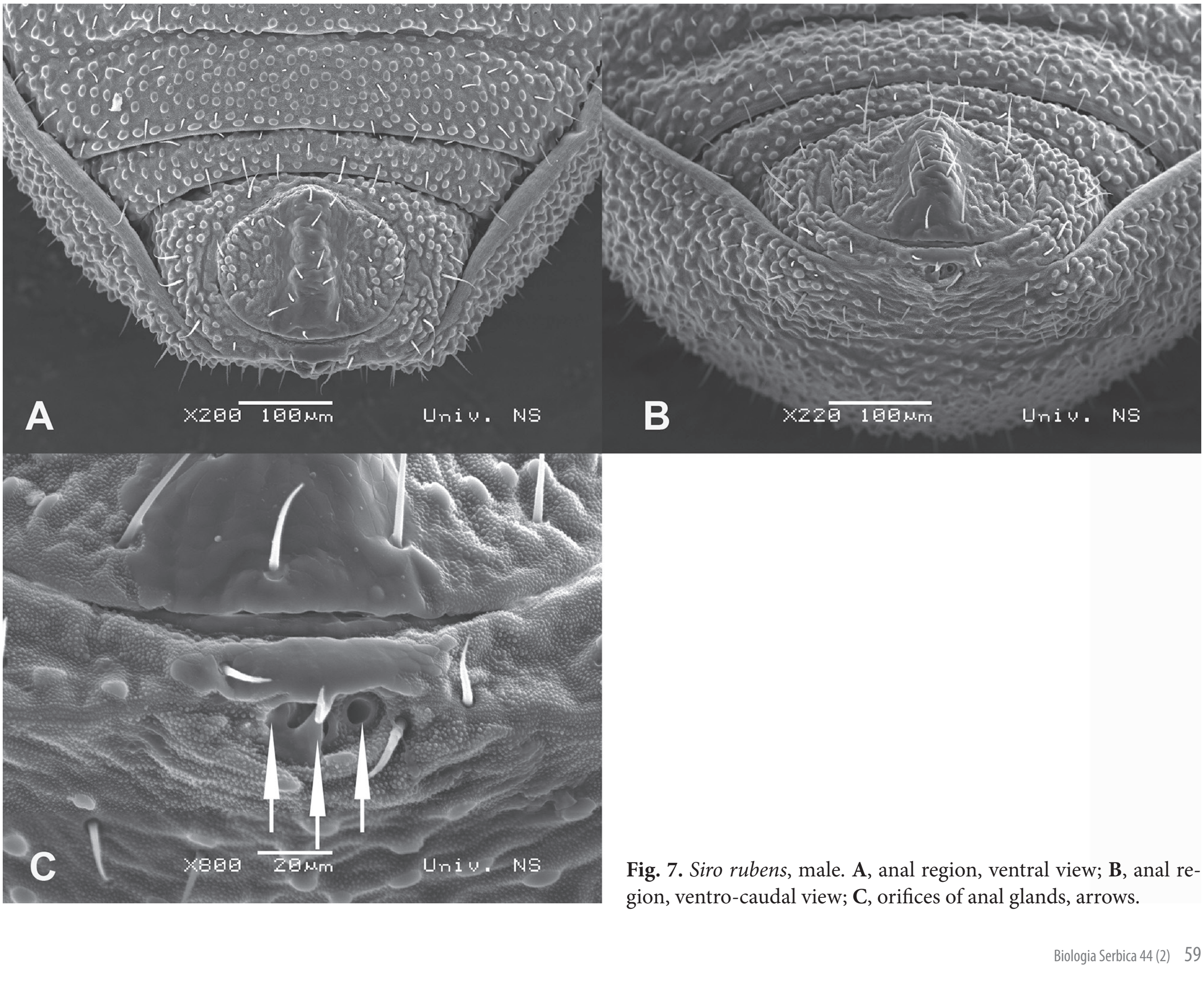

Fig. 7. *Siro rubens*, male. **A**, anal region, ventral view; **B**, anal region, ventro-caudal view; **C**, orifices of anal glands, arrows.

In the same sources the illustrations of females correspond to *Siro rubens*. As this error is repeated, it is clear that these specimens stem from mixed material of two species (*S. rubens* and *Cyphophthalmus* sp.), indicating their possible syn-

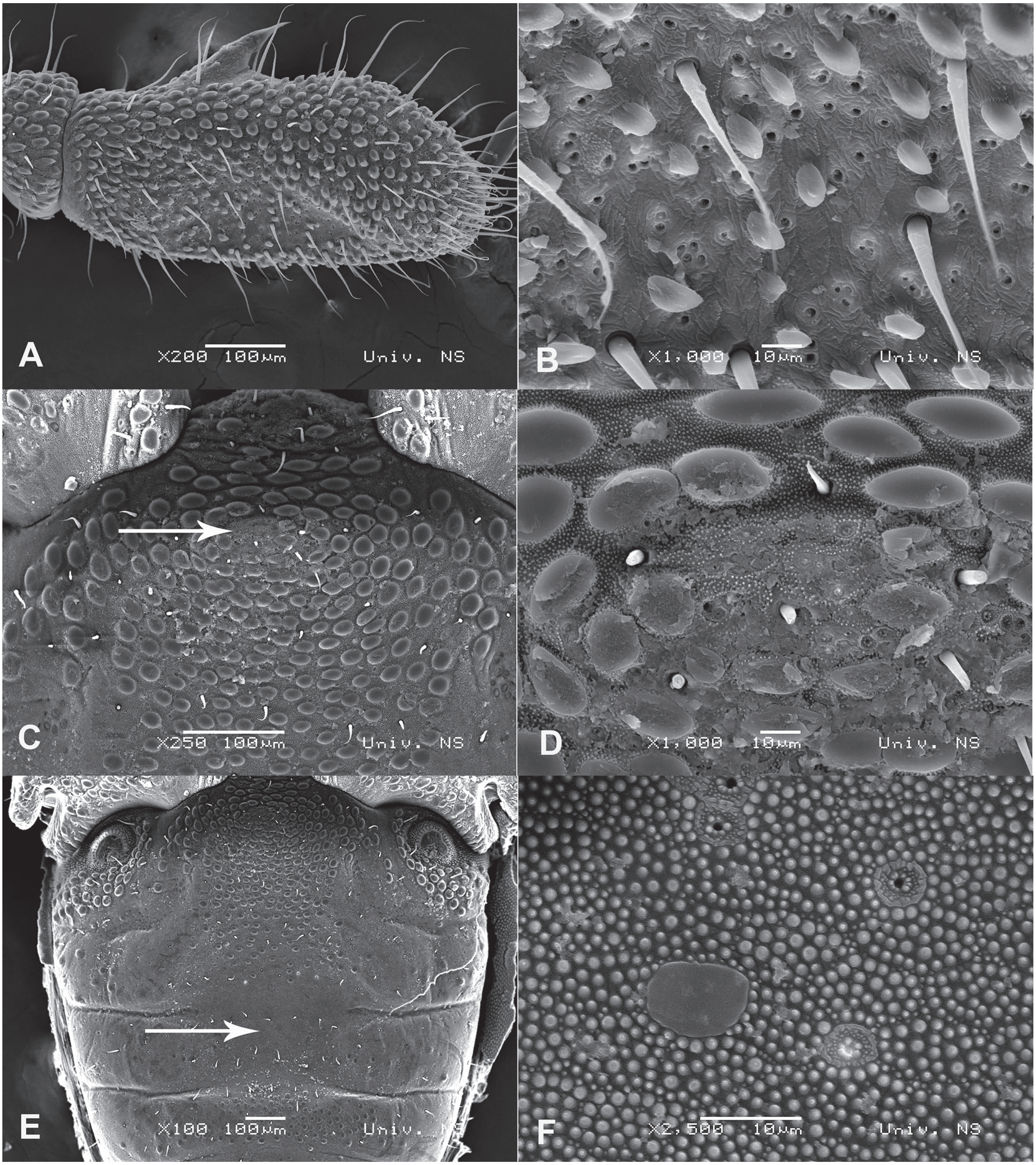

Fig. 8. *Meghalaya* sp. male, Trang Province, Thailand. **A**, tarsus IV depressed surface, ventro-prolateral view; **B**, cluster of glandular orifices in the depression of the tarsus IV; **C**, concetration of gland orifices on sternum II (arrow); **D**, cluster of glandular orifices on sternum II; **E**, depressed sternum surface without coarse ornamentation (first rank granules); **F**, surface of the depression, with granules of the second, and third rank only.

topic occurrence in these areas. Correspondingly, an incorrect illustration of *S. rubens* male is presented in Delfosse and Iorio (2009, Fig. 3a). As corrections to the given illustrations, I present SEM of relevant details of *S. rubens* males (Fig. 7) which fully correspond to the precise drawings of this species in Juberthie (1967). There are some cases of the spread of some old Aegean fauna into western Mediterranean, as in terrestrial isopods *Graeconiscus* (Garcia et al. 2020), *Cordioniscus* (Reboleira et al. 2015), *Macedonethes* (Karaman 2003), cave cricket genus *Dolichopoda* (Karaman et al. 2011) and probably others. Assuming a sympatrical occurrence of species at the locality of Mt Aigual in France (cited as the source of the analyzed samples in de Bivort and Giribet 2004), and thanks to the published coordinates in Giribet and Shear (2010), I found only relatively numerous populations of *S. rubens*. However, I do not exclude the possibility of sympatrical occurrence of two species there. Another possibility is that the samples from Greece and France were accidentally mixed in the laboratory.

Cyphophthalmus is the most diversified genus in the family and possibly in the whole suborder, reflecting the turbulent history of the archipelagos in the western Neo-Tethys Ocean, which rifted from northern Gondwana and collided with the Laurasian paleocontinental margin. It also reflects the complex orogeny of the Balkan penninsula. The species from Cyprus (based on a juvenile specimen) that seems to belong to this genus, possibly has a separate history but the same origin. I would complement the differential characteristics of the genus presented in Karaman (2009) – lobes II with almost straight posterior margins, medially fused along their length; lobes III long (longer than wide at the narrower part), straight anterior margins, posteriorly abruptly narrowing to widen out fan-like (hourglass shape) (Figs 2D, 9E). Spermatopositor with well-developed exterior pair of strong movable fingers with converging tips, inner movable fingers less developed; terminal lobe elongated and smooth. Male anal plate is with pronounced medial ridge and granular flat surfaces. Two anal gland pores tightly to widely separated (up to 1/3 anal plate width).

Genera *Paramiopsalis* Juberthie, 1962 and *Iberosiro* de Bivort & Giribet, 2004

Both genera are distributed in the western parts of the Iberian Peninsula. *Paramiopsalis* with four species and *Iberosiro* with two described species (Giribet et al. 2017). While other sironids have convoluted shapes of lateral margins of coxal lobes II, they are parallel in whole length in these two genera and form one broad continuous smooth surface with coxal lobes III and the anterior part of coxal lobes IV (Fig. 2E). That is the striking synapomorphic character of these two genera. Spermatopositor terminal lobe narrow; movable fingers more terminally located than in other sironids. Double adenostyle on the male tarsus IV in *Iberosiro* versus one in *Paramiopsalis*, which is the only diagnostic character to separate these two genera. Coxal lobes III in both genera are short and not meeting each other in the midline. A diagnosis for *Paramiopsalis* is given by Juberthie (1962) and for *Iberosiro* by de Bivort and Giribet (2004). The situation with the number of male anal gland orifices among the described species is interesting (Juberthie 1962; de Bivort and Giribet 2004; Giribet et al. 2017). Possession of two anal gland orifices is stable and a specific character in the genus *Cyphophthalmus* which is closely related to these two genera (Giribet et al. 2017). In *Paramiopsalis ramulosus* Juberthie, 1962 there is only one, while in *Iberosiro rosae* Giribet, Merino-Sáinz & Benavides, 2017 and *Paramiopsalis anadonae* Giribet, Merino-Sáinz & Benavides, 2017 there are two orifices as well as in "*Paramiopsalis ramulosus*" presented in Rambla and Fontarnau (1984). In *Paramiopsalis ramblae* Benavides & Giribet, 2017 there are three main orifices and several small ones. Similar small orifices are present in *P. ramulosus* (Fig. 6 in Juberthie 1962). The tendency to reduce the number of anal gland orifices from three to two and one is expressed here in one genus – *Paramiopsalis.* A further tendency towards displacement of these glands from the anal position to other positions is expressed in the genus *Meghalaya* Giribet, Sharma & Bastawade, 2007 (Stylocellidae). Clouse (2012) mentions the presence of a small male anal gland pore in one undescribed species of this genus. In other species of this interesting genus, gland drainage orifices, probably with the same function, can be seen as clusters of individual smaller dermal gland-like openings in the depression of the ventroprolateral side of tarsus IV (Figs 8A-B) (mislabeled as Ramblas organ by Clouse 2012). The function of these glands is probably related to the presence of the ventral opisthosomal depression and the absence of coarse ornamentation on its surface (Figs 8E-F). In at least one species of this genus there are clusters of small dermal gland-like openings in the position of the male sternal glands in Ogoveoidea (Figs 8C-D). In this genus, it seems that the transition of the position of the exocrine glands from the anal to sternal is at work.

North American sironids

North American sironids are a relatively diversified group with 10 species known to date (Giribet and Shear 2010; Giribet et al. 2017), but the actual species diversity seems to be higher than is actually known (as noted by Giribet and Shear 2010). Based on Newell's (1943, 1947) and Hoffman's (1963) excellent descriptions, it was clear that in North America at least two sironid genera exist, separated from European genus *Siro*. The description of the extremely unusual *Siro sonoma* Shear, 1980 created the impression of

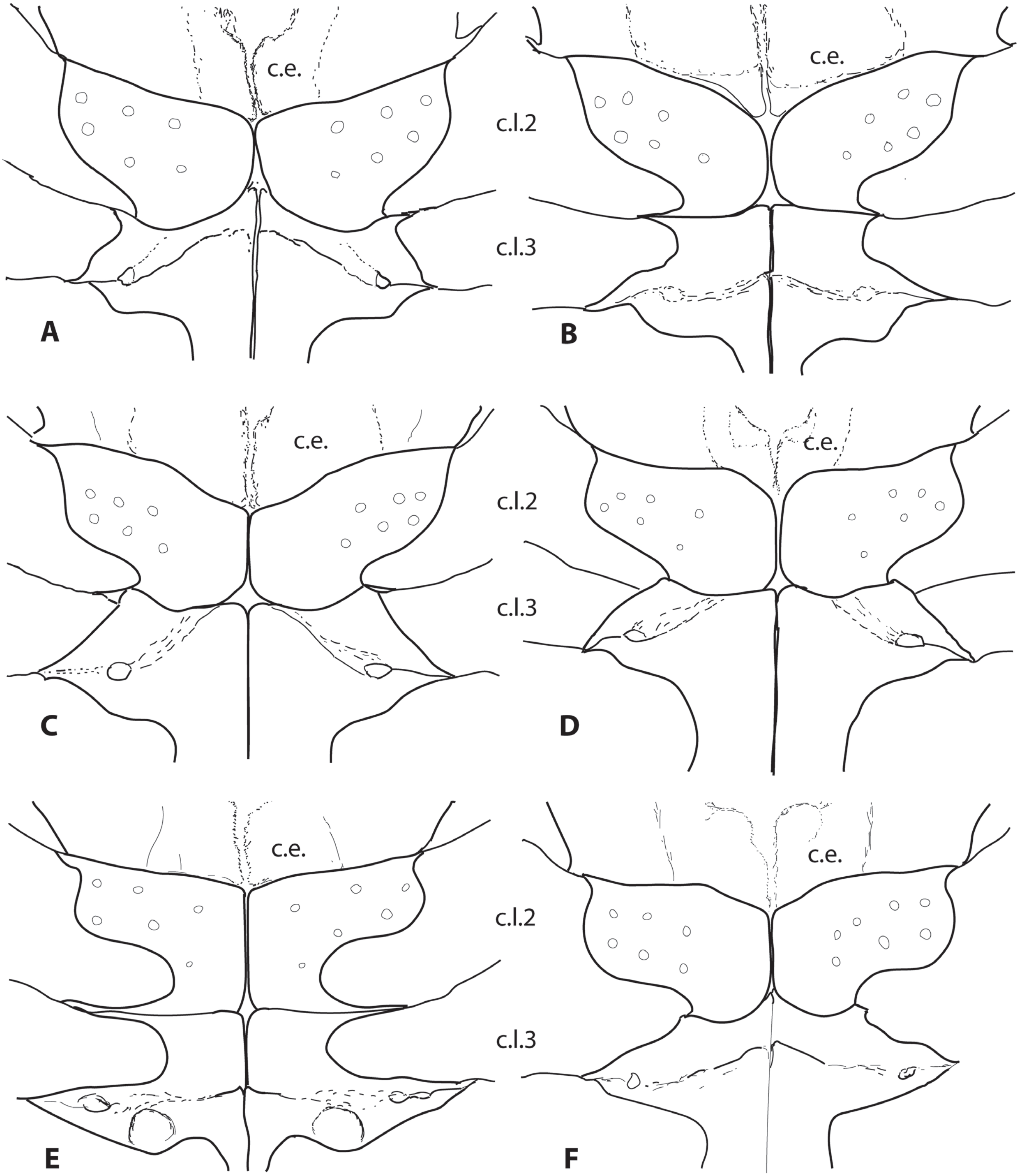

Fig 9. Coxosternal region drawings of males of some sironid genera. **A**, *Siro rubens*; **B**, *Holosiro calaveras*; **C**, *Neosiro exilis*; **D**, *Neosiro* (*Tillamooksiro*) *martensi* n. sp.; **E**, *Cyphophthalmus duricorius*; **F**, *Arhesiro clousi*. c.e.- coxal endite of coxal lobe 1; c.l.2 - coxal lobes II; c.l.3 -coxal lobes III (B and F based on Figs 11C and 15B in Giribet and Shear 2010).

even greater diversification of sironids in North America. I was convinced of that myself many years ago by reviewing the material that Shear kindly loaned to me, as well as later by analyzing specimens from the collection of Professor Martens. However, I could not come to any final conclusions except to determine that the diversity is much greater than previously presented. *Neosiro kamiakensis* Newell, 1943 and related *Siro exilis* Hoffman, 1963 were the only North American sironids correctly described and with relatively clear taxonomical situation. A key problem in resolving taxonomy of North American sironids is the fact that the initially described *Holosiro acaroides* Ewing, 1923 and specimens presented as conspecific (as *Siro acaroides* by synonymizing genus *Holosiro* with *Siro*) by Newel (1947) (also in Giribet and Shear 2010) do not represent the same species.

The unusual body form visible on Ewing's drawing and given proportions of the female holotype is so different from presented illustrations and proportions of this species in Newel (1947) that it clearly represents a different species. Newell's (1947) description of "*S. acaroides*" is not related to that species and represents a so far unnamed other species. A major mistake regarding this case was made in assuming that only one species lives in a wider area without considering the possible sympatric and parapatric existence of different species. I learned this very early by working on the genus *Cyphophthalmus*. If the differences among sympatric species are not easy noticeable in terms of body dimensions, such cases are easily overlooked. Even the existence of three different *Cyphophthalmus* species (two sympatric and one parapatric) in an area (much smaller than "foothills of Coast Range Mountains, Benton County, Oregon") is no exception. The precise position of the type locality "foothills of Coast Range Mountains, Benton County, Oregon" of *H. acaroides* is unknown. Newell (1947) did not compare his specimens directly to the holotype, the whereabouts of which in the meantime have become unknown (Shear 1980), aggravating the problem regarding the first described North American sironid and nominal of the genus *Holosiro*. In the original description of *H. acaroides* some relevant details are missing and the illustration of the coxosternal area was not so convincing that I would treat it as reliable enough to conclude anything related to this species and its position among the others satisfactorily described species from North America. The description of *Siro calaveras* Giribet & Shear 2010 created the conditions to solve the problem. The unusual body shape and proportions of the female of *S. calaveras* fully correspond to the specimen described by Ewing as *H. acaroides*. Comparing the illustrations of these two species, it turned out that Ewing was very precise in illustrating the structure of the coxal lobes. Due to the geographical distance of the localities and some minor differences visible in the illustrations, it is most likely that these are two closely related species. Based on the details illustrated in the description of *S. calaveras,* I could deduce that Ewings specimen is congeneric with specimens presented as belonging to *H. acaroides* (as *Siro acaroides*).

Based on specimens that I was able to investigate and published data (Giribet and Shear 2010; Giribet et al. 2017) I thus recognize three separate genera among North American sironids: resurrected ***Holosiro*** Ewing, 1923, resurrected ***Neosiro*** Newell, 1943 and ***Arhesiro*** gen. nov. New genus is established based on the of presented characteristics of *Siro clousi* Giribet & Shear 2010 and *Siro sonoma* Shear, 1980. The form of coxal lobes is crucial for mutual distinction of North American sironid genera and their separation from the genus *Siro* (Fig. 9). Common to the genera *Holosiro* and *Neosiro* is the spermatopositor with elongated digiti mobiles which reach up or exceed the terminal lobe of the spermatopositor, in contrast to the species of the genus *Siro* in which digiti mobiles are considerably shorter. The spermatopositor structure of *Arhesiro* gen. nov. species is unknown.

Genus *Holosiro* Ewing, 1923

Diagnosis

Coxal lobes II deeply separated by medially protruded posterior margins of Coxal lobes 1; medially shortly meeting; anterior margins mutually diverging (Fig. 10A-B). Coxal lobes III short, medially meeting throughout their length; anterior margins slightly protruded medially. Spermatopositor digiti mobiles strong and elongated, exceed the proximal margin of the terminal lobe. Male anal plate smooth, without medial ridge (Fig. 10E). Three anal gland pores widely separated.

Composition

Holosiro acaroides Ewing, 1923, *H. calaveras* (Giribet & Shear, 2010) comb. n., *H. shasta* (Giribet & Shear, 2010) comb. n. and *H. ewingi* sp. n.

Holosiro ewingi sp. n.

(Figs 10-14)

Material examined

1 ♂ holotype; 7 ♂, 6 ♀ paratypes, 6 juv., Corvallis, Oregon, USA, 15. 10. 1949, leg. V. Rirk.

Deposition

Holotype (Inv. No. 4415/1) and paratypes (Inv. No. 4415/2) are deposited in the Jochen Martens collection, Mainz.

Etymology

The species is named after Henry Ellsworth Ewing, American arachnologist who collected and described the first cyphophthalmid species from North America.

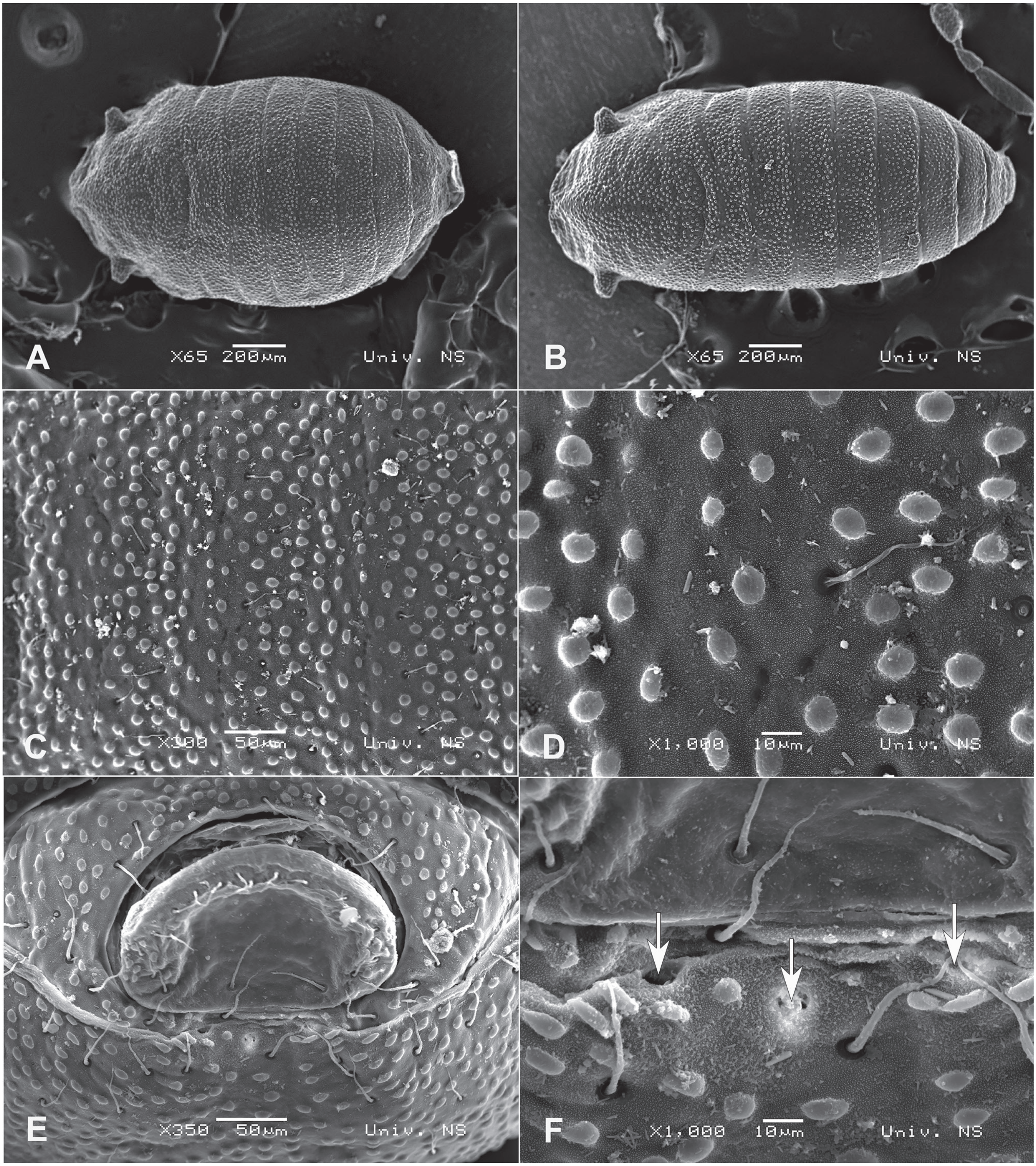

Fig 10. *Holosiro ewingi* n. sp. **A**, holotype dorsum; **B**, paratype female dorsum; **C**, dorsum granulation (sixth to tenth tergite); **D**, detail of granulation of the eighth tergite; **E**, male anal region, ventral view; **F**, terminal posterior part of the male dorsum with pores of anal glands (arrows).

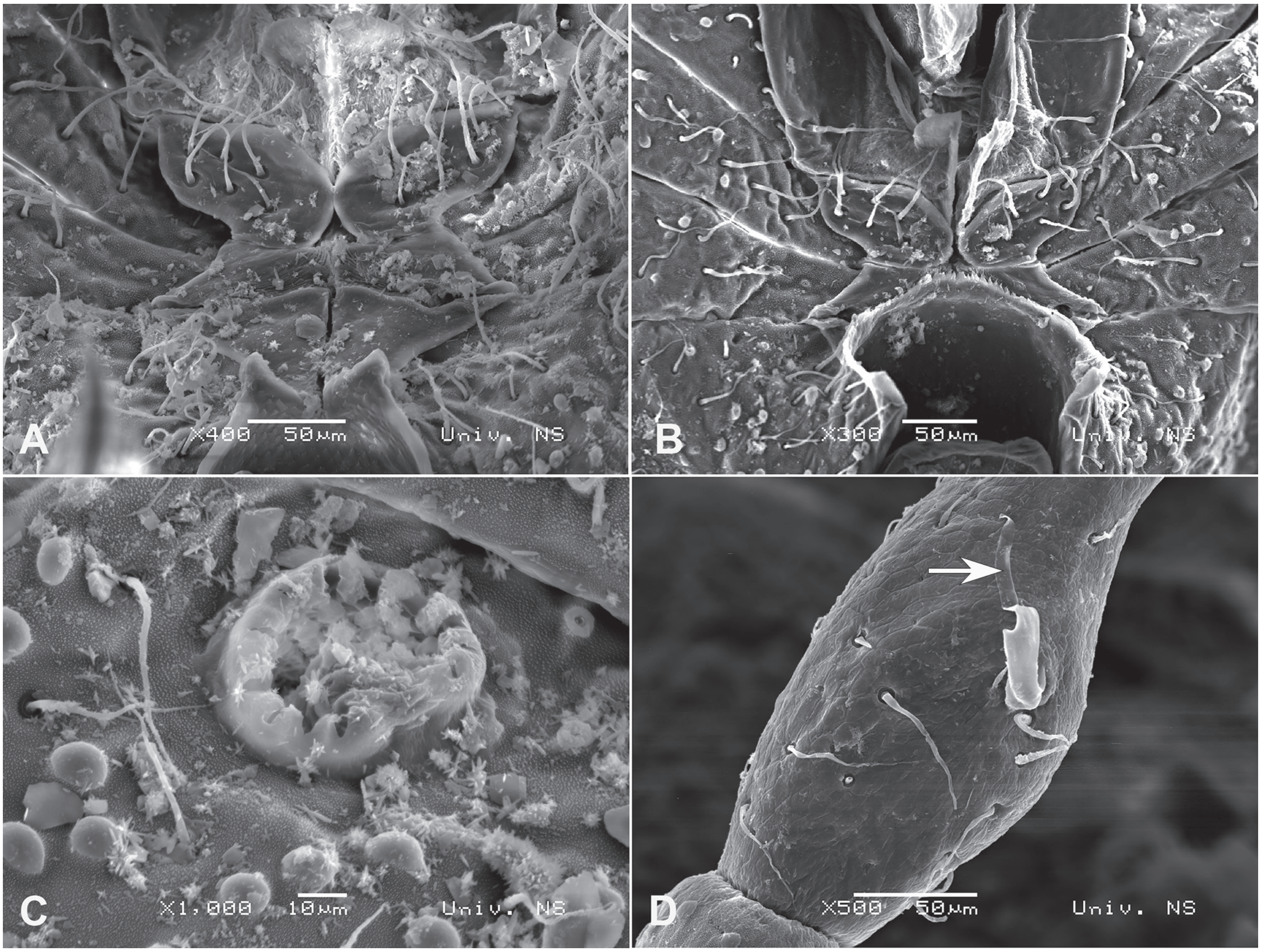

Fig 11. *Holosiro ewingi* n. sp. **A**, paratype male ventral prosomal complex; **B**, female ventral prosomal complex; **C**, Spiracle; **D**, dorsal view of adenostyle on male telotarsus IV, with elongated lamelliform process (arrow).

Diagnosis

Small sironid species, with short legs and large claws. Ozophores short. Anal plate completely depressed. Integument sparsely ornamented. Spermatopositor movable fingers and sensory papillae positioned close to terminal lobe,

Description

Male holotype body length 1.67 mm (males: 1.47-1.67). Anterior margin of dorsal scutum concave with small shallow notch. Ozophores conical, short (wider than long), dorso-laterally orientated of type II (sensu Juberthie, 1970). Dorsum wide (Fig. 10A); eighth tergite is concave. Granules of first rank (convex tubercles) oval in shape, small, sparsely distributed (Figs 10C-D). Anal plate completely depressed with wide smooth surface laterally and anteriorly bounded by narrow granulated bands (Fig. 10E). Three anal gland pores widely spaced to each other (Fig. 10F). Spiracles in the form of an open circle (Fig. 11C).

Chelicerae short (Fig. 12D), (basal article 0.69 mm long; second article 0.66 mm long). Basal article sparsely granulated on lateral and ventral side. Dorsal depression shallow, ventral bulge emphasized. Second article smooth, 4 times longer than wide**.** Teeth on fixed finger (6), basal ones widely spaced, on movable finger (7) tightly spaced.

Pedipalps short of normal proportions (Fig. 12E), (1.15 mm long without coxa and apotele). Trochanter shorter than patella, more than a half of the femur length. Tarsus as long as patella, shorter than tibia.

Legs basitarsi I-II and all telotarsi without ornamentation; basitarsi III-IV ornamented. Telotarsus I shape as in Fig. 12A (L/W ratio: 2.5), with soleae along terminal ¾ of its length. Claws I smooth sickle form, slightly elongated. Telotarsus IV (L/W ratio: 2.5) with adenostyle on the beginning of the second third of its length, (Fig. 12B). Adenostyle, lamelliform with elongated processus (Fig. 11D). Measurements of legs (without coxae and claws, in mm): I -1.78; II -1.49; III -1.21; IV -1.67.

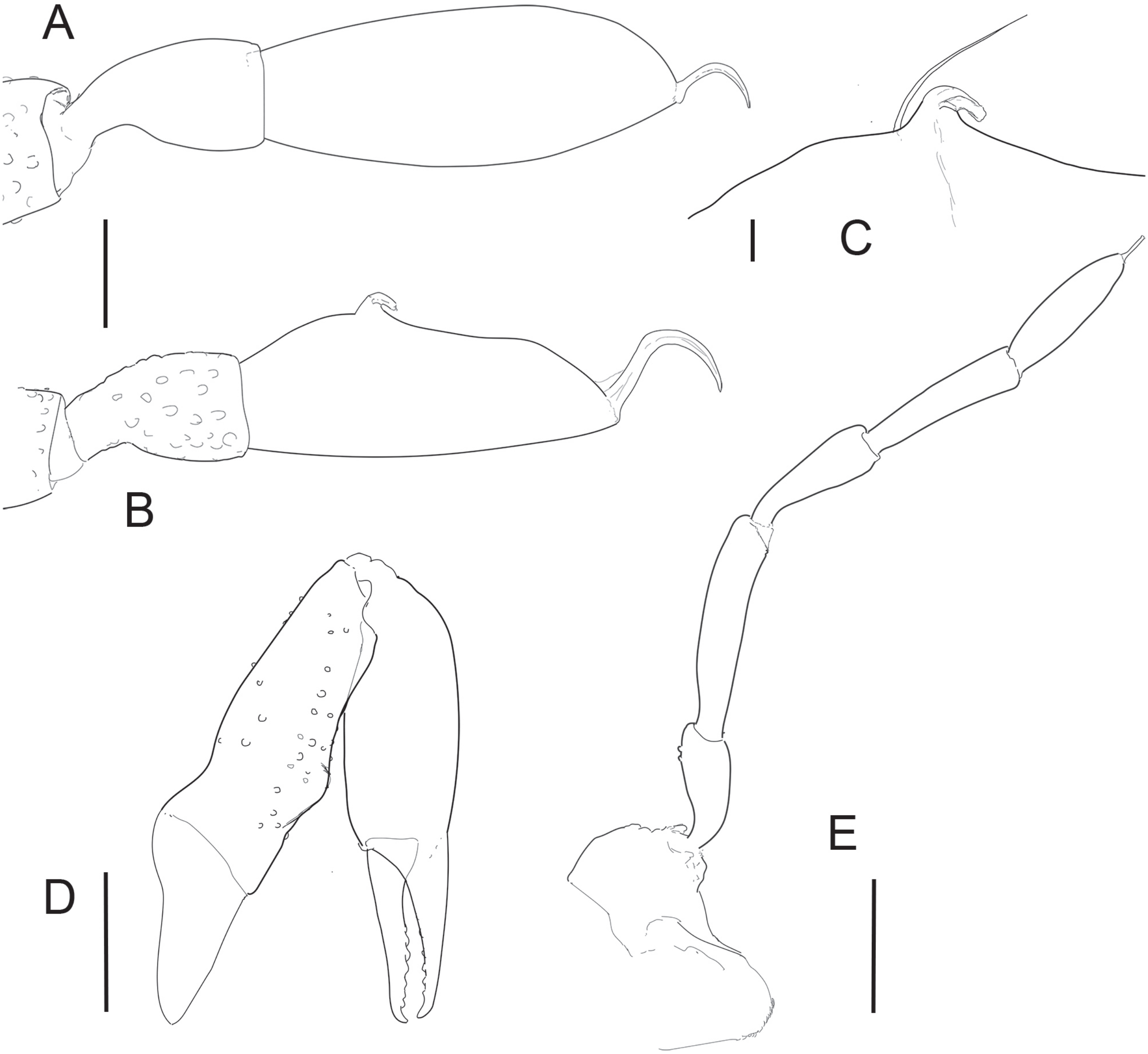

Fig. 12. *Holosiro ewingi* n. sp., holotype. **A**, basitarsus and telotarsus leg I; **B**, basitarsus and telotarsus leg IV; **C**, adenostyle; **D**, chelicerae, medial view; **E**, pedipalp, medial view. (Scale bars: A-B = 100 µm, C = 20 µm, D-E = 200 µm.)

Ventral prosomal complex (Fig. 11A): Coxal lobes II three times wider than long, abruptly narrowed in last third of their length; posterior width 3/5 of the anterior width; anterior margins medially diverging at right angle, laterally diverging slightly. Coxal lobes III short, medially meeting with the length that is a quarter of the length of their anterior margin. Coxal lobes IV frontal margin medially slightly convex; conical processes situated laterally on frontal margin of gonostome, separated.

Spermatopositor (Fig. 13) wide (less than 1.5 times as long as wide) with very short widely rounded terminal lobe. Terminal lobe smooth, with rare denticles apically. Setae terminales (4) short, medial pair widely separated. Setae dorsales (6) short, medial pair does not reach the medial lobe. Four setae laterales on each side. Setae ventrales (4) grouped closer to the base of the terminal lobe, medial pair slightly indented proximally. Movable fingers elongated, slightly sclerotized, diverge, by one third of their length they exceed the margin of apical lobe. Sensory papillae simple, positioned at the level of lateral pair of terminal setae.

Fig. 13. *Holosiro ewingi* n. sp., paratype. Spermatopositor (dorsal view). (Scale bar = 50 µm.)

Female body length 1.63-1.90 mm. Dorsum narrow, elongated (almost twice as width) (Fig. 10B) terminally attenuate; ventral prosomal complex (Fig. 11B), coxal lobes II as in male; coxal lobes III short, medially meeting very little. Ovipositor apical lobes short (Fig. 14), 2.5 times longer than terminal article. Terminal article as long as wide in its base. Openings of receptacles situated on the half of the length of apical lobes. Receptacles of saccate form**.** Each apical lobe bearing one terminal, one ramified and 12 simple setae. Measurements of legs, without coxae and claws (in mm) (female 1.8 mm body length): I -1,55; II -1.27; III -1.10; IV -1.37.

Remarks

The new species is close to *Holosiro shasta* (Giribet and Shear, 2010) comb. n. from north California, but it is conspicuously smaller. Clearly differs also in the details of the structure of coxal lobes II, III and spermatopositor.

All specimens examined have lost their original color and their cuticle is thinned, so some structures are prone to deformations, such as the dorsum of the female on Fig. 10B. Presented profiles of appendages could be slightly deformed as well.

Genus *Neosiro* Newell, 1943

Diagnosis

Coxal lobes II medially meeting throughout their length. Coxal lobes III short, medially not meeting. Coxal lobes IV in males medially protruded and inserted separating coxal lobes III. Spermatopositor digiti mobiles elongated, reaching or exceeding the proximal margin of the terminal lobe. Male anal plate with a wide smooth surface laterally bounded by narrow granulated bands and medial ridge. Three anal gland pores tightly spaced to each other. Based on differences in relevant taxonomical characters within the genus I distinguish two subgenera: ***Neosiro*** Newell, 1943 and ***Tillamooksiro*** sbg. nov.

Diagnosis of the subgenus ***Neosiro***: coxal lobes II anterior margins medially slightly mutually diverging, laterally parallel (straight, almost at right angle to the longitudinal body axis). Male coxal lobes IV medially sharply protruded. Anal plate medial ridge wide and inconspicuous, extends the entire length of the plate. Ovipositor wide, last article wider than long.

Composition

Neosiro kamiakensis Newell, 1943; *N. exilis* (Hoffman, 1963) comb. n.; *N. boyerae* (Giribet & Shear, 2010) comb. n.; *N. ligiae* (Giribet, 2017) comb. n.; *N. richarti* (Benavides & Giribet, 2017) comb. n. and fossil *N. balticus* (Dunlop & Mitov, 2011) comb. n.

Diagnosis of the subgenus ***Tillamooksiro*** sbg. nov.: coxal lobes II anterior margins almost straight, at right angle to the longitudinal body axis; male coxal lobes IV medially bluntly protruded. Anal plate, medial ridge pronounced, narrow and short, extends along the posterior half of the plate. Ovipositor narrow, last article as long as wide in the base.

***Neosiro* (*T.*) *martensi* sp. n.**

(Figs 9D, 15-19)

Material examined

1 ♂ holotype; 7 ♂, 6 ♀ paratypes, Sand Beach Campground, Suislaw Nat. For. Road, S30, 1,5 mi S, 2 mi W Sand Lake, Oregon, Tillamook Co. USA, 4. 11. 1972, leg. E. M. Benedict.

Type locality

Sand Beach Campground, Tillamook Co, Oregon, USA

Deposition

Holotype (Inv. No 2183/1), paratypes (Inv. No. 2183/2) are deposited in the Jochen Martens collection, Mainz.

Etymology

The species is dedicated to Professor Jochen Martens, great zoologist and renowned Opiliones expert.

Diagnosis

Small sironid species, with slender body and short legs. Anterior margin of prosoma with moderately deep, rounded notch. Male dorsum is globous posteriorly. Adenostyle short and stout with terminal spure. Spermatopositor with three lobed sensory papillae.

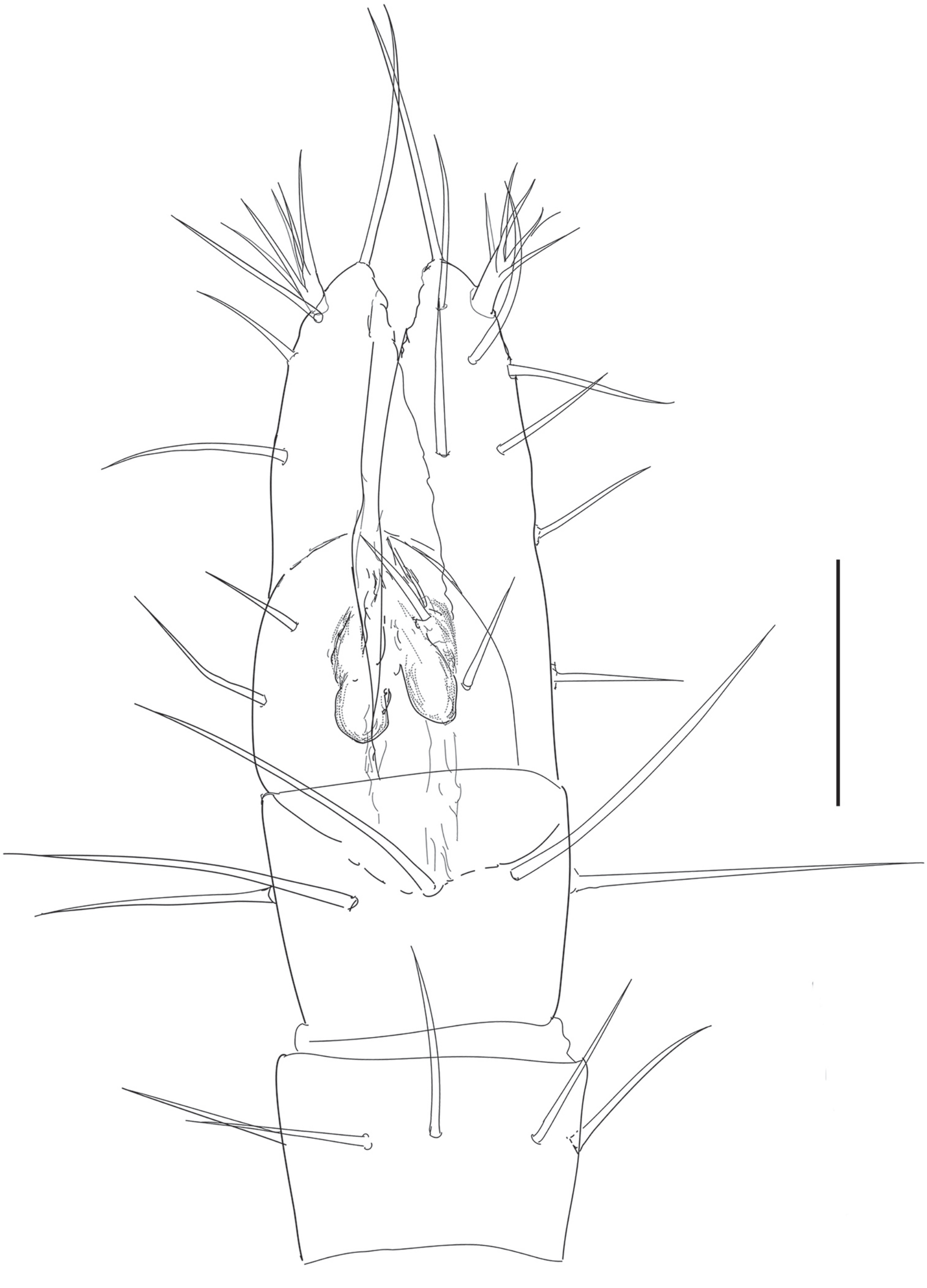

Fig. 14. *Holosiro ewingi* n. sp. Distal portion of ovipositor, ventral view. (Scale bar = 100 μm.)

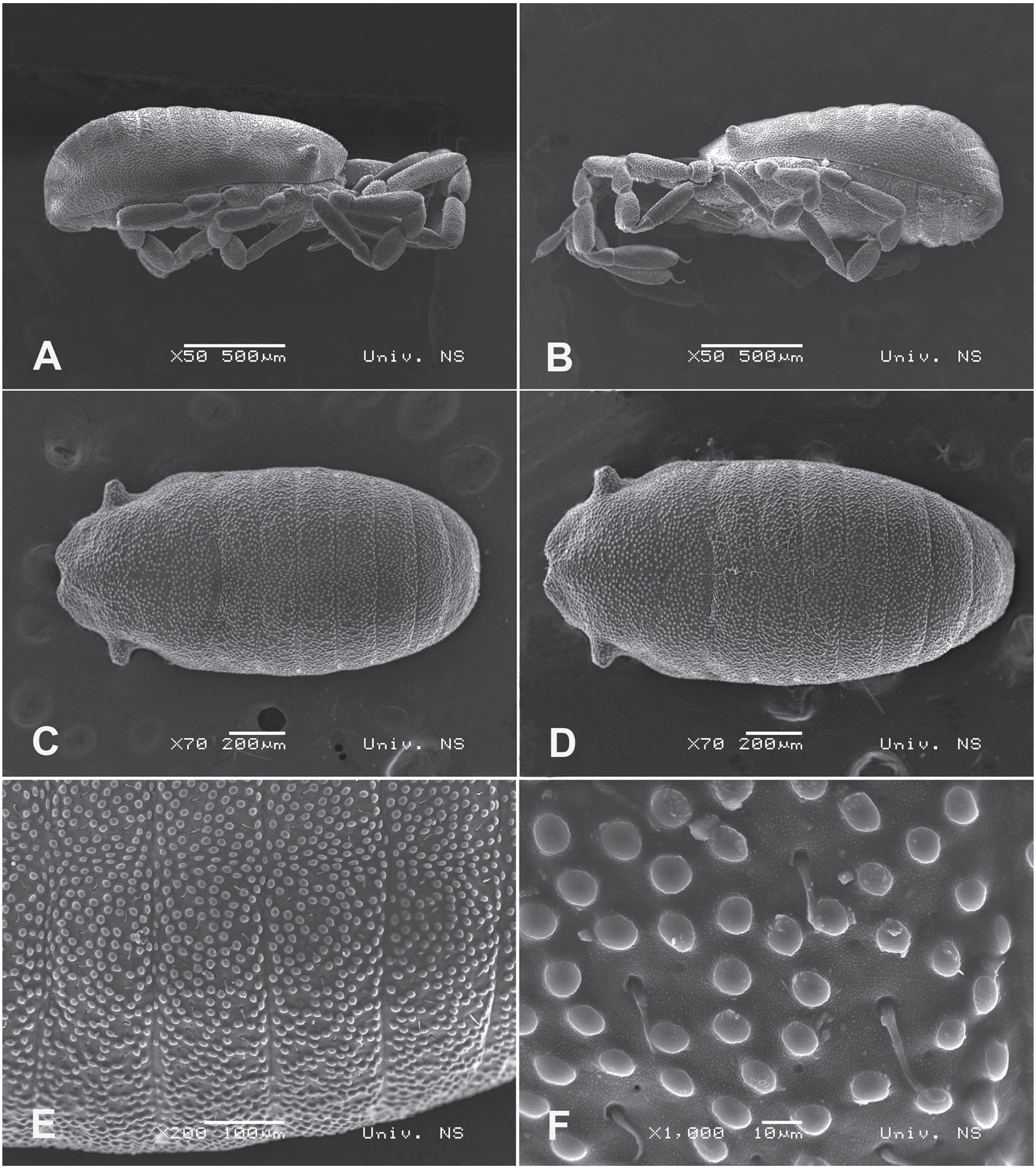

Fig 15. *Neosiro* (*Tillamooksiro*) *martensi* n. sp. **A**, paratype male lateral view; **B**, paratype female lateral view; **C**, male dorsum; **D**, female dorsum; **E**, dorsum granulation (sixth to tenth tergite); **F**, detail of granulation of the eighth tergite.

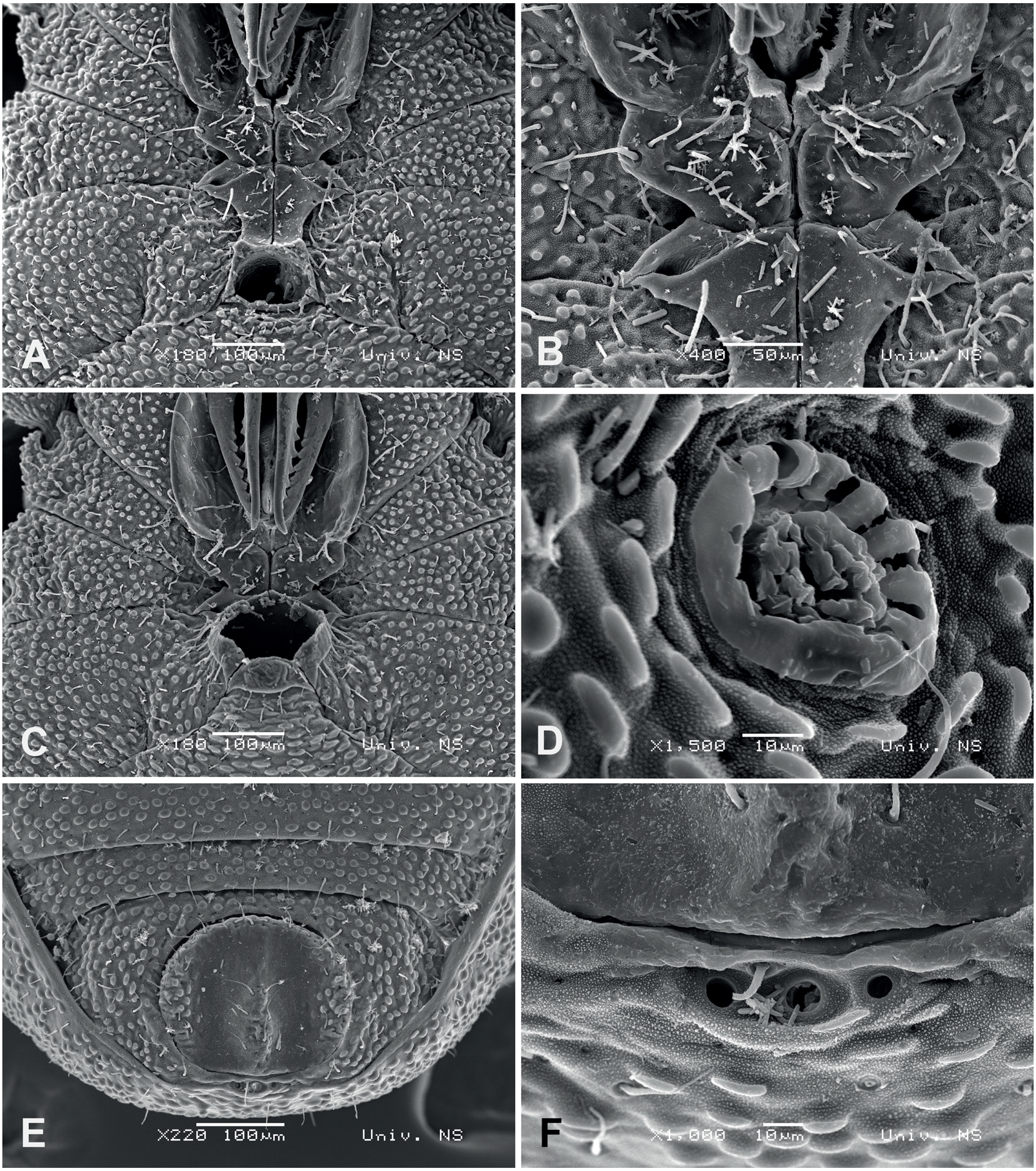

Fig 16. *Neosiro* (*Tillamooksiro*) *martensi* n. sp. **A**, male ventral prosomal complex; **B**, detail of male ventral prosomal complex; **C**, female ventral prosomal complex; **D**, spiracle; **E**, male anal region, ventral view; **F**, terminal posterior part of the male dorsum with pores of anal glands.

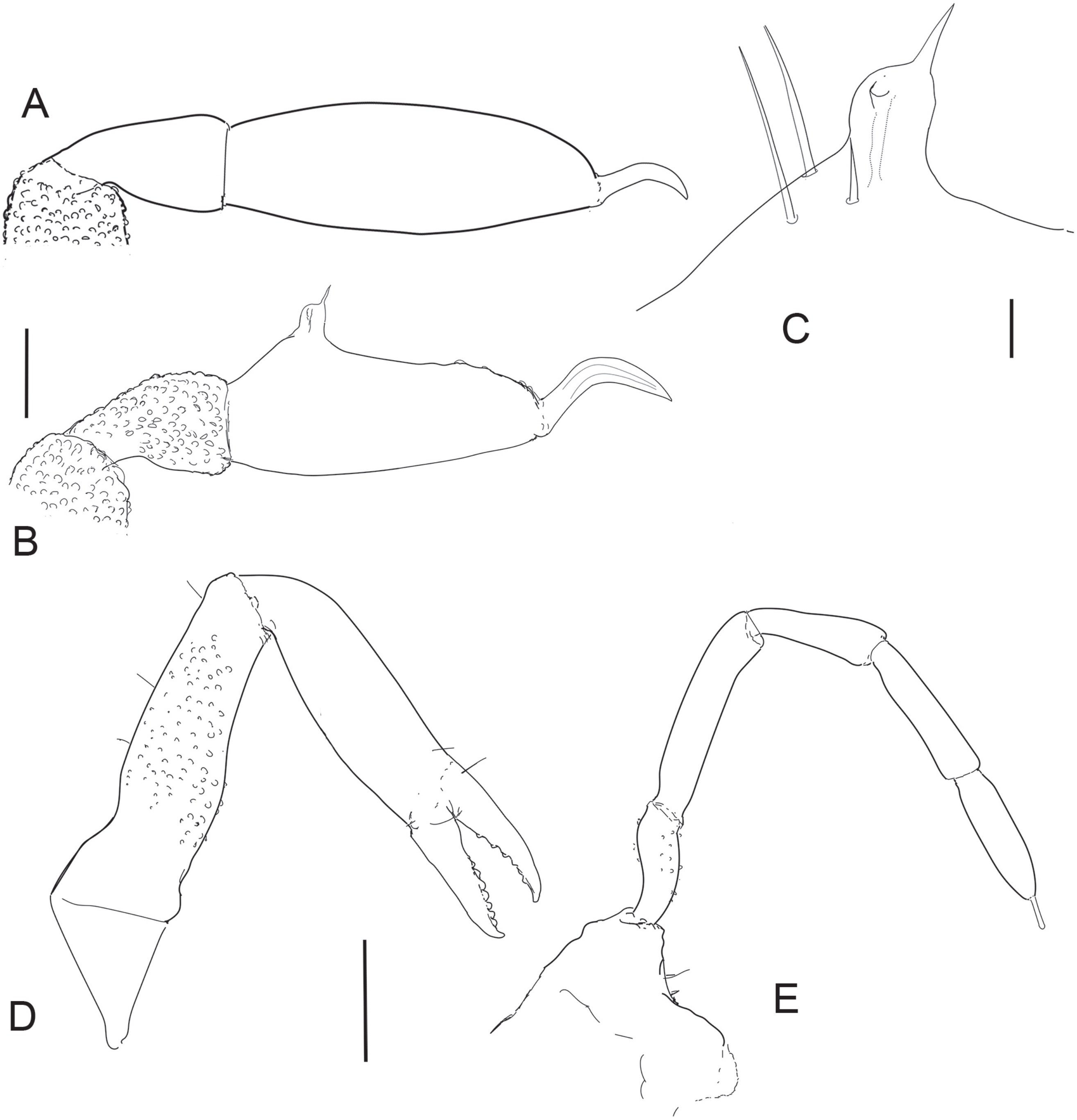

Fig. 17. *Neosiro* (*Tillamooksiro*) *martensi* n. sp. **A**, basitarsus and telotarsus, leg I; **B**, basitarsus and telotarsus, leg IV; **C**, adenostyle; **D**, chelicerae, medial view; **E**, pedipalp, medial view. (Scale bars: A-B, D-E = 200 μm, C = 20 μm.)

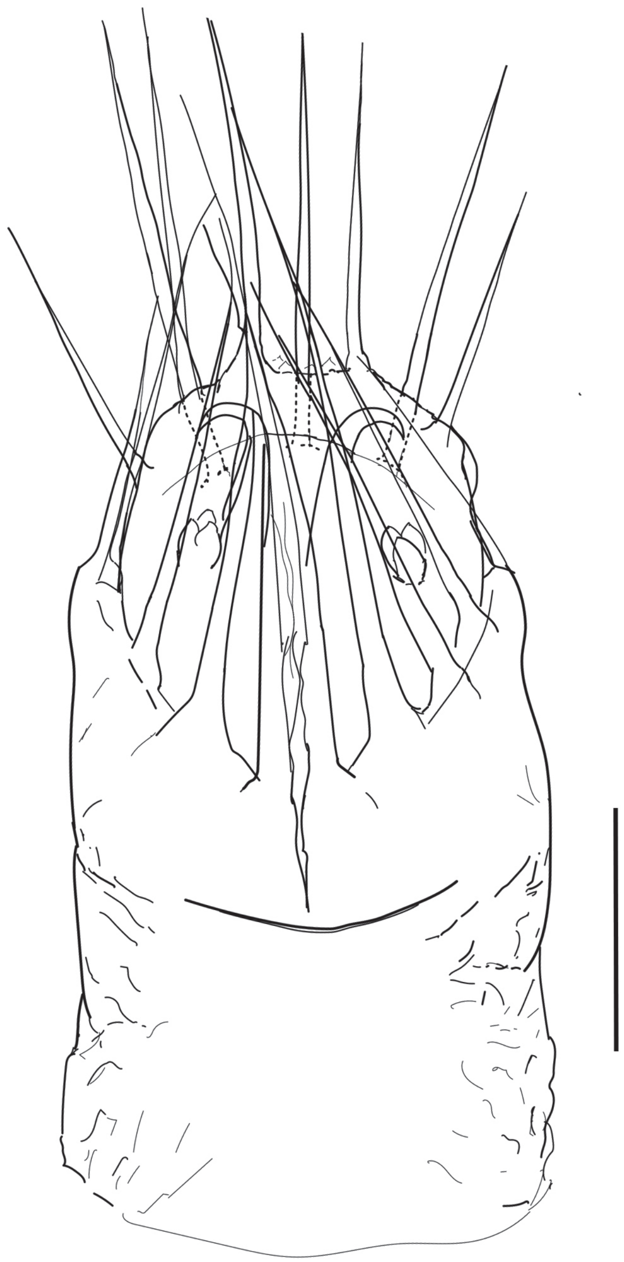

Fig. 18. *Neosiro* (*Tillamooksiro*) *martensi* n. sp. Spermatopositor (dorsal view). (Scale bar = 50 µm.)

Description

Male holotype body length 1.51 mm (males: 1.50-1.60 mm). Body uniformly brown in color. Dorsum narrow, elongated (as twice as width), (Fig. 15C); anterior margin of prosoma with moderately deep, rounded notch; anterolateral margins short, sinuate; posterior margin of opisthosoma bluntly rounded, globous in lateral projection (Fig. 15A). Ozophores as long as wide at their bases, dorso-laterally orientated (type 2). Anal plate with wide smooth surface laterally bounded by narrow granulated bands and pronounced narrow, rough medial ridge (Fig. 16E). Medial ridge short, extends along the posterior half of the anal plate. Three anal gland pores tightly spaced to each other (Fig. 16F). Lateral ones spaced one-fifth apart the width of the plate.

Chelicerae slightly elongated (Fig. 17D), (in 1.50 mm paratype male: basal article 0.79 mm long; second article 0.72 mm long). Basal article granulated on lateral and ventral side, sparsely dorsal; medially only ventral rim sparsely granulated. Dorsal depression shallow, ventral bulge weakly emphasized. Second article smooth, 5 times longer than wide. Teeth on fixed finger (6) widely spaced, on movable finger (8) tightly spaced.

Pedipalps of normal proportions (Fig. 17E), (in 1.50 mm paratype male: 1.20 mm long without coxa and apotele); Trochanter shorter than patella, more than a half of the femur length. Tarsus as long as patella, shorter than tibia.

Legs basitarsi I-II and all telotarsi without ornamentation; basitarsi III-IV ornamented. Telotarsus I shape as in Fig. 17A (L/W ratio: 3), with distinct soleae along terminal ¾ of its length. Claws I smooth and short. Telotarsus IV relatively short (L/W ratio – somewhat less than 3) with adenostyle on the first third of its length, (Fig. 17B). Adenostyle short, cylindrical, stocky, slightly longer than wide, on distal edge with short spur (Fig. 17C). Measurements of legs (paratype 1.53 mm) (without coxae and claws, in mm): I -1.80; II -1.51; III -1.27; IV -1.55.

Ventral prosomal complex (Figs. 16A-B): Coxal lobes II three times wider than long, abruptly narrowed in half its length; posterior width 2/5 of the anterior width; anterior margin almost straight medially interrupted by short protrusion of coxal lobes I. Coxal lobes III short, medially do not meeting. Coxal lobes IV in males protruded medially at an obtuse angle and inserted separating coxal lobes III; conical processes situated laterally on frontal margin of gonostome, connected by a transverse ridge.

Spermatopositor (Fig. 18) narrow (more than 1.5 times as long as wide) with short terminal lobe. Terminal lobe with sparse denticles apically. Setae terminales (5) short, lateral pair positioned more ventral at the level of setae ventrales; Setae dorsales (6) long, two lateral pairs almost as long as spermatopositor. Three setae laterales on each side. Setae ventrales (3) standing close to terminal setae, longer than them; Movable fingers elongated, slightly sclerotized, curved outward, almost reach to apical lobe; Sensory papillae three-lobed, positioned at the level of terminal pair of lateral setae.

Female body length 1.54-1.71 mm. Dorsum narrow, elongated (length: twice as width) (Fig. 15D); ventral prosomal complex (Fig. 16C) coxal lobes II as in male; coxal lobes III short, medially not meeting. Ovipositor apical lobes

(Fig. 19) three times longer than terminal article. Terminal article as long as wide in its base. Openings of receptacles situated in the base of terminal half of the apical lobes length. Receptacles of saccate form. Each apical lobe bearing one terminal, one ramified and 12 simple setae. Measurements of legs, without coxae and claws (in mm) (female 1.66 mm body length): I -1.74; II -1.45; III -1.15; IV -1.54.

Remarks

Among North American sironids, *Neosiro* (*T.*) *martensi* sp. n. stands out with a series of characters that I consider apomorphic. Because of this, it is difficult to recognize its clear phyletic position. Several characters suggest its closeness to the genus *Neosiro*. These are the structure of coxosternites III and IV in males; length and position of spermatopositor movable fingers and tightly spaced anal gland pores. The deeply arched dorsum posteriorly is a character present in *Neosiro* species but not so pronounced as in *N.* (*T.*) *martensi* sp. n.

The tendency to shorten coxosternite III to provide direct contact of male coxosternite IV with coxosternite II is obvious and occurs independently in most sironids and some other Cyphophthalmi. I believe it has to do with the production of spermatophores.

Spermatopositor with three lobed sensory papillae in *N.* (*T.*) *martensi* sp. n. is an apomorphy. The usual structure of sensory papillae in sironids implies a pair of them with sim-

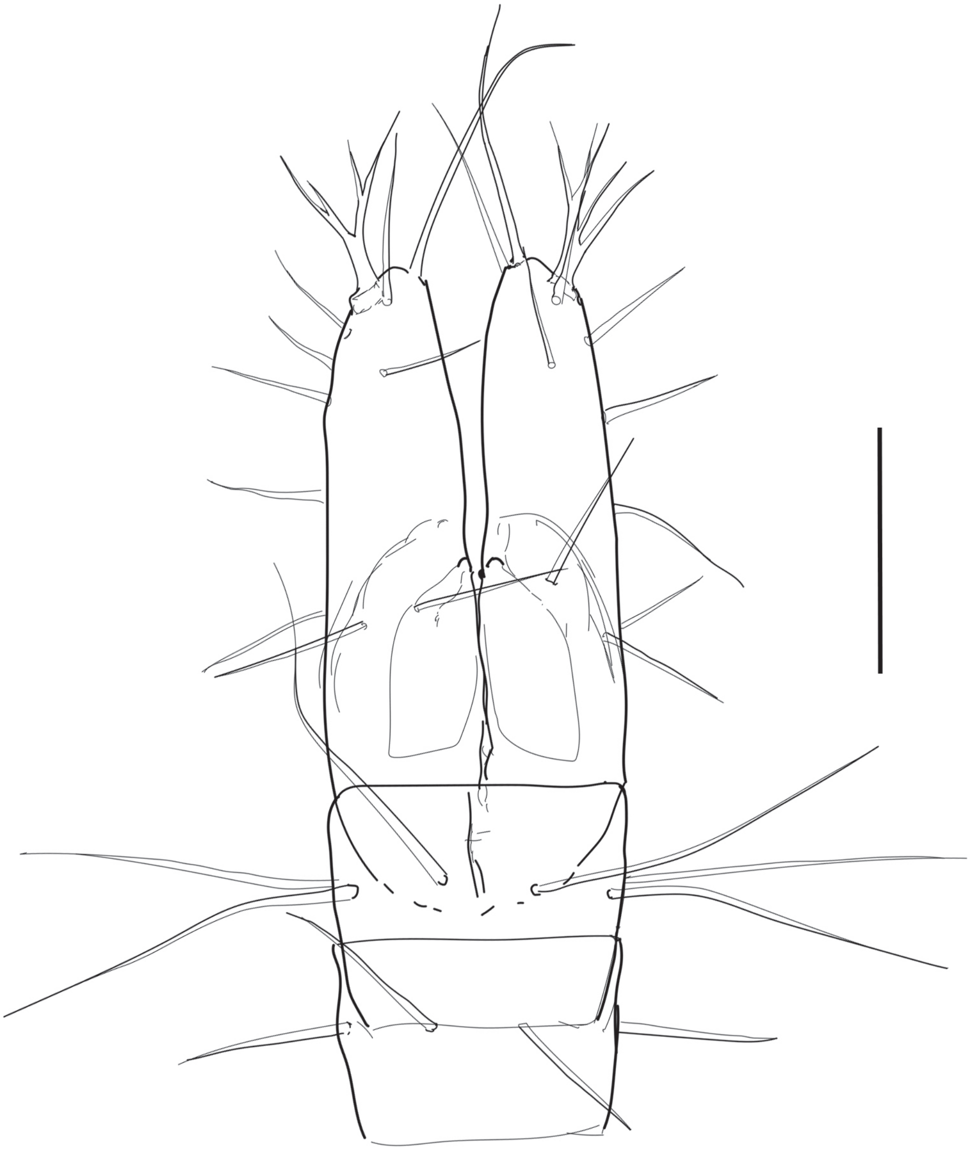

Fig. 19. *Neosiro* (*Tillamooksiro*) *martensi* n. sp. Distal portion of ovipositor, ventral view. (Scale bar = 100 µm.)

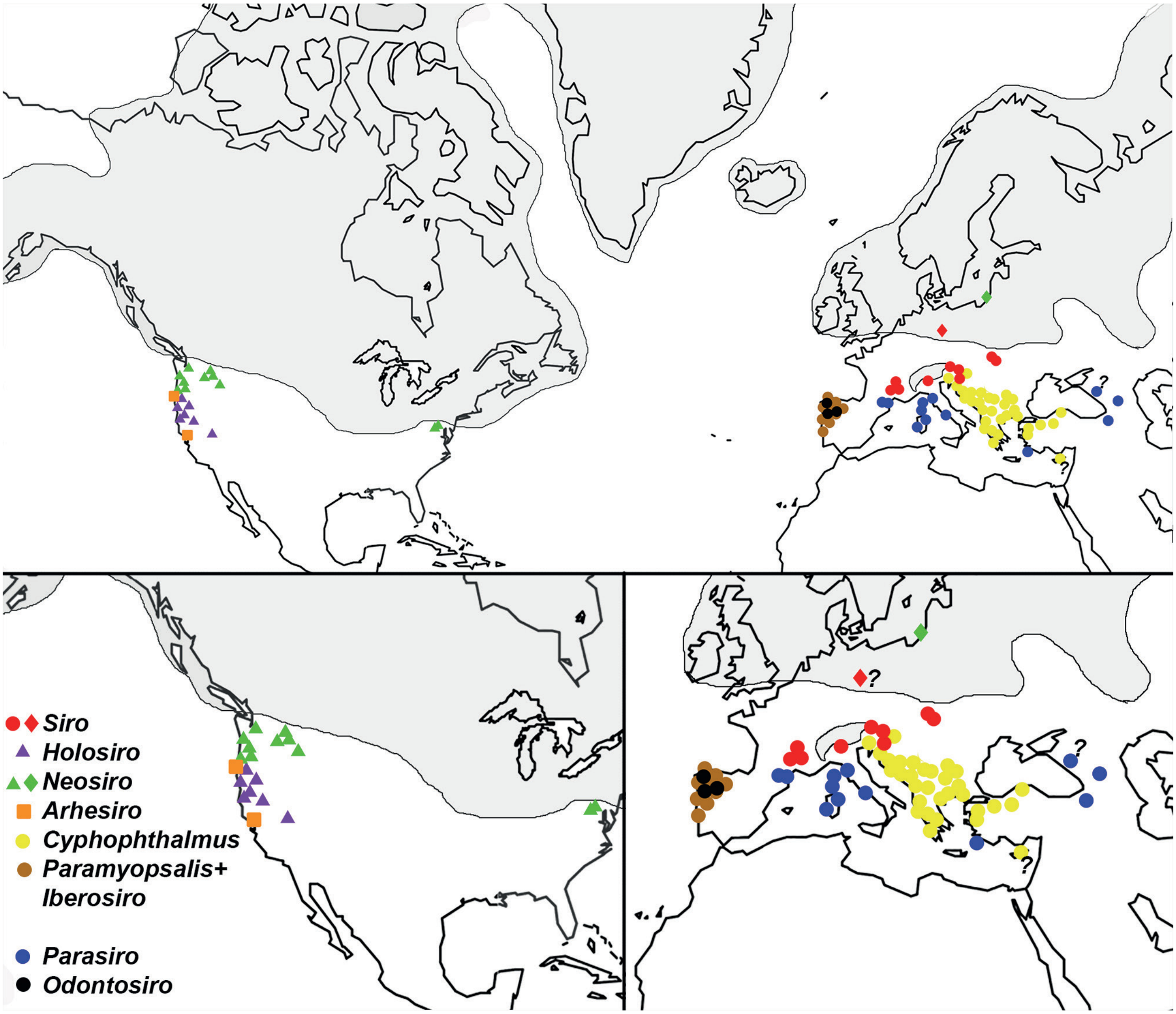

Fig. 20. Distribution of Sironidae genera + *Parasiro* and *Odontosiro*. Rhombus shape marks refer to fossil species; "?" - questionable affiliation to the genus. Shaded areas - approximate extent of the ice sheets during the glacial maximum in North America and Europe during Pleistocene.

ple nipple-like shape ending by two processes, as illustrated by Rafalski (1958) for *Siro carpaticus* and *Cyphophthalmus duricorius*. But this form is not very stable among congeners in Sironidae. In *S. rubens* there are two pairs of such papillae, each with one processus as illustrated by Juberthie (1967). In a specimen of *Siro crassus* from Austria I have dissected, sensory papillae are hypertrophied, irregular in shape. At this moment I could not conclude whether it is an aberration or a species characteristic.

At the type locality *N.* (*T.*) *martensi* sp. n. occurs sympatrically with *Neosiro* cf *ligiae*.

Genus *Arhesiro* gen. nov.

Diagnosis. Coxal lobes II medially meeting throughout their length; anterior margins almost straight, at right angle to the longitudinal body axis; lateral margins parallel with longitudinal body axis; abruptly narrowing at the last third of their length (Fig. 9F). Coxal lobes III short, medially meeting; protruded and inserted medially separating the posterior end of coxal lobes II. Males coxal lobes IV anterior margin medially protruded. Three anal gland pores. Spermatopositor structure is unknown. Chelicerae basal article with abruptly lowered dorsal surface ("dorsal crest"), similar as in genus *Parasiro*, but not so pronounced. In other sironids this terminal edge of dorsal cheliceral depression is gradual and less pronounced. This detail ("dorsal crest") is widely present across cyphophthalmid families and in most additionally emphasized by a transverse ridge (crest). It is actually the place of contact of the cheliceral dorsal surface

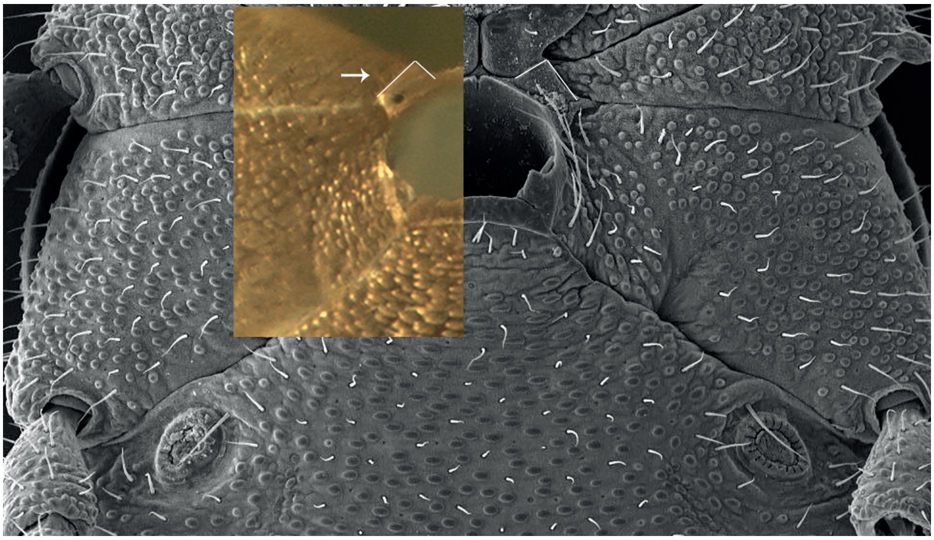

Fig. 21. Coxosternal region of *Neosiro exilis* (SEM) partially overlaid with a color photo of the same detail of the *Neosiro balticus* amber fossil specimen (Dunlop and Mitov 2011, Fig. 3, part).

with the frontal dorsum edge, providing manipulative abilities of the chelicera and greater compactness of that part of the body. Pedipalp tarsi longer than patella. Basitarsi of legs elongated, more than half of the telotarsi length. Sparsely ornamented anal carina surrounded with ornamented surface of anal plate. Anal carina covers 2/3 anal plate length. The distance between the outermost lateral openings of the anal glands is about 1/3 of the width of the anal plate.

Composition: *A. clousi* (Giribet & Shear 2010) comb. n. (type species); *A. sonoma* (Shear, 1980) comb. n. Both species are known from individual localities on Pacific Coast Range of North America (California Northern Coast Range and Central Oregon Coast Range).

The genus is clearly distinguished from the other North American genera and the genus *Siro* based on the shape of coxal lobes II, the profiles of which resemble those of genus *Cyphophthalmus*. From the latter it is clearly distinguished by shorter coxal lobes III and medially protruded anterior margin of coxal lobes III and males coxal lobes IV. Species of this genus are characterized by elongated basitarsi, characters they share with species of the genus *Parasiro*.

DISCUSSION

According to the current distribution of Sironidae (Fig. 20), we can conclude that the genera *Holosiro* and *Neosiro* have a common origin in the area of northern Laurasia. In the area of the then tropical belt, these two genera separated from the genus *Siro* even before the opening of the North Atlantic Ocean. However, the genus *Arhesiro* seems to have had a different history. Based on the known morphological characteristics it is not closely related to the other North American genera, *Holosiro* and *Neosiro*. Molecular analyses of *Arhesiro clousi* (Giribet et al 2017) are in line with this. The actual position and connection of the genus *Arhesiro* with the diversity center of the family Sironidae in the western part of Tethys realm suggests a different direction of the westward dispersal of this genus. It may have happened during the breakup of Pangea and the opening of the Atlantic Ocean. Also, this dispersal can be explained by Carnian pluvial episodes during Triassic and the existence of late Carboniferous rainforests that covered the equatorial region of Pangea, the slopes of the Central Pangean Mountains, and the present areas of Europe and North America. Traces of this immigration in the form of surviving relict species of the genus *Archesiro* in the space between may have been erased by CAMP (Central Atlantic Magmatic Province) eruptions also causing the Triassic–Jurassic (Tr-J) extinction event (Blackburn et. al. 2013). The CAMP eruptions must have left a significant mark on the present-day distribution of the family Sironidae because they covered a big part of the original family areal.

The great distance of *Archesiro* from the center of diversity of the family is caused not only by the opening and expansion of the Atlantic Ocean, but also by the clockwise rotation of North America, which took place almost continuously beginning at end of the Triassic.

The genera *Holosiro* and *Neosiro* separated in northern Laurasia most likely during the early Cretaceous by the opening of the Western Interior Basin. Diversification of *Holosiro* is connected with the central part of Laramidia and *Neosiro* with Northern Appalachia. The *Neosiro* range covered the northern parts of the American continent with the core towards the west, while in the southeast reaching the Appalachian Mountains (relatively recently, which is manifested by only one species present there - *N. exilis*) and in the east across Greenland to today's Baltic. Pleistocene glacial cycles eliminated most of the fauna of this genus. The fossil *Neosiro balticus* comb. n. marks the easternmost known point of the range of this genus. The relatedness of the two easternmost species of the genus, the extant *N. exilis* and fossil *N. balticus* is evident, although only a part of the body of the latter species is fossilized. Dunlop and Mitov (2011) pointed out the closeness of this fossil species to North American sironids, but without clear support for that claim. Coxal lobi III of *N. exilis* and *N. balticus* as well of all representatives of the genus *Neosiro* are widely separated. But in *N. exilis* and *N. balticus* they are almost of a right-angled triangle shape (Fig. 21). Frontal and lateral margins of their coxal lobi III form a right angle. Both margins in other known *Neosiro* species form more or less obtuse angle (Fig. 5 in Newel 1943; Figs 7D and 21C in Giribet and Shear 2010; Fig. 21H and 26H in Giribet et al. 2017).

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