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The phylogeny of the genus *Ischioscia* Verhoeff, 1928, with redescriptions of three species (Crustacea: Isopoda: Oniscidea)

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Abstract

The genus *Ischioscia* Verhoeff, 1928 is reviewed. 26 species are considered valid. A key for their identification is given, as well as a map showing the geographic distribution. The known range of the genus covers a large area from the central Amazon region to the mountains of Guatemala. The species of *Ischioscia* have a typical "philosciid" habitus ("runner" type); they can be distinguished from other Neotropical species with similar habitus by the following apomorphies: (1) male pereiopod 1 carpus enlarged to a plate-like extension, (2) scale field on male pereiopod 1 covering entire frontal side of the carpus, (3) male pereiopod 7 ischium with a ventral scale field, (4) dactylus in both sexes with a long inner claw. The groundpattern of *Ischioscia* is reconstructed, and an analysis of the phylogenetic relations within the genus is made on the basis of morphological data. The species are very similar to each other, most differences are found in the male structures of sexually dimorphic features. *Ischioscia sturmi* (Vandel, 1972), *I. amazonica* Lemos de Castro, 1955 and *I. bolivari* Vandel, 1968 are redescribed in detail.

Key words: Oniscidea, *Ischioscia*, phylogeny, taxonomy, South America

Introduction

The genus *Ischioscia* Verhoeff, 1928 is one of the most diverse genera of crinochete Oniscidea found in northern South America and the Central American land bridge. Our first knowledge is from Miers (1878) and Budde-Lund (1893) who described species in *Philoscia* Latreille, 1804 which were subsequently placed in the genus *Ischioscia*. Similarly, *I. variegata* (Dollfus, 1893) – the type species of *Ischioscia* by synonymy (Leistikow 2001d) with *I. lobifera* Verhoeff, 1928 – was first described as a member of *Philoscia*, but then transferred to *Ischioscia*. Budde-Lund (1908) apparently noticed differences between the European members of *Philoscia* and South American species which at that time were also classified in this genus. He established the subgenus *Hesca* for *P. nitida* Miers, 1878 and *P. debilis* Budde-Lund, 1893, but did not provide a description or diagnosis for the new subgenus. For this reason, *Hesca* was not used by subsequent authors, but van Name (1936) and Vandel (1952) listed it as a senior (!) synonym of *Ischioscia*. As explained in the "Taxonomic section" below, we consider *Hesca* Budde-Lund a nomen dubium, and *Ischioscia* Verhoeff as the valid genus name for the species treated here.

I. variegata was reported from several localities outside the area where it was first encountered, Venezuela. Richardson (1914) mentioned the species from Colombia, Arcangeli listed records from Costa Rica (1930) and the Lesser Antilles (1932). In the following decades, two new species were described: *I. mineri* (van Name, 1936) from Dominica, and *I. amazonica* Lemos de Castro, 1955 from the state of Amazonas. Furthermore, Vandel (1952) recorded new data on *I. variegata* from Venezuela.

Some samples from Ecuador were recognized by Vandel (1968) as belonging to a separate genus, *Proischioscia* Vandel, 1968, with the single species *P. andina* Vandel, 1968. That genus differs from *Ischioscia* in the following characters: linea frontalis present, no scale

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fields on male pereiopod 7 ischium. Schmalfuss (1980) in his revision of the genus *Ischioscia* found new species intermediate in their character sets between *Proischioscia* and *Ischioscia*. Moreover, he recognized that the characters presumably distinguishing *Proischioscia* mostly are plesiomorphies and could not be used for the definition of a genus. Thus, *Proischioscia* was thought to be a junior synonym of *Ischioscia*. A preliminary cladogram for the genus was presented.

New data on this interesting genus were supplied by Leistikow (1997; 1999b; 2000; 2001b, d) who described several new species from Costa Rica, Panama and Venezuela. Particularly, the new data made possible a reconstruction of the phylogenetic relationships within the genus.

The re-examination of several of Vandel's species of the genus *Ischioscia* (Vandel 1968, 1972) and some additional data on *Ischioscia* from Central America are presented in this study. Line drawings for the re-examined species are given, and a key to all known species of *Ischioscia* is presented.

Material and methods

The phylogeny of the genus is reconstructed by means of the Hennigian principles of phylogenetic systematics using parsimony and the outgroup comparison (cf. Hennig 1950). The morphological data were also evaluated using the computer program PAUP.

Outgroups for the phylogenetic analysis were *Deto echinata* Guérin, 1836, *Ligia baudiniana* Milne Edwards, 1840, *Philoscia muscorum* (Scopoli, 1763), *Prosekia rutilans* (Vandel, 1952), and *Androdeloscia ferrarai* Leistikow, 1999.

Data for *Ischioscia* species were taken from the original descriptions or redescriptions, as indicated below in the list of species (see Results, Taxonomic section).

The specimens redescribed in this paper where examined by means of a light microscope and a stereoscope. Line drawings were made with a camera lucida.

Acronyms: ICZN (International Code of Zoological Nomenclature), MNHN (Muséum National d'Histoire Naturelle, Paris), MNRJ (Museu Nacional, Rio de Janeiro), SMNS (Staatliches Museum für Naturkunde, Stuttgart).

Results

Reconstruction of the groundpattern of *Ischioscia*

The analysis below permits the formation of an hypothesis on the character set of the most recent common ancestor of all *Ischioscia* species:

Crinochete with philosciid habitus, i.e. tergites smooth and shining, pleon distinctly narrower than pereion, second antennae and pereiopods long and slender. This corresponds to the "runner-type" of Schmalfuss (1984). The coloration is uniformly brownish, with the exception of the pale muscle insertion spots. On the smooth tergites long sensilla are scattered, but no noduli laterales can be discerned. The cephalothorax has laterally protruding eyes and therefore shows a T-shape in frontal view (a synapomorphy with *Tropiscia* Vandel). Both linea frontalis and linea supra-antennalis are present.

First antenna 3-jointed, the distal article with some aesthetascs. Basal article on the frontal face with a shield-like extension of its distal margin, covering two thirds or more of the second article. The second antenna flagellum is 3-jointed. The apical cone is as long as or longer than the distal flagellar article.

Mandibles asymmetrical. The left mandible has a larger lacinia mobilis and two hairy setae on the hairy lobe, whereas the right mandible has a smaller lacinia mobilis and one hairy seta on the hairy lobe. One hairy seta between the hairy lobe and the pars molaris. The latter is represented by a tuft of several hairy setae (excact number cannot be identified). First maxilla inner endite bearing two penicils, and with a rounded distolateral corner. Lateral endite with outer group of 4 large, simple tooth setae, one smaller triangular lobe and one very slender seta, and inner group of 6 more setae, 4–5 of them apically cleft. In a subapical position on the caudal face, a pair of small setae is found. Second maxilla distally bilobate, with a field of sensilla on the medial lobe and 2 single sensilla between the medial and the lateral lobe. Maxilliped palp 3-jointed, the basal article with a large medial and a smaller lateral seta. Second article with a proximal tuft of setae and a distal tuft of more setae, located on a common socket. Distal article with a distal tuft of equal setae. Lateral margin of second article with one broad and one slender seta. Maxilliped endite bearing a subapical penicil.

Pereiopods long and slender, increasing in length from P1 to P7. In males the pereiopod carpus 1 is enlarged to a plate-like extension, and most of its frontal face is covered by a scale field. The male pereiopod 7 ischium bears a fringe of hair-like scales on its ventral side. Dactyli have a long inner claw, and the dactylar seta is long and apically fringed with setules.

Pleopod exopodites without lungs or distinct respiratory fields. The respiratory surface is presumably on the ventral face of the exopodites. The margin of exopodites 2–5 has a row of simple setae. Exopodites 1 (of males and females) have a smooth margin without setae. Exopodites 5 have a transverse stripe of several rows of pectinate scales. The male pleopod 1 endopodite is simply constriced towards the apex, and has a row of small setae along the spermatic furrow on the dorsal (caudal) side. The uropods are composed of a sympodite on which the smaller endopodite is inserted more proximally than the larger, lanceolate exopodite.

The pleotelson is roughly triangular.

The apomorphies for the taxon *Ischioscia* are [plesiomorphies in square brackets]:

- ■ Male carpus of pereiopod 1 enlarged to a plate-like extension [male carpus not extended, similar to the female]
- ■ Scale fields of male pereiopod 1 covering frontal side of the carpus [scale field only in distal half of carpus 1]
- ■ Male pereiopod 7 ischium with a ventral field of hair-like scales [no such field on the male pereiopod 7 ischium]
- ■ Dactylus with long inner claw [inner claw short].

Phylogeny within the genus *Ischioscia*

The phylogeny of the genus *Ischioscia* was dealt with in several contributions, most recently by Schmalfuss (1980), and Leistikow (1997, 1999b, 2000). The study of further species and the discovery of six new species from Venezuela (Leistikow 2001b) and one from Colombia (Leistikow 2001d) make a reconsideration of the earlier results advisable.

The phylogeny of the species of *Ischioscia* is one of the first to be resolved among all known genera of the philosciid facies. The autapomorphies of this taxon were given above. From this analysis, *I. andina, I. irmleri, I. longicauda, I. stenocarpa,* and *I. hanagarthi* were excluded because for these species not the entire set of morphological characters, as listed below, was known (Vandel 1968, Schmalfuss 1980). The cladogram for the genus is presented in Fig. 10.

The following listing presents the characters and character states used in the analysis, numbered in square brackets. Each number to the left of a dash specifies the character in consecutive order; numbers (0 or 1) to the right of a dash denote the character state as scored for the cladistic analysis. Autapomorphies are marked with the symbol "■" in the section "Clades and supporting characters".

Cephalothorax (Fig. 1):
[1-0] Cephalothorax without lateral extensions
[1-1] Cephalothorax with eyes laterally protruding
[2-0] Cephalothorax with both linea supra-antennalis and linea frontalis present
[2-1] Linea frontalis absent

The eyes of *Ischioscia* specimens are situated on lateral protrusions of the cephalothorax. The same situation is also found in *Tropiscia* and in Scleropactidae. It is also the case in at least some Armadillidae (not among the outgroups for the present cladistic analysis). In Oniscidea, there may be two distinct transverse ridges on the frontal face of the cephalothorax. The linea supra-antennalis is just above the insertions of the second antennae, and the linea frontalis is on the upper margin of the cephalothorax, directly below and between the eyes. In different taxa of the Oniscidea either both lines are present, or only one of them, or, less frequently, both are absent. The most parsimonious explanation is to assume that both lines belong to the groundpattern, and that reduction of one or the other occurred frequently. As a reductive trait, no a priori estimation of the homology can be made. However, a clear distinction between 'linea frontalis present' or 'linea frontalis absent' cannot always be made. There are also specimens which may described as having an 'indistinct linea frontalis', or a 'sharp frontal edge of the cephalothorax'.

Tergites: In the groundpattern of the Oniscidea the tergites were smooth, as can be deduced from the presence of smooth tergites in species of *Ligia* Fabricius, 1798, of Synocheta, and in numerous diverse taxa of the Crinocheta. Among the taxa of the present analysis, only *Deto* Guérin, 1836 does not have smooth tergites.

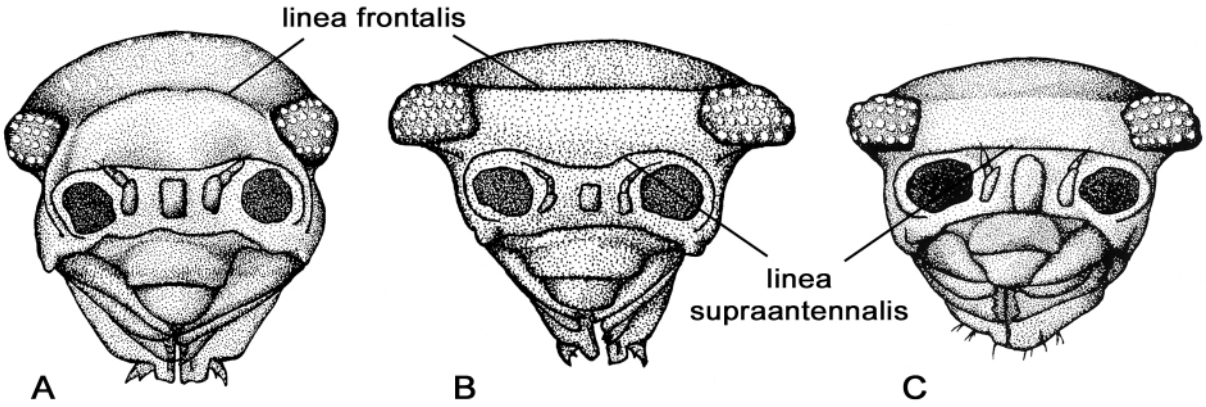


Fig. 1. Cephalothorax. A. *Prosekia rutilans*: no lateral extensions [1-0], with linea frontalis and linea supra-antennalis [2-0]; B. *Ischioscia amazonica*: with lateral extensions [1-1], with both lineae [2-0]; C. *Ischioscia cadoangelis*: with lateral extensions [1-1], with linea supra-antennalis only [2-1]. (A, C from Leistikow 2001b, 2000).

First antenna (Fig. 2):
[3-0] 'Normal'
[3-1] Basal article with a shield-like projection.

The shield-like projection of the basal article of the first antenna is found only in *Tropiscia* and *Ischioscia* among the taxa considered here. Leistikow (2001c) found this character to represent an apomorphy of the Ischiosciini, a taxon also including *Ecuadoroniscus* Vandel, 1968, *Oreades* Vandel, 1968, and *Mirtana* Leistikow, 1997.

Second antenna (Fig. 3):
[4-0] Flagellum with apical tuft or short cone with long lateral sensilla
[4-1] Flagellum with long cone and short lateral sensilla.

The derived condition is found in tropical Philosciidae and Scleropactidae. An apical tuft of sensilla is found in all Oniscidea not belonging to the Oniscoidea. (cf. Schmidt, in press). This character, as well as the preceding, is not informative for the phylogeny within the genus *Ischioscia*.

Pereiopod dactyli (Fig. 4):
[5-0] Inner claw short, less than half as long as outer claw
[5-1] Inner claw long, as long or nearly as long as outer claw
[6-0] Dactylar seta apically plumose
[6-1] Dactylar seta apically not plumose
[7-0] Dactylar seta plumose or simple
[7-1] Dactylar seta with a spatulate tip.

In the Oniscidea groundpattern, the dactylus has a long outer claw and a much shorter inner claw. Since Mesoniscidae, Synocheta and basal Crinocheta lack the inner claw, a reduction in the stem-lineage of the Orthogonopoda can be assumed. Within the Crinocheta, an inner claw of differing length evolved secondarily, probably from a modified seta (Schmidt, in prep.). Since the aim of the present study is the reconstruction of the phylogenetic relations between the species of *Ischioscia* only, the short inner claws of *Ligia* and of species of the Crinocheta are subsumed in the plesiomorphic character state [5-0].

In the case of the dactylar seta, three character states can be observed: simple, spatulate, and plumose. A plumose dactylar seta is clearly the plesiomorphic state, since this is present in many basal Crinocheta, Synocheta, Ligiidae, and also in marine isopods. The spatulate tip of some *Ischioscia* species therefore is a derived character. A spatulate seta somewhat similar to that of some *Ischioscia* species is also present in *Alloniscus*

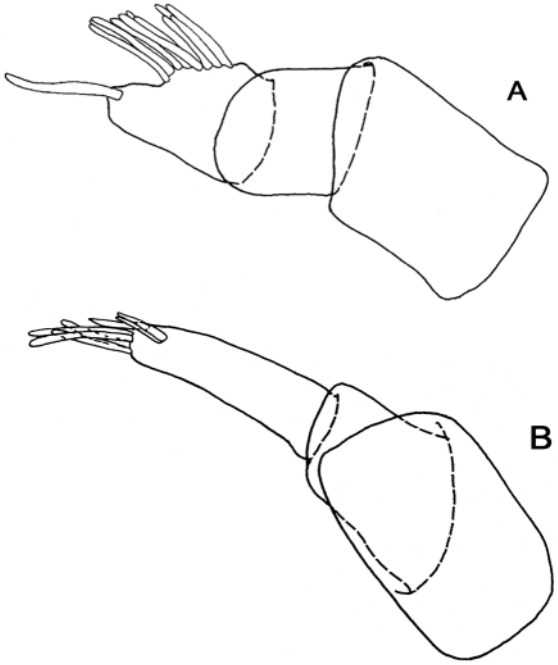


Fig. 2. First antenna, frontal. A. *Androdeloscia ferrarai*: proximal article simple [3-0]; B. *Ischioscia amazonica*: proximal article with shield-like projection [3-1] (A from Leistikow 1999a).

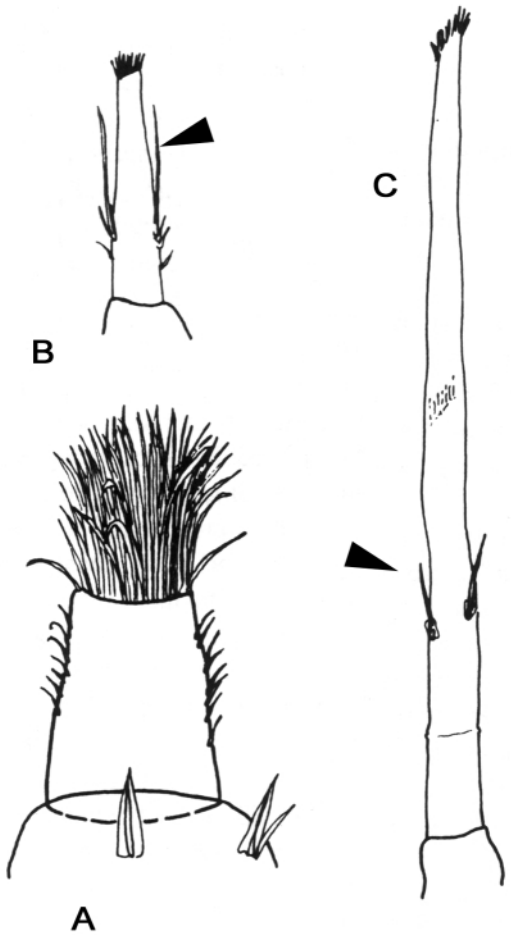


Fig. 3. Apical organ of second antennae. A. *Deto echinata*: tuft of sensilla [4-0]; B. *Philoscia muscorum*: short apical cone with long lateral sensilla [4-0]; C. *Ischioscia pariae*: long apical cone with short lateral sensilla [4-1]. (A, B, C from Leistikow 2001d, g, c).

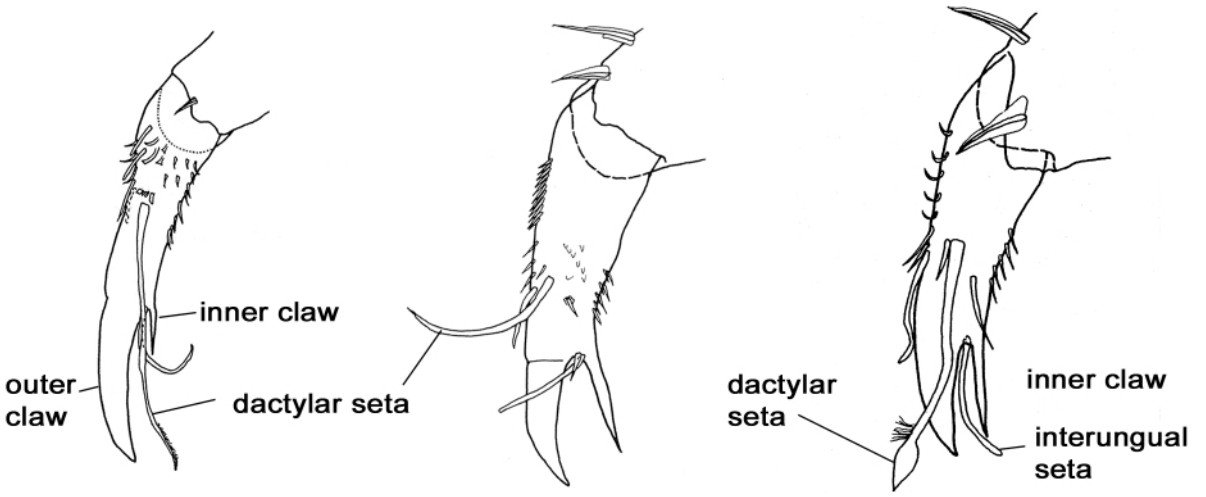
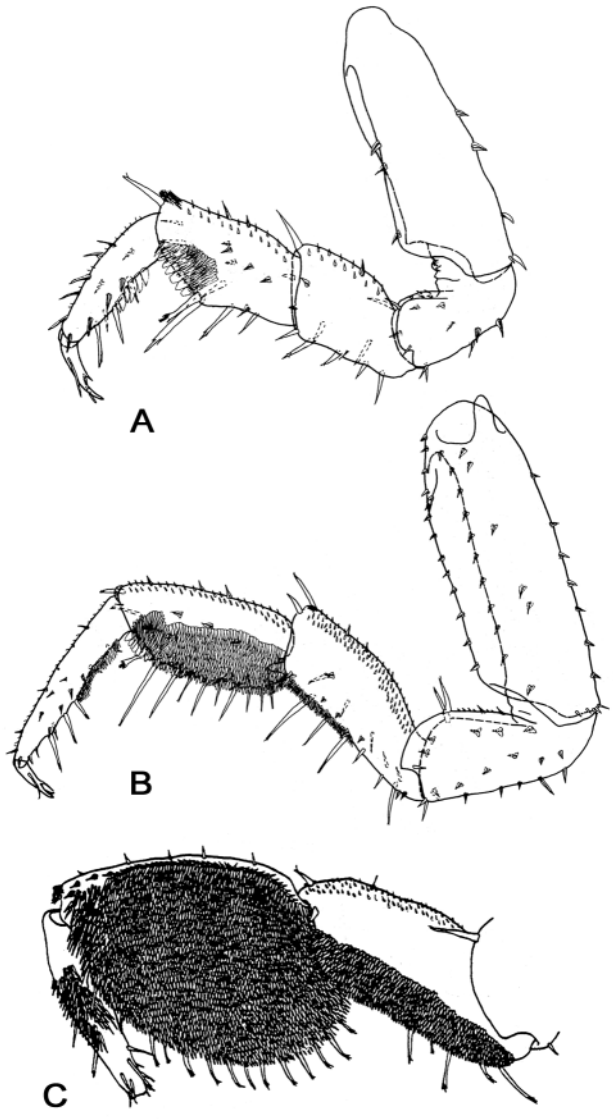


Fig. 4. Pereiopod dactylus in frontal view. A. *Prosekia rutilans*: with short inner claw and plumose dactylar seta [5-0, 6-0, 7-0]; B. *Ischioscia marmorata*: inner claw long [5-1], dactylar seta simple [6-1, 7-0]; C. *Ischioscia sturmi*: inner claw long [5-1], dactylar seta with spatulate tip and some subapical hairs [6-1, 7-1]. (A, B from Leistikow 2001b, 2000).



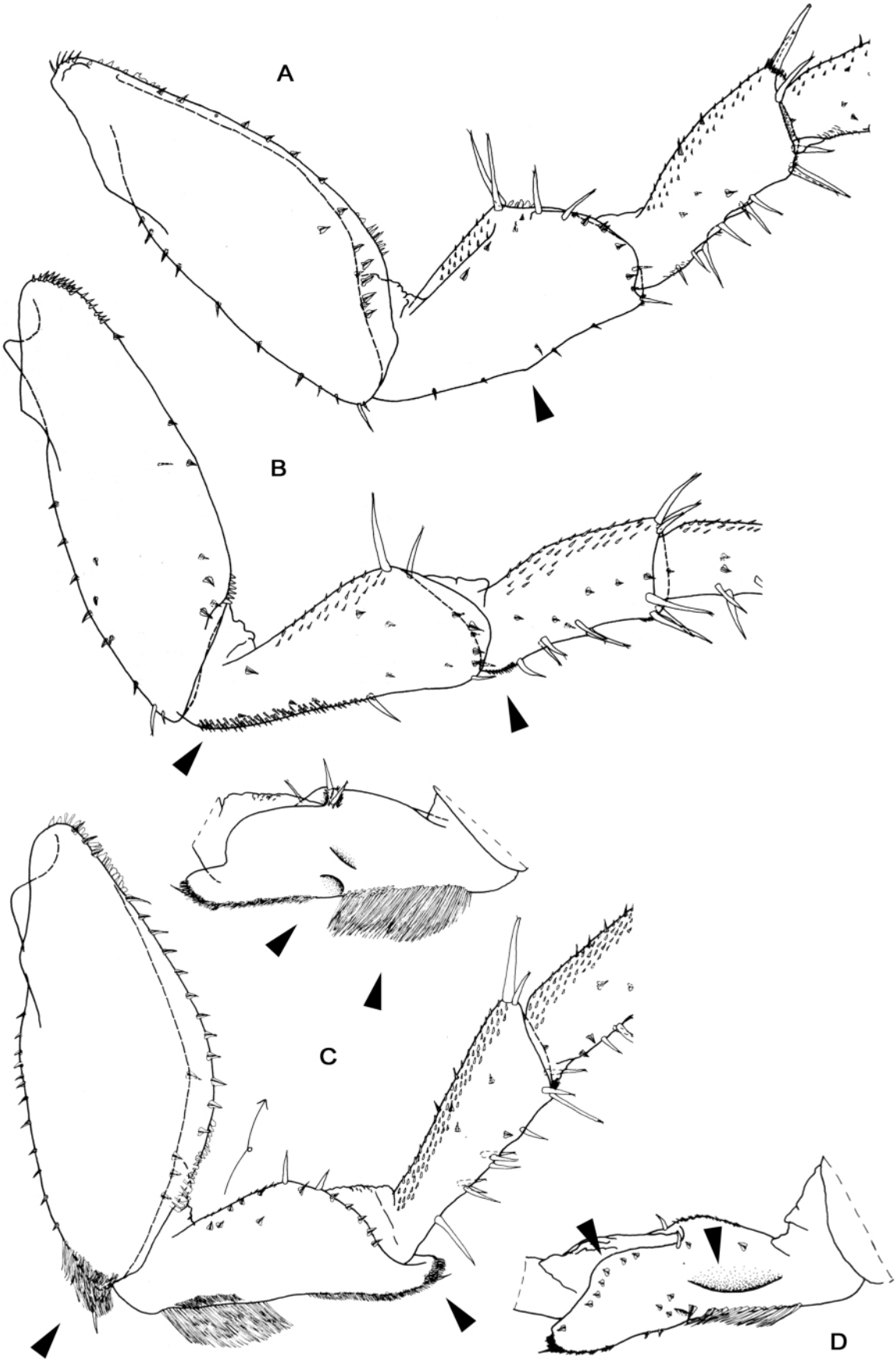
Dana, 1845 (Schmidt, in prep.), probably by convergence. An entirely simple dactylar seta is also derived, but since it is a reductive trait, we do not know whether the simple dactylar seta inside *Ischioscia* is derived from a dactylar seta with a spatulate tip or directly from the apically plumose seta. The phylogeny hypothesis for the (mainly Neotropical) genera of "Philosciidae" (Leistikow 2001b) gives the implication that the simplification of the dactylar seta occurred independently within *Ischioscia* and in the outgroup taxa. Therefore the simple seta of the outgroup taxa here is coded together with the plesiomorphic state, while the simple seta of *Ischioscia* species is coded together with the spatulate seta.

Male pereiopod 1 (Fig. 5):

[8-0] Carpus not extended, as in female
[8-1] Carpus extended
[9-0] Without sexual differentiation or scale field
[9-1] With scale fields on merus, carpus and propodus
[10-0] Carpus not or slightly extended
[10-1] Carpus enlarged to form a plate-like extension, width ≥ 0.4 length.

These structures have a function in mating behaviour. Scale fields improve the adhesion on the smooth tergites of females, and their surface is increased by enlargment of the carpus. In the plesiomorphic state there is no difference between male and female. Other taxa have the

Fig. 5. Male pereiopod 1. A. *Androdeloscia ferrarai*: with carpus not extended [8-0, 10-0], without scale fields in addition to the antenna-grooming brush [9-0]; B. *Ischioscia fasciifrons*: carpus slightly extended [8-1, 10-0], with scale field [9-1]; C. *Ischioscia variegata*: carpus strongly enlarged [10-1]. (A, B, C from Leistikow 1999a, 2001c, 1997).


A
B
C
D

number of ventral setae multiplied and thereby achieve the same function. Since this is the case in basal representatives (*Alloniscus; Oxalaniscus* Leistikow, 2000; *Quintanoscia* Leistikow, 2000) and in most of the 'higher' Crinocheta, as revealed by a previous study (Leistikow 2001b), brushes composed of numerous setae are considered as plesiomorphic with respect to scale fields. Enlargements of the carpus, covered with a scale field, were also described from species of "Philosciidae" outside the Neotropics, e.g. *Burmoniscus* (?) *rowei* Taiti & Manicastri, 1988, or *Halophiloscia couchi* (Kinahan, 1858; illustrations in Schmidt in press).

Male pereiopod 2:
[11-0] Carpus not enlarged
[11-1] Carpus enlarged, as in pereiopod 1
[12-0] Carpus without scale field
[12-1] Carpus with scale field.

The structures described above may be restricted to the first pereiopod, or may also affect the second and third pereiopod.

Male pereiopod 3:
[13-0] Carpus 3 without scale field
[13-1] Carpus 3 with scale fields as on carpus 1-2
[14-0] Carpus not enlarged
[14-1] Carpus enlarged, as in pereiopods 1-2.

If the pereiopod 1 has a scale field on the carpus, then pereiopod 2 also always shows this structure. On pereiopod 3, in contrast, the scale field may be present or absent. An unmodified pereiopod 3 is here tentatively regarded as plesiomorphic.

Male pereiopod 7 (Fig. 6):
[15-0] Basipodite without modification
[15-1] Basipodite with ventrodistal tuft of hairs
[16-0] Ischium without sexual differentiation concerning the cuticular scales
[16-1] Ischium with field of hair-like scales
[17-0] Ventral brush of ischium either absent or longer than half of the ischium
[17-1] Brush of hair-like scales confined to ≤0.5 of ischium length, preceded by a proximal part without scales
[18-0] Ischium without transverse furrow
[18-1] Ischium with medio-rostral transverse furrow
[19-0] Ischium without depression
[19-1] Ischium with depression on rostral surface
[20-0] Ischium without ventrodistal elongation
[20-1] Ischium with elongate ventrodistal process
[21-0] Fronto-distal margin of ischium straight
[21-1] Fronto-distal margin of ischium with a semicircular lobe
[22-0] Ventral margin of ischium straight
[22-1] Ventral margin of ischium with slight bump
[23-0] Merus with scattered sensory setae on the ventral margin
[23-1] Merus with a single row of prominent setae on the ventral margin
[24-0] Merus on ventro-proximal edge with simple (scale-like) scales
[24-1] Merus on ventro-proximal edge with hair-like scales.

The pereiopod 7 of Crinocheta (and also of Synocheta) frequently shows sexual dimorphism. Various protrusions, lobes, tubercles, concave depressions, scale fields, brushes etc. can be found in different species. These special structures are extremely diverse, and often similar shapes can be found in only distantly related taxa. On the other hand, even closely related species may have very different special structures, as illustrated

Fig. 6. Male pereiopod 7. A. *Tropiscia flagellata*: ventral margin with slight bump [22-1], otherwise not modified (from Leistikow 2001a); B. *Ischioscia zebricolor*: ischium with field of hair-like scales [16-1] longer than 0.5 ischium length [17-0], and merus on ventro-proximal edge with hair-like scales [24-1] (from Leistikow 1999b); C. *Ischioscia hirsuta*: basipodite with ventrodistal tuft of hairs [15-1], ischium with field of hair-like scales less than 0.5 ischium length [16-1, 17-1], medio-frontal furrow [18-1], and ventrodistal process [20-1]. D. *Ischioscia pariae*: ischium with semicircular lobe [21-1] and depression [19-1] on frontal surface. (C, D from Leistikow 2001c).

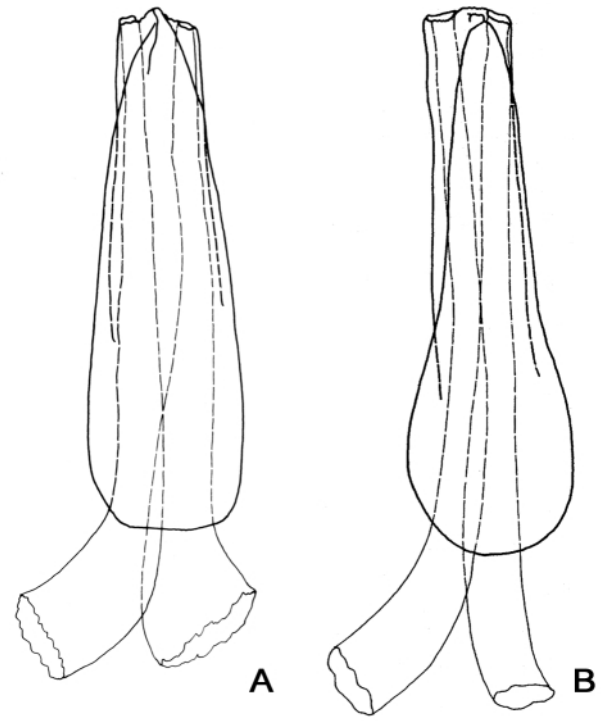


Fig. 7. Male genital papilla. A. *Ischioscia plurimaculata*: with convex, approximately parallel sides [25-0] (from Leistikow 2000); B. *Ischioscia amazonica*: with concave sides, 'pear-shaped' [25-1].

by the present study. Therefore they are regarded as not informative on a higher taxonomic level. Nevertheless, they may provide useful hints for the inference of phylogenetic relations among species, if the relatedness of these species is supported by other (more complex) characters.

Male genital papilla (Fig. 7):

[25-0] Ventral shield approximately parallel-sided or absent

[25-1] Ventral shield pear-shaped.

Only within the Crinocheta a ventral shield with strong cuticle is part of the genital papilla, but some

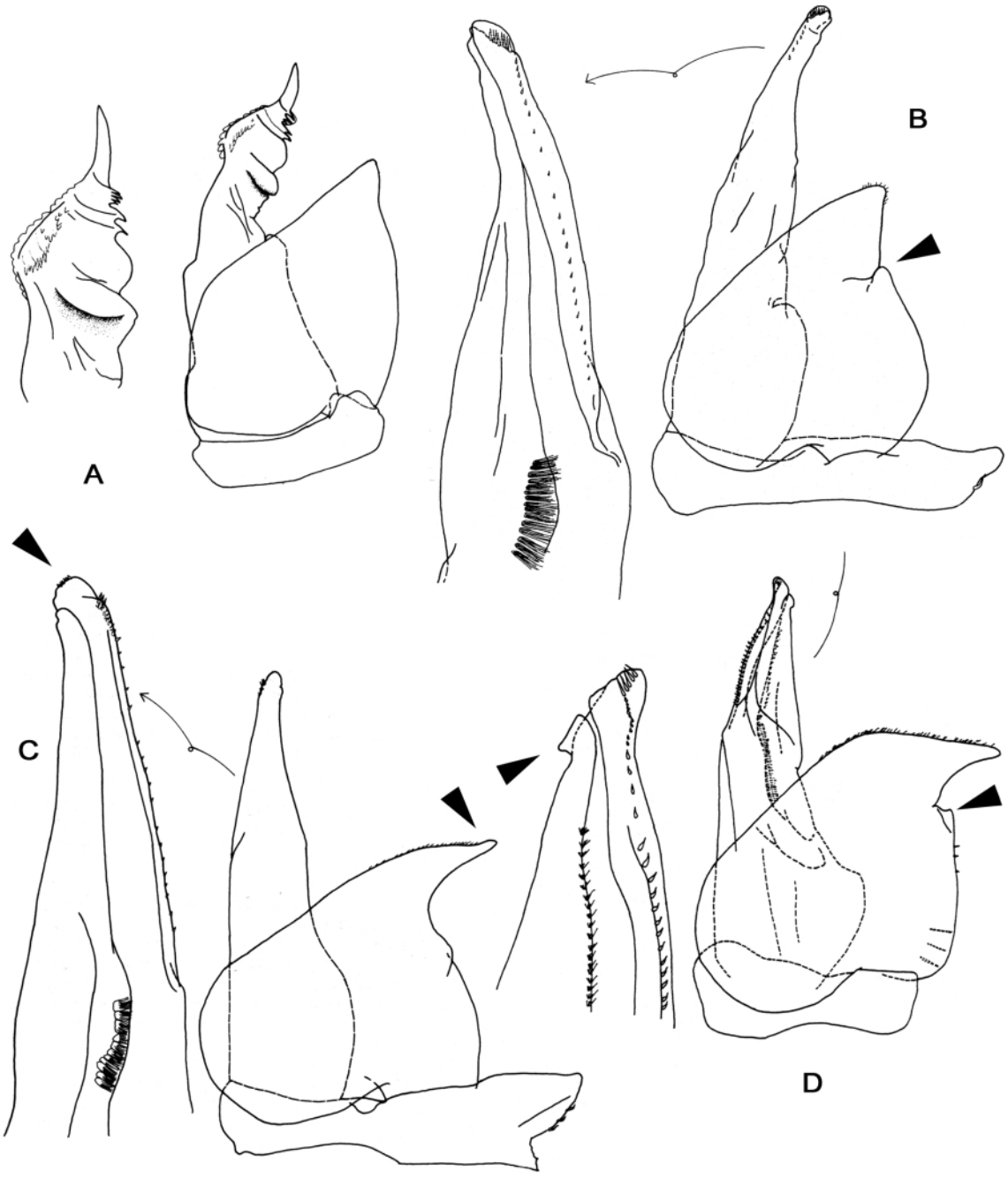


Fig. 8. Male pleopod 1. A. *Androdeloscia ferrarai*: exopodite with simple lateral margin [26-0, 28-0, 29-0], endopodite with complicated structure [30-0]; B. *Ischioscia amazonica*: exopodite with slight lateral incision [26-1, 27-0], distal end simply angulate [20-0]; C. *Ischioscia fasciifrons*: exopodite with slight lateral incision [26-1, 27-0], no lateral protrusion [28-0], distally drawn out to a laterally directed tip [29-1], endopodite with set of very small subapical terminal spines [31-1]; D. *Ischioscia martinae*: exopodite with deep lateral incision [26-1, 27-1], lateral subapical protrusion [28-1], distally drawn out to a laterally directed tip [29-1], endopodite with a subapical hook [30-1]. (A, C, D from Leistikow 1999a, 2001c, 1997).

basal representatives have a simple genital papilla without ventral shield. The situation present in the outgroup taxa, with 2 papillae in *Ligia*, a papilla without shield in *Deto*, and lanceolate shields are here all subsumed under the plesiomorphic character state [25-0], because these differences are not relevant for the phylogeny inside the genus *Ischioscia*.

Male pleopod 1 (Fig. 8):
[26-0] Exopodite 1 with simple lateral margin
[26-1] Exopodite 1 with an incision on the lateral margin
[27-0] Exopodite at most with a slight lateral incision
[27-1] Exopodite with a deep lateral incision
[28-0] Exopodite 1 without lateral protrusion
[28-1] Exopodite 1 with subapical lateral protrusion, proximal of an incision
[29-0] Exopodite 1 distally rounded or angulate
[29-1] Exopodite 1 distally drawn out into a laterally directed, slender tip
[30-0] Endopodite 1 simply constricted apically, or with complicated structure
[30-1] Endopodite 1 with a subapical hook or tubercle
[31-0] Endopodite apex without very small spines (or setae) that do not belong to the row of small sensory setae along the spermatic furrow.
[31-1] Apex of male pleopod 1 endopodite obtuse, with set of very small spines terminally, quite distinct from the medio-caudal row of spine-like setae.

The comparison with marine isopods reveals that feathery marginal setae represent the plesiomorphic condition. Within the Crinocheta, some basal species still have feathery marginal setae. Other Crinocheta have either simple marginal setae (Porcellionidae, Trachelipodidae, Oniscidae, Armadillidae, etc.) or the first exopodite lacks marginal setae completely (most tropical "Philosciidae", some Scleropactidae and Platyarthridae). The presence of small marginal setae in some species of *Ischioscia* may be interpreted as plesiomorphic; if *Ischioscia* is part of a monophylum in which the other members lack marginal setae (Leistikow 2001b), their presence in *Ischioscia* species may also be regarded as a 're'-appearance and thus as apomorphic.

Male pleopod 2 (Fig. 9):
[32-0] Endopodite without protrusion
[32-1] Endopodite with elongate protrusion.

Behavioural characters:
[33-0] Animals attempt to escape predators by fast running, no jumping ability
[33-1] In addition to the running, the animals are able to jump, like amphipods.

The jumping behaviour has been observed in *I. variegata* which jumps about 30 cm, and in *I. pariae* which jumps only about 5 cm, when disturbed. This behaviour seems to be part of the escape reaction. Species in which no jumping behaviour was observed by the authors of this paper are scored as "0". For other species, only preserved material could be studied. These were scored as "?" in the data matrix.

Colour pattern:
[34-0] Coloration uniformly brown, or with darker median stripe
[34-1] Coxal plate lighter than tergites.

The colour pattern has to be taken with caution, because (a) similar coloration in not closely related species is frequent in Oniscidea, (b) intraspecific variation oc-

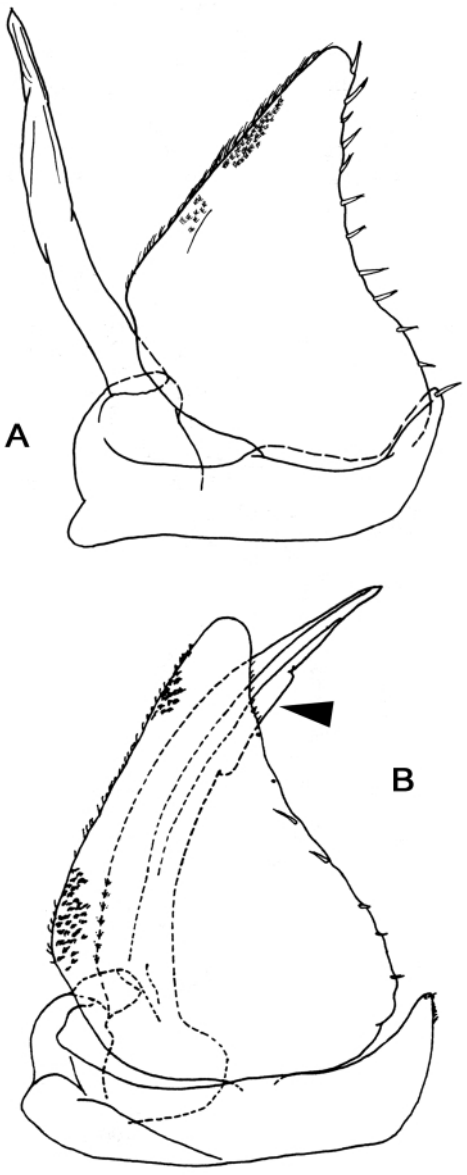


Fig. 9. Male pleopod 2. A. *Ischioscia trifasciata*: endopodite simple [32-0]; B. *Ischioscia martinae*: endopodite with elongate protrusion [32-1]. (A, B from Leistikow 2001c, 1997).

curs in some species, (c) coloration may be altered by preservation.

Clades and supporting characters

The morphological characters listed and discussed above were evaluated both by brain and using the computer program PAUP. For the latter procedure a data matrix was constructed (see Appendix). The matrix includes only informative characters. Autapomorphies of single species, as mentioned in their original descriptions, are not included. Characters 11–14 and 34 were given the weight 1, all remaining characters were given the weight 2. Characters 11–14 were given a lower weight because they represent only gradual changes of already present features. E.g., the appearance of scale fields on pereiopod 1 is thought to be a more complex character than the appearance of such scale fields on pereiopods 2 or 3, if they were already present on pereiopod 1. Character 34 (colour pattern) was downweighted because there seems to be much intraspecific variation at least in some species, and because the coloration is not known for a number of species described after preserved specimens that had bleached. All characters were assigned the character type "ordered".

With PAUP, a heuristic search found 5 shortest trees the consensus of which is presented below (see Fig. 10). The shortest trees had a length of 145 steps and a consistency index of 0.4345.

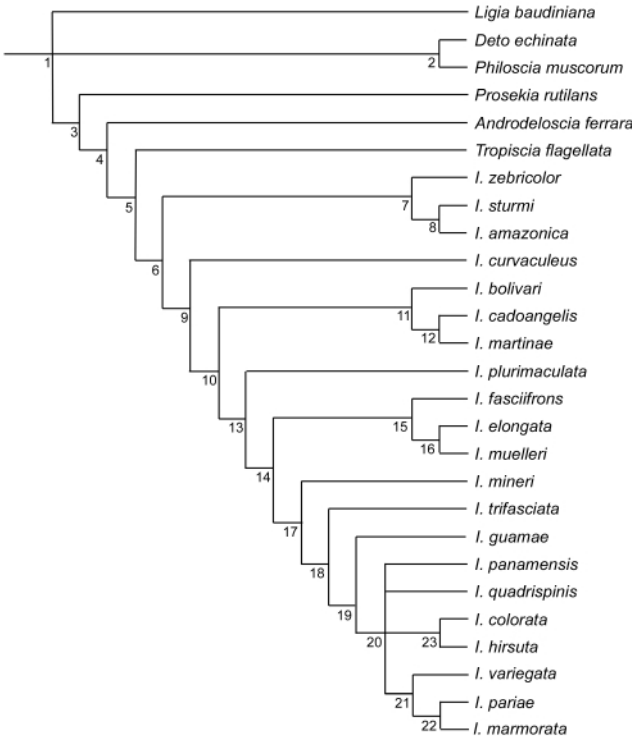


Fig. 10. Phylogenetic relations of the species of *Ischioscia*. Consensus diagram of 5 shortest trees derived from the data set with PAUP.

A bootstrap analysis with 100 replicates led to a less resolved tree. The clades 1-10, 16 and 23 were found by the bootstrap procedure. Thus, the monophyly of the genus *Ischioscia*, its sistergroup relation with *Tropiscia*, and its subdivision in the clades 7 and 9 are better supported than most other nodes. Also sister-species relations between *I. sturmi* and *I. amazonica* (clade 8), *I. hirsuta* and *I. colorata* (clade 23), and *I. muelleri* and *I. elongata* (clade 16) seem well supported.

In the following, the clades present in the consensus tree are discussed. The respective numbers of parallelisms and reversals refer to the whole cladogram (thus including the apomorphy behind which they are indicated).

Clade 1: A basal trifurcation. Since the analysis is aiming at the relations among the species of *Ischioscia*, no characters supporting the monophyly of the Crinocheta (all taxa except *Ligia*) were included in the data matrix.

Clade 2: *Deto echinata* and *Philoscia muscorum:*

■ [2-1] Linea frontalis absent (3 parallelisms, 1 reversal).

These species are united here on the basis of a reductive character. In fact, *Philoscia muscorum*, together with the remaining Crinocheta of this analysis, belongs to the clearly monophyletic taxon Oniscoidea, based on a number of apomorphic characters (Schmalfuss 1989, Schmidt in press) which, for the reason mentioned above, were not included in the data matrix. Therefore, this 'clade' does not require further attention.

Clade 3: *Prosekia, Androdeloscia, Tropiscia, Ischioscia*

■ [4-2] Second antenna flagellum with long apical cone, and a pair of short lateral sensilla on the cone.

These taxa, together with the Scleropactidae and several genera of "Philosciidae", were grouped in "Taxon C" by Leistikow (2001d), based on the same apomorphy.

Clade 4: *Androdeloscia, Tropiscia, Ischioscia*

■ [26-1] Male pleopod 1 exopodite with an incision on the lateral margin.

Leistikow (2001d) included *Androdeloscia* Leistikow, 1999 and *Prosekia* Leistikow, 2001 in the Prosekiini Leistikow, 2001, a monophylum supported by two apomorphies: (1) first antenna with a subapical tuft of aesthetascs which are not appressed to the article and divided from a distal pair of aesthetascs by a gap; (2) male pleopod 1 endopodite with hyaline lamella near apex. These characters were also not included in the data matrix, therefore the taxon Prosekiini could not be found. An incision on the lateral margin is a character that is widespread within the Crinocheta and probably is not useful for reconstructing the phylogeny of higher taxa.

Clade 5: *Tropiscia* and *Ischioscia*

- [1-1] Cephalothorax with eyes laterally protruding
- [3-1] First antenna with a shield-like projection of the basal article.

Both genera, together with *Oreades, Ecuadoroniscus* and *Mirtana*, form the Ischiosciini Leistikow, 2001. The shield-like projection of the basal article of the first antenna is present in all these forms and represents an apomorphy for the taxon. A second apomorphy of the Ischiosciini is a ventral semicircular pit of the pleotelson. The shape of the cephalothorax [1-1] is found in *Tropiscia* and *Ischioscia* and constitutes a synapomorphy of these two genera (Leistikow 2001a, d). Outside of the taxa included in the present analysis, laterally protruding parts of the cephalothorax bearing the eyes are also found in the conglobating "Scleropactidae" and Armadillidiidae. While the latter are phylogenetically more distant, the "Scleropactidae" probably have close relations with some "Philosciidae" (Leistikow 2001d, Schmidt in press). Unfortunately, there is no evidence for the monophyly of the Scleropactidae; only after a revision of the Scleropactidae, hypotheses on their phylogenetic relations with some Philosciidae can be based on sufficient data.

Clade 6: *Ischioscia*

- [5-1] Inner claw of pereiopod dactyli long
- [8-1] Male pereiopod 1 carpus extended (1 reversal)
- [9-1] Male pereiopod 1 merus, carpus and propodus with scale fields
- [12-1] Male pereiopod 2 carpus with scale field
- [16-1] Male pereiopod 7 ischium with field of hair-like scales (3 reversals)
- [27-1] Male pleopod 1 exopodite with a deep lateral incision (1 parallelism, 1 reversal).

The monophyly of *Ischioscia* is clearly supported. Five of the six apomorphies concern the sexually dimorphic characters of the males. The inner claw present in the Oniscidea groundpattern is supposed to have been reduced and later, within the Crinocheta, to have been replaced by a specialized seta. This seta in the more primitive forms is short, whereas in most Oniscoidea it is nearly as long as the outer claw (Schmidt in press). Probably an elongation of the inner claw took place several times. In Oniscidea, specialization of the anterior pereiopods of the males is frequently found. The carpus may be extended, and the anterior face can be covered by a field of scales. Such a field of scales improves the adhesion on the smooth tergites of the females. Besides *Ischioscia*, similar extensions and scale fields are also found, e.g., in *Halophiloscia* Verhoeff, 1908 and Scleropactidae. Thus, parallelism does not occur within the present data set, but it must be assumed when the Oniscidea or the Crinocheta are regarded. The scale field on the ischium is a weak character as it was lost four times even in the species considered for the present analysis, but a similar scale field is also found in numerous Scleropactidae. A deep incision on the lateral margin of the male pleopod 1 exopodite evolved convergently in *Philoscia*, which is only distantly related with *Ischioscia* (Leistikow 2001d), and some other taxa. In the present case, a deep incision has disappeared in *I. sturmi*. However, it can be admitted that a change between a weak and a deep incision on the margin of a pleopod exopodite is a character of low complexity. In the case of prominent scale fields it should be kept in mind that all legs are covered with scales, and that a scale field becomes obvious if scales in a certain area are elongate and not appressed to the cuticle.

Schmalfuss (1980) found four apomorphies for the genus *Ischioscia*. Of these, the enlargement of the carpus on male pereiopods 1-2 and the scale fields on merus, carpus and propodus of pereiopods 1-3 of the males, and the lateral incision on the male pleopod 1 exopodite were approximately found in the present study. In contrast to Schmalfuss, our hypothesis requires the assumption that only the carpus 1 was enlarged, and that merus, carpus and propodus of pereiopod 1 only have scale fields. However, this difference is a small one. The lateral extension of the cephalothorax in the present study is regarded as a synapomorphy of *Ischioscia* and *Tropiscia*. Since Schmalfuss did not include *Tropiscia* in his considerations, he regarded that character as an apomorphy of *Ischioscia* alone.

Clade 7: *I. zebricolor, I. sturmi, I amazonica*

- [6-1] Dactylar seta apically not plumose (3 parallelisms)
- [7-1] Dactylar seta with a spatulate tip (3 parallelisms)
- [24-1] Male pereiopod 7 merus at the ventroproximal edge with hair-like scales
- [25-1] Male genital papilla pear-shaped.

In Crinocheta, the dactylar seta was originally bifurcate and plumose. In the Oniscoidea it is simple but still plumose. Among the taxa included in the present analysis, the hairy dactylar seta changed to a simple seta in *Androdeloscia*, clade 22, and in the present taxon. But a simple dactylar seta is present on most Oniscoidea and the reduction may have occurred even more often. A spatulate tip of the same seta is something more exceptional. According to the results of the present analysis, a spatulate tip evolved three times convergently: in the more distantly related *Philoscia*, in *I. pariae* and in the present taxon. Among the taxa not considered here, a spatulate tip is also found in *Alloniscus* (Schmidt in press). The other two characters are unique among the taxa studied. However, a more or less pear-shaped ventral shield of the genital papilla is also found in numerous taxa of the Oniscidea.

In contrast to the sister group (clade 9), a distinct linea frontalis is present.

Clade 8: *I. sturmi* and *I. amazonica*
- 11-1] Carpus of male pereiopod 2 enlarged (3 parallelisms)
- [14-1] Carpus of male pereiopod 3 enlarged (3 parallelisms)
- [23-1] Merus of male pereiopod 7 with a single row of large setae on the ventral face.

The sistergroup relation of *I. sturmi* and *I amazonica* is supported by three apomorphies. If the carpus of male pereiopod 1 is enlarged and provided with a large scale field, then it is imagineable that this specialization can be easily expressed also on the following legs. Therefore, characters 11 and 14 were downweighted before the analysis. The single row of large setae on the ventral face of merus 7, instead of an arrangement in two or three rows of setae, is unique at least among the taxa included in the present analysis.

Clade 9: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis*, *guamae*, *trifasciata*, *mineri*, *fasciifrons*, *elongata*, *muelleri*, *plurimaculata*, *martinae*, *cadoangelis*, *bolivari*, *curvaculeus*
- [2-1] Linea frontalis absent (3 parallelisms, 1 reversal)
- [29-1] Male pleopod 1 exopodite distally projected into a laterally directed, slender tip
- [30-1] Male pleopod 1 endopodite with subapical hook or tubercle.

As mentioned above, the linea frontalis was lost many times within the Oniscidea. However, on a smaller scale it can be used for phylogeny reconstruction. The same is true for the shape of the male pleopod 1 exopodite. A laterally directed, slender tip is also found, e.g., in *Trachelipus* Budde-Lund (Schmidt 1997) and *Benthana* Budde-Lund (Lemos de Castro 1958). The subapical tubercle is unique to *Ischioscia*. In other taxa, some subapical hooks or tubercles are also present, but these have a different shape. However, in *I. fasciifrons* no distinct subapical differentiation was found. Given the present cladogram, this must be regarded as a secondary simplification.

Clade 10: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis*, *guamae*, *trifasciata*, *mineri*, *fasciifrons*, *elongata*, *muelleri*, *plurimaculata*, *martinae*, *cadoangelis*, *bolivari*
- [10-1] Male pereiopod 1 carpus enlarged to form a plate, width ≥ 0.4 length (1 parallelism, 1 reversal)
- [17-1] Male pereiopod 7: ventral brush of hair-like scales confined to ≤ 0.5 of ischium length, preceded by a proximal part without such scales (2 reversals).

This clade is also supported by weak characters only. The extreme enlargement of the male pereiopod 1 carpus has evolved convergently in *I. sturmi* and the present clade. Within the latter, the carpus is secondarily less extended only in *I. bolivari*. When compared with the plesiomorphic state, a less extended carpus which nevertheless has a well-developed scale field, it is obvious that this character is not of high complexity. The same can be said about the second putative apomorphy, which has undergone two reversals: in *I. marmorata* and clade 15.

Clade 11: *I. martinae, cadoangelis, bolivari*
- [28-1] Male pleopod 1 exopodite with a lateral protrusion proximal of the incision (3 parallelisms)
- [32-1] Male pleopod 2 endopodite with elongate protrusion (3 parallelisms, 1 reversal).

The lateral subapical protrusion on the male pleopod 2 exopodite evolved two times convergently according to the present analysis. The other case is in clade 19. An elongate protrusion on the endopodite 2 evolved convergently in clade 20, in *I. pariae* and the present clade, and was reduced in *I. hirsuta*.

Clade 12: *I. martinae* and *I. cadoangelis*
- [11-1] Male pereiopod 2 carpus enlarged (3 parallelisms)
- [19-1] Ischium with depression on the frontal surface (4 parallelisms).

The male pereiopod 2 carpus is enlarged, in addition to carpus 1, in clades 14 and 8 and the present one. A large concavity on the frontal face of the ischium 7 evolved three more times in parallel: in *I. amazonica*, clade 20, and clade 16. The assumption of multiple evolution of this concavity poses the question, whether a single evolution and subsequent reduction might be a more plausible explanation. On the base of the cladogram, the assumption of an eleven-fold reduction would be required.

Clade 13: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis*, *guamae*, *trifasciata*, *mineri*, *fasciifrons*, *elongata*, *muelleri*, *plurimaculata*
- [14-1] Male pereiopod carpus 3 enlarged, as carpi 1 and 2 (3 parallelisms).

This clade is especially weakly supported, by only one character. Why this character has a low complexity is explained above. The other cases are clade 8 and *I. martinae*.

Clade 14: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis*, *guamae*, *trifasciata*, *mineri*, *fasciifrons*, *elongata*, *muelleri*
- [11-1] Male pereiopod 2 carpus enlarged (3 parallelisms)
- [31-1] Apex of male pleopod 1 endopodite with very small spines different from the row of setae along the spermatic furrow (3 parallelisms, 1 reversal).

For [11-1] see above. For the additional small spines at the tip of the pleopod 1 endopodite it is assumed that

they evolved in *I. zebricolor, I. trifasciata* and in the present clade, and were lost within the latter.

Clade 15: *I. fasciifrons*, *elongata*, *muelleri*
- [16-0] Male pereiopod 7 without sexual differentiation concerning the cuticular scales (3 parallelisms)
- [17-0] Male pereiopod 7: ventral brush either absent or longer than half of the ischium.

The brush of hair-like scales on the ventral face of the male P7 ischium putatively belonged to the groundpattern of *Ischioscia*. The present analysis found 3 convergent reductions of this brush, in *I. sturmi, I. marmorata,* and clade 15. The following character in the plesiomorphic state includes complete absence of a ventral brush or a brush that is longer than half of the ischium. In the three species the brush is entirely absent, thus in this case character [17-0] in fact is not different from [16-0].

Clade 16: *I. elongata* and *I. muelleri*
- [15-1] Male pereiopod 7 basipodite with ventrodistal tuft of hair-like scales (3 parallelisms)
- [19-1] Ischium 7 with depression on the frontal surface (4 parallelisms)
- [28-1] Exopodite 1 with subapical lateral protrusion, proximal of an incision (3 parallelisms).

A tuft of hair-like scales is also present in *I. amazonica* and clade 23.

The depression on ischium 7 evolved convergently in *I. amazonica*, clade 20, and clade 12.

The lateral subapical protrusion on the male pleopod 2 exopodite evolved three times convergently according to the present analysis. The other cases are clades 11 and 19.

Clade 17: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis*, *guamae*, *trifasciata, mineri*
- [13-1] Male pereiopod 3 carpus with scale field as on carpi 1-2 (1 reversal)
- [20-1] Male pereiopod 7 ischium with ventrodistal elongation
- [34-1] Coxal plates lighter than middle of tergites.

On carpus 3 there is a scale field as on carpi 1-2. Only in *I. guamae* this is not the case. The absence of a scale field on carpus 3 of *I. guamae* is explained by reduction. The ventrodistal process on ischium 7 is unique to the species grouped here. Outside of the taxa in the present analysis, a somewhat similar process is found in *Amazoniscus* Lemos de Castro, 1967 (Scleropactidae). Regarding the coloration a reversal is assumed for *I. marmorata*. Character 34 is a weak one, because a colour pattern with dark tergites and brighter coxal plates is found in numerous taxa of the Crinocheta and is by no means exclusive to clade 17. Moreover, in three species the coloration is unknown because only preserved material with faded colour was available for examination.

Clade 18: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis*, *guamae, trifasciata*
- [21-1] Fronto-distal margin of male P7 ischium with a semicircular lobe (1 reversal).

A loss of this lobe is assumed for *I. marmorata*.

Clade 19: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis, guamae*
- [28-1] Exopodite 1 with subapical lateral protrusion proximal of an incision (3 parallelisms).

The lateral subapical protrusion on the male pleopod 2 exopodite evolved three times convergently according to the present analysis. The other cases are clades 11 and 16.

Clade 20: *I. variegata*, *marmorata*, *pariae*, *hirsuta*, *colorata*, *quadrispinis*, *panamensis*
- [19-1] Ischium 7 with depression on the frontal surface (4 parallelisms)
- [32-1] Male pleopod 2 endopodite with elongate protrusion (3 parallelisms, 1 reversal).

The depression on ischium 7 evolved convergently in *I. amazonica*, and clades 16 and 12. An elongate protrusion on the endopodite 2 evolved convergently in clade 11, in *I. pariae* and in the present clade. The weakly supported node is a trifurcation.

Clade 21: *I. variegata*, *marmorata*, *pariae*,
- [31-0] Male pleopod 1 endopodite lacking apical small spines (reversal)
- [33-1] Escape behaviour includes jumping.

The apical small spines, probably an apomorphy of clade 14, are assumed to be reduced in these three species. In *I. variegata*, in addition the row of small setae along the spermatic furrow is vestigial.

The behavioral character is interesting. Jumping behaviour among Oniscidea is extremely rare. Within *Ischioscia* it probably occurs only in some species. It is documented only for *I. variegata* and *I. pariae*. In other species it has not been observed, but due to the scarcity of observations we cannot be sure that those species really lack jumping ability.

Clade 22: *I. marmorata* and *I. pariae*
- [6-1] Dactylar seta apically not plumose (3 parallelisms)
- [18-1] Male P7 ischium with medio-frontal transverse furrow (4 parallelisms).

The plumosity of the dactylar seta was also lost in *Androdeloscia*, clade 22, and clade 7. A transverse furrow on the P7 ischium evolved convergently in *I. fasciifrons*, *I. plurimaculata*, and clade 23.

Clade 23: *I. hirsuta* and *I. colorata*

- [15-1] Male pereiopod 7 basipodite with ventrodistal tuft of hair-like scales (3 parallelisms)
- [18-1] Male P7 ischium with medio-frontal transverse furrow (4 parallelisms).

A transverse furrow on the P7 ischium evolved convergently in *I. fasciifrons*, *I. plurimaculata*, and clade 22. A tuft of hair-like scales is also present in *I. amazonica* and clade 16.

Ischioscia zebricolor:

- [8-0] Male pereiopod 1 carpus not extended, as in female (reversal)
- [31-1] Apex of male pleopod 1 endopodite with very small spines different from the row of setae along the spermatic furrow (3 parallelisms, 1 reversal)

The extended carpus 1 of the males evolved in clade 6. The close relations of *I. zebricolor, I. sturmi* and *I. amazonica* (clade 7) require the assumption of a reversal to an undifferentiated carpus 1.

For the additional small spines at the tip of the pleopod 1 endopodite it is assumed that they evolved convergently in *I. zebricolor*, *I. trifasciata* and in clade 14, and were lost within the latter.

Ischioscia sturmi:

- [10-1] Male pereiopod 1 carpus enlarged to form a plate, width ≥ 0.4 length (1 parallelism, 1 reversal)
- [16-0] Male pereiopod 7 without sexual differentiation concerning the cuticular scales (3 parallelisms)
- [27-0] Male pleopod 1 exopodite with a deep lateral incision (reversal).

The extreme enlargement of the male pereiopod 1 carpus has evolved convergently in *I. sturmi* and clade 10. Within the latter, the carpus is secondarily less extended only in *I. bolivari*.

The brush of hair-like scales on the ventral face of the male P7 ischium putatively belonged to the groundpattern of *Ischioscia*. The present analysis found three convergent reductions of this brush, in *I. sturmi, I. marmorata*, and clade 15. The lack of a deep lateral incision on pleopod 1 expododite is a reversal of a groundpattern character of *Ischioscia*.

Ischioscia amazonica:

- [15-1] Male pereiopod 7 basipodite with ventrodistal tuft of hair-like scales (3 parallelisms)
- [19-1] Ischium 7 with depression on the frontal surface (4 parallelisms).

A tuft of hair-like scales is also present in clades 16 and 23.

The depression on ischium 7 evolved convergently in clades 16, 12 and 20.

Ischioscia marmorata: ([16-0] Male pereiopod 7 ischium without sexual differentiation concerning the cuticular scales (3 parallelisms)

- [17-0] Ventral brush of male P7 ischium either absent or longer than 0.5 of ischium length (reversal)
- [21-0] Fronto-distal margin of male P7 ischium straight (reversal)
- [34-0] Coloration uniformly brown, with pale muscle insertion spots (reversal).

The brush of hair-like scales on the ventral face of the male P7 ischium putatively belonged to the groundpattern of *Ischioscia*. The present analysis found three convergent reductions of this brush: in *I. sturmi, I. marmorata*, and clade 15. The following character in the plesiomorphic state includes complete absence of a ventral brush or a brush that is longer than half of the ischium. In the three species the brush is entirely absent, so in this case character [17-0] in fact is not different from [16-0]. A semicircular lobe on the fronto-distal margin of male P7 ischium evolved in clade 18, a loss of this lobe is assumed only for *I. marmorata*. A colour pattern with lighter coxal plates evolved in clade 17 and is assumed to have been lost in the present species. Moreover, a similar colour pattern is found in many species of Crinocheta. The coloration is unknown for several species included in the present analysis.

Ischioscia pariae:

- [7-1] Dactylar seta with a spatulate tip (3 parallelisms)
- [32-1] Male pleopod 2 endopodite with elongate protrusion (3 parallelisms, 1 reversal).

According to the results of the present analysis, a spatulate tip evolved three times convergently, in the more distantly related *Philoscia*, in *I. pariae*, and in clade 7.

Ischioscia hirsuta:

- [32-0] Male pleopod 2 endopodite without protrusion (reversal).

Ischioscia panamensis:

- [2-0] Cephalothorax with linea frontalis and linea supra-antennalis.

This is a reappearance of the linea frontalis, that was reduced in clade 9 which contains the majority of the species of *Ischioscia*. The linea frontalis was lost in many different taxa of the Crinocheta. Probably the impression of a 'reappearance' of the linea frontalis is given by a secondarily sharpened frontal edge of the cephalothorax.

Ischioscia guamae:

- [13-0] Male P3 carpus without scale field (reversal).

A reduction of the scale field that is a putative apomorphy of clade 17. As explained, the appearance of a scale field on the P3 carpus in addition to similar scale fields on the P1 and P2 carpi is a weak character, and also a secondary loss may easily occur.

Ischioscia trifasciata:

■ [31-0] Male pleopod 1 endopodite with row of small setae along the spermatic furrow, but no additional apcial spines (reversal).

This is a reversal of a character that evolved three times convergently.

Ischioscia fasciifrons:

■ [18-1] Male P7 ischium with medio-frontal transverse furrow (4 parallelisms)

■ [30-0] Male pleopod 1 endopodite simply constriced apically, without subapical hook (reversal).

A transverse furrow on the P7 ischium evolved convergently in *I. fasciifrons*, *I. plurimaculata*, clade 22, and clade 23. The subapical, lateral hook or tubercle on the male pleopod 1 endopodite, that is characteristic for clade 9, is assumed to have been lost in *I. fasciifrons*.

Ischioscia elongata:

■ 16-0] Male pereiopod 7 without sexual differentiation concerning the cuticular scales (3 parallelisms).

This is a mistake, because the reduction of the ventral brush on the male P7 ischium is also counted as a putative apomorphy of clade 15 which includes *I. fasciifrons*, *I. muelleri* and *I. elongata*. The same character cannot support a clade and one of its subordinate taxa.

Ischioscia plurimaculata:

■ [18-1] Male P7 ischium with medio-frontal transverse furrow (4 parallelisms).

A transverse furrow on the P7 ischium evolved convergently in *I. fasciifrons*, *I. plurimaculata*, and in clades 22 and 23.

Ischioscia martinae:

■ [14-1] Carpus of male pereiopod 3 enlarged (3 parallelisms).

The carpus of the male P3 is also enlarged in clades 8 and 13.

Ischioscia cadoangelis:

■ [22-1] Ventral margin of male P7 ischium with a slight bump (3 parallelisms).

In most species the ventral margin of the male P7 ischium is straight or concave. A slight bump is found also in *Tropiscia flagellata* Vandel, 1968 and *Prosekia rutilans*.

Ischioscia bolivari:

■ [10-0] Male pereiopod 1 carpus not or slightly extended (reversal).

This clade is also supported by the reduction of the extreme enlargement of the male pereiopod 1 carpus, that has evolved convergently in *I. sturmi* and clade 10. Within the latter, the carpus is secondarily less extended only in *I. bolivari*.

Affinities of the remaining species

Some species were not included in the cladistic analysis, because no sufficient data were available for them.

Ischioscia hanagarthi: This species has the carpi of male pereiopods 1-3 enlarged, and the pereiopod 7 ischium is ventrodistally elongated and has a semicircular lobe on the frontodistal margin. Therefore it could be included in clade 17, from which it differs by the plesiomorphic long ventral brush of the ischium 7 and the presence of a linea frontalis.

Ischioscia longicauda* and *I. irmleri: The long ventral brush of the male ischium 7 is thought to be plesiomorphic with respect to the restricted ventral brush as present in clade 10. The male pleopod 1 exopodite is apically acute, but not a slender tip as in clade 9. These characters and the plesiomorphic presence of a linea frontalis suggest that theses species branched off before clade 9.

Ischioscia stenocarpa: This species also has a linea frontalis (plesiomorphic). The absence of a ventral brush on ischium 7 may be plesiomorphic, as suggested by Schmalfuss (1980). In that case the ventral brush of ischium 7 could not be regarded as an apomorphy of the genus *Ischioscia*, but of a subordinate taxon. By the lack of this brush and the convex, not straight, ventral margin of the male ischium 7, I. *stenocarpa* resembles *I. sturmi*.

Taxonomic section

Genus *Ischioscia Verhoeff*, 1928

Type species: *Ischioscia lobifera* Verhoeff, 1928 (by monotypy); synonym of *Philoscia variegata* Dollfus, 1893 (non Dollfus, 1898).

Number of species: 26, all from the Neotropics.

Distribution: northwestern South America and Central America north to Guatemala (see map in Fig. 28).

Remarks: Verhoeff (1928) established the genus *Ischioscia* for the species *I. lobifera* Verhoeff, 1928 from Maracay, Venezuela. Van Name (1936) and Vandel (1952) listed *Hesca* Budde-Lund, 1908 as synonymous with *Ischioscia*, but against the ICZN principle of priority maintained Verhoeff's name because Budde-Lund's had not been accompanied by a description. This practice has been followed by most subsequent authors dealing with this genus. However, no observation or justification supporting the synonymy has ever been published, and reversal of the ICZN principle of priority was not possible under the Codes in effect at the respective time, therefore this opinion on the problem is not accepted here.

Budde-Lund (1908) had introduced *Hesca* as a subgenus of *Philoscia*, including the species *Philoscia niti-*

da Miers and *P. debilis* Budde-Lund, but he did not give a description or definition of the new subgenus, and none has ever been published. Nevertheless, the name is available according to ICZN Article 12 (International Commission on Zoological Nomenclature 1999), because the two species included by Budde-Lund (1908) serve as a sufficient "indication" (ICZN Article 12.2.5.). However, the original descriptions of the two species originally included in *Hesca* do not contain any information allowing identification, not even assignment to any genus of "Philosciidae" (Schmalfuss 1980), and thus they have been considered nomina dubia (Leistikow 2001c). In the absence of diagnostic characters or identifiable included species to define *Hesca* Budde-Lund we regard it as a nomen dubium and follow Schmalfuss (1980) in not accepting it as a synonym of *Ischioscia*.

Dollfus (1898) described under the name *Philoscia variegata* a species from Sulawesi (the former Celebes), without noticing that he had established a species with exactly the same name from Venezuela five years earlier (Dollfus 1893). In accordance with ICZN Article 23.9.5. (International Commission on Zoological Nomenclature 1999), the junior primary homonym must not be replaced until any work published after 1899 is discovered in which the two homonyms were considered congeneric. The present authors are unaware of such a publication, but an exhaustive search of the literature on species of *Burmoniscus* – to which *P. variegata* Dollfus, 1898 currently belongs – was beyond the scope of this study. If necessary, *Burmoniscus cinctellus* (Dollfus, 1898), synonymized with the junior homonym by Taiti et al. (1992), would be available as a replacement.

A summary of the generic characters of *Ischioscia* is given in Leistikow (1997). Several new species from Costa Rica and Venezuela were described by Leistikow (1999b, 2000 and 2001b).

The genus *Ischioscia* is very distinct and cannot be confused with any other South American taxon of the philosciid facies except *Tropiscia flagellata* Vandel which is the adelphotaxon of *Ischioscia*.

List of species

Ischioscia amazonica Lemos de Castro, 1955 – redescription below
Ischioscia andina (Vandel, 1968)
Ischioscia bolivari Vandel, 1968 – redescription below
Ischioscia cadoangelis Leistikow, 2000
Ischioscia colorata Leistikow, 2001
Ischioscia curvaculeus Leistikow, 2001
Ischioscia elongata Leistikow, 1997
Ischioscia fasciifrons Leistikow, 2001
Ischioscia guamae Leistikow, 2001
Ischioscia hanagarthi Schmalfuss, 1980
Ischioscia hirsuta Leistikow, 2001
Ischioscia irmleri Schmalfuss, 1980
[*Ischioscia lobifera* Verhoeff, 1928 – junior synonym of *I. variegata*]
Ischioscia longicauda Schmalfuss, 1980
Ischioscia marmorata Leistikow, 2000
Ischioscia martinae Leistikow, 1997
Ischioscia mineri (van Name, 1936) – redescription by Leistikow (2001f)
Ischioscia muelleri Leistikow, 1997
Ischioscia panamensis Leistikow, 1999
Ischioscia pariae Leistikow, 2001
Ischioscia plurimaculata Leistikow, 2000
Ischioscia quadrispinis Leistikow, 2000
Ischioscia stenocarpa Schmalfuss, 1980
Ischioscia sturmi (Vandel, 1972) – redescription below
Ischioscia trifasciata Leistikow, 2001
Ischioscia variegata (Dollfus, 1893) – redescription by Leistikow (1997)
Ischioscia zebricolor Leistikow, 1999

Key to the species of *Ischioscia* Verhoeff, 1928

Specimens can be identified to genus with a key to the Neotropical genera of "philosciid" Crinocheta (Leistikow 2001d).

1 Pereionites coloured uniformly white or umber, zebra-patterned due to dark and light stripes; length max. 5 mm ..... *I. zebricolor*
1* Pereionites mottled in brown colours, with light patches at muscle insertions; length > 6 mm 2
2 Cephalothorax with linea frontalis and linea supra-antennalis 19
2* Cephalothorax with linea supra-antennalis only, linea frontalis reduced 3
3 Pereiopods 1-3 of adult male with carpus enlarged 4
3* Pereiopod 3 carpus of adult male not enlarged .. 12
4 Pereiopod 7 ischium with medio-distal process and latero-distal semicircular lobe on rostral surface . 5
4* Ischium of pereiopod 7 lacking semicircular lobe, medio-distal process inconspicuous 10
5 Male pleopod 1 endopodite with or without extremely small spines in caudal row, if present their position marked by dark structures (the holes in the cuticle through which the spines are innervated) ..... *I. variegata*
5* Caudal row of spines on pleopod 1 endopodite well developed 6
6 Colour of dorsal side looking marbled, with several light areas; two teeth of lateral endite of first maxilla double-cleft ..... *I. marmorata*
6* Colour more uniformly brown with light muscular insertion patches and dark medial line; all teeth of first maxilla cleft simply 7

7 Male pereiopod 7 merus with four distinct groups of sensory setae medially grouped in a 1-3-3-1 pattern; ischium 7 with prominent proximal brush, distal half with short-haired brush, basis with a medio-distal hairy tuft . . . . . *I. hirsuta*
7* Male pereiopod 7 without prominent setal tuft on basis, merus with fewer spines 8
8 Male pleopod 1 endopodite apically obtuse, without proximally directed subapical lobe; endopodite 2 apically slightly bulbous, bearing faint cuticular scales; dactylar seta with plumose distal part one third of total length . . . . . *I. colorata*
8* Male pleopod endopodite 1 with subapical lobe; endopodite 2 pointed, without cuticular scales; dactylar seta with plumose part one fifth of length or replaced by cuticular plaque 9
9 Dactylar seta with indistinct plumose distal part; male pleopod 1 exopodite without lateral protrusion; pereiopod 7 merus with 1-2-2-0-3 pattern of sensory setae, proximal pair very short . . . . . *I. trifasciata*
9* Dactylar seta with cuticular vane distally; pleopod 1 exopodite with protrusion; pereiopod 7 merus with 2-0-1-0-3 pattern of sensory setae . . . . . *I. pariae*
10 Pereiopods 1-3 with scale field on propus . . . . . *I. quadrispinis*
10* Only propus of pereiopod 1 with antenna-grooming brush 11
11 Male pleopod 1 exopodite with incision proximal of lateral protrusion, endopodite without faint hairs . . . . . *I. martinae*
11* Pleopod 1 exopodite lacking incision, endopodite apically with tufts of faint hairs . . . . . *I. mineri*
12 Dactylus with very short inner claw . . . . *I. bolivari*
12* Dactylus with long inner claw, almost as long as interungual seta 13
13 Pereiopod 3 carpus with or without small medio-proximal scale field on carpus 14
13* Pereiopods 1-3 with scale field on carpus 16
14 Limited scale fields present on pereiopod 3 medio-proximal area of carpus and medio-distal area of merus; no scale field on ischium 7 . . . *I. fasciifrons*
14* No scale fields on pereiopod 3; scale field present on ischium 7 15
15 Male pereiopod 7 merus with ventroproximal hook; male pereiopod 2 merus and carpus with vestigial scale field; distal lobe of male pleopod 1 exopodite apically rounded, with convex medial margin . . . . . *I. curvaculeus*
15* Male pereiopod 7 merus without hook; male pereiopod 2 merus and carpus with scale fields as well developed as in pereiopod 1; distal lobe of male pleopod 1 exopodite apically acute, with concave medial margin . . . . . *I. cadoangelis*
16 Setal tuft medio-distally on basis of pereiopod 7, no scale field medially at midlength of ischium 7 . . 17
16* Ischium 7 with depression on rostral surface and scale field medially at midlength 18
17 Pleopod 1 exopodite medio-distally rounded; no scale field on pereiopod 7 ischium . . . . *I. elongata*
17* Pleopod 1 exopodite medio-distally straight; setose area proximally on pereiopod 7 ischium *I. muelleri*
18 Telson bearing many tricorn-like setae; male pereiopod 7 ischium bearing two prominent and one small sensory spine on medial margin . . *I. plurimaculata*
18* Telson with two pairs of tricorn-like setae; male pereiopod ischium bearing one long and three shorter sensory setae . . . . . *I. guamae*
19 Male pereiopod 7 ischium without medial scale field 20
19* Male pereiopod 7 with more or less prominent medial scale field 22
20 Male pleopod 1 exopodite triangular, without incision, with a slight protuberance laterally . *I. sturmi*
20* Male pleopod 7 exopodite with lateral incision . 21
21 Carpal brushes present on male pereiopods 1-3 . . . . . *I. andina*
21* Carpal brushes present on male pereiopod 1. . . . . *I. stenocarpa*
22 Scale field on male pereiopod 7 ischium in proximal half, with medio-distal lobe . . . . . *I. panamensis*
22* Scale field along entire medial margin or more in distal half, no medio-distal lobe 23
23 Scale field of ischium 7 in distal half, carpi of pereiopods 1-3 enlarged . . . . . *I. hanagarthi*
23* Scale field of ischium 7 on entire medial margin, carpus 3 not enlarged 24
24 Male pereiopod 4 merus with scale field medially . . . . . *I. amazonica*
24* No scale field on pereiopod 4 merus 25
25 Medial margin of male ischium 7 straight . . . . . *I. longicauda*
25* Medial margin of male ischium 7 conspicuously concave . . . . . *I. irmleri*

Redescriptions and new records

Ischioscia sturmi (Vandel, 1972) (Figs 11–16)

Proischioscia sturmi Vandel, 1972

Material: Male (syntype), body length 7.5 mm; female (syntype), 8.5 mm: Colombia, Paramo de Chisaca, 40 km southwest of Bogotá, 25.VI.1966, leg. H. Sturm, MNHN (uncataloged).

Description: Colour: dorsum and cephalothorax buff with umber patches in medial line, coxal plates II to VII also with umber patches. Muscle insertions almost invisible on pereionites, conspicuous on vertex, coxal plates covered with dark chromatophores except for lateral border, ventral side and appendages light yellowish.

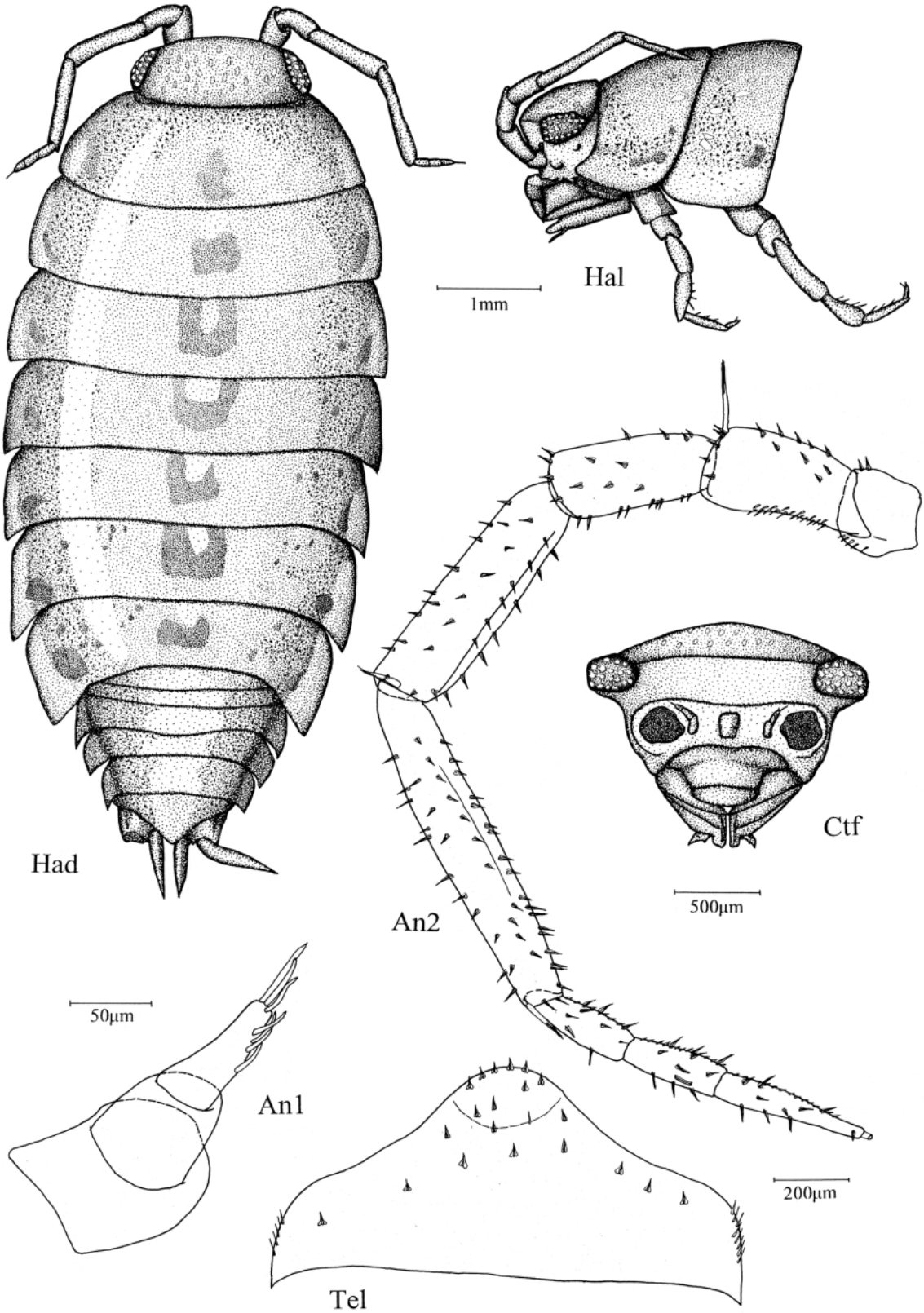


Fig. 11. *Ischioscia sturmi* (Vandel): syntype male, 7.5 mm. An1 antennula; An2 antenna; Ctf cephalothorax in frontal view; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

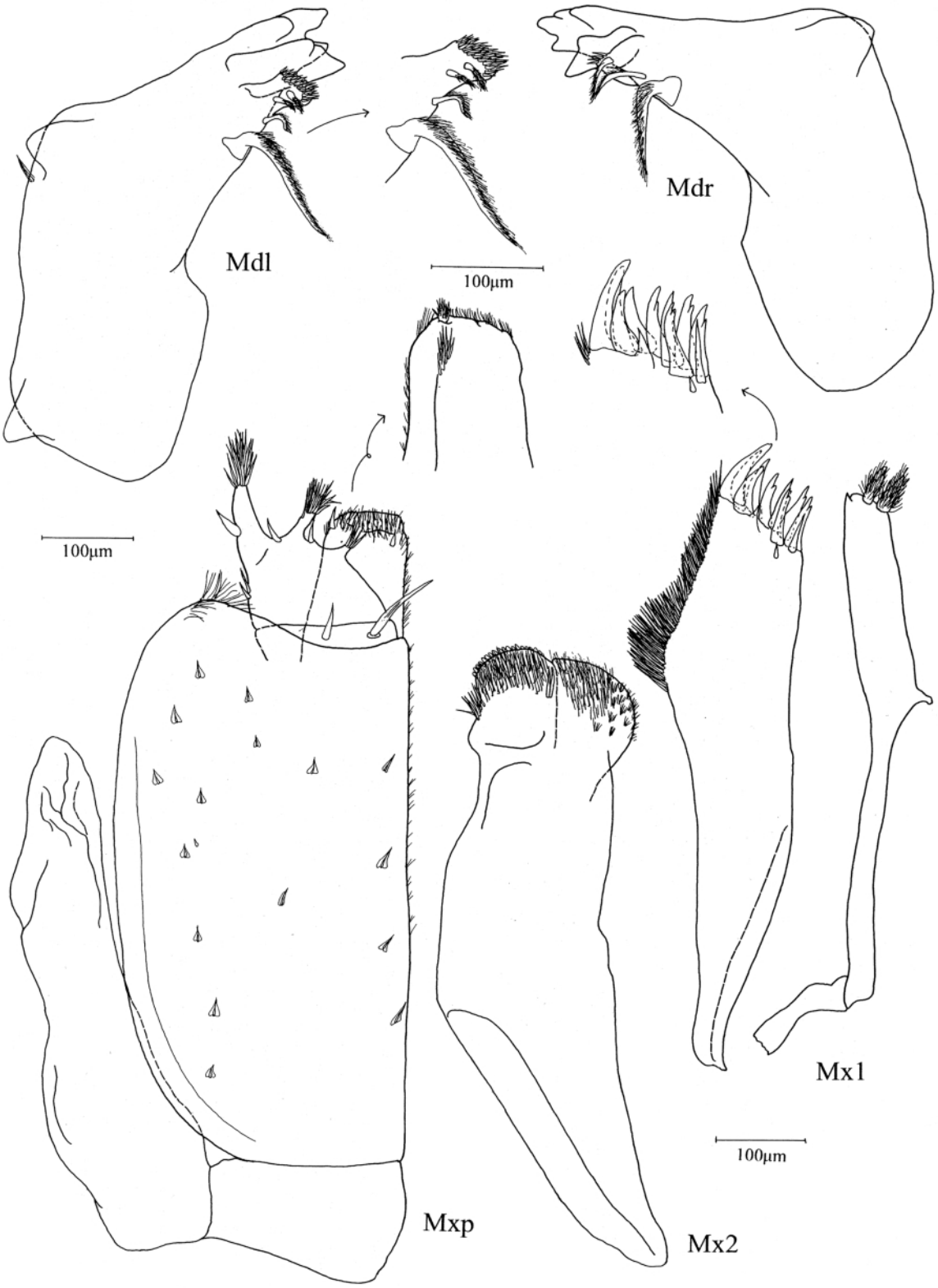


Fig. 12. *Ischioscia sturmi* (Vandel): syntype male. Mdl/Mdr left and right mandible, with detail of left pars intermedia; Mxp maxilliped, with detail of endite in rostral view; Mx1 first maxilla, with detail of apical lateral endite in rostral view; Mx2 maxilla.

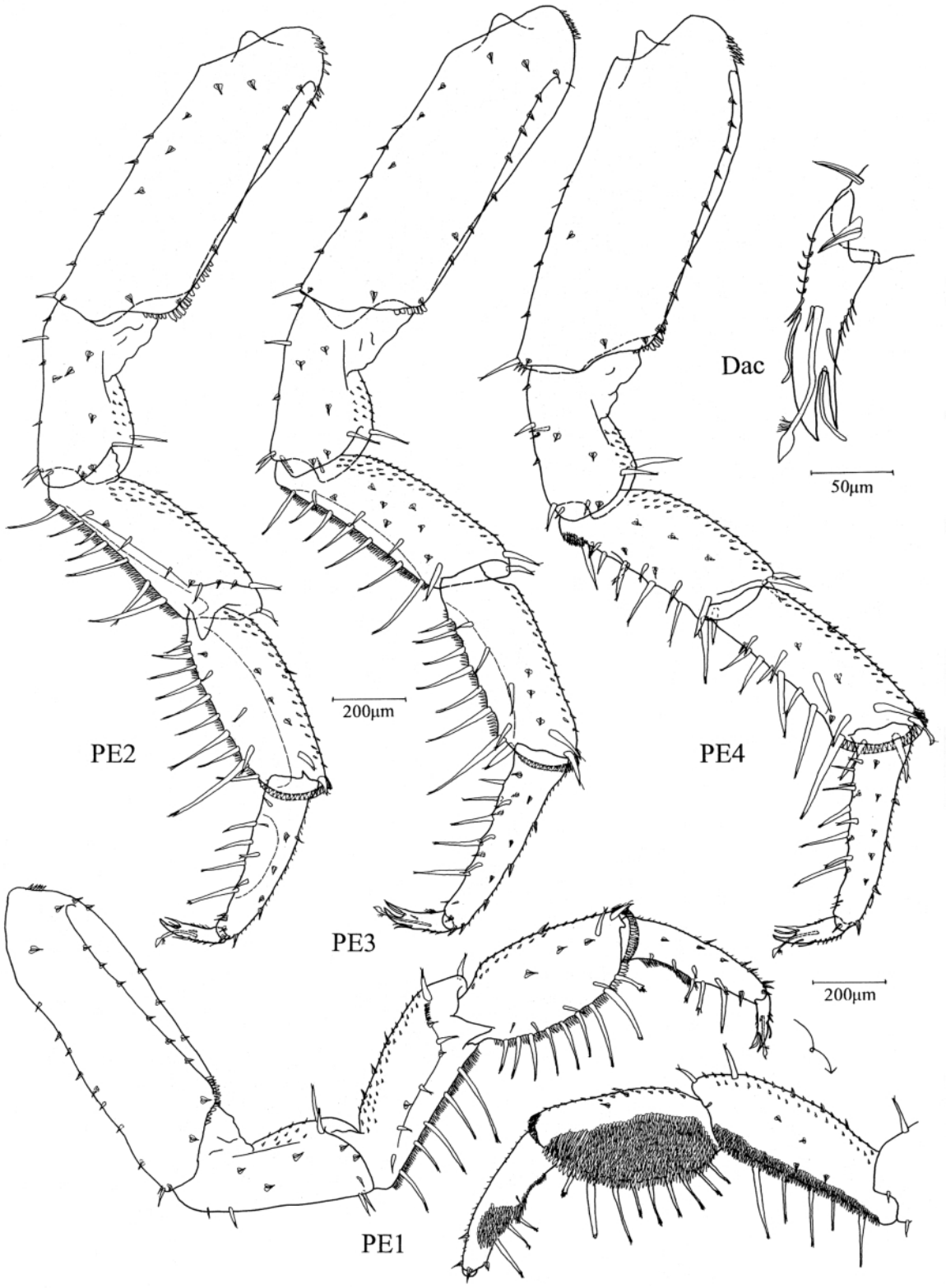


Fig. 13. *Ischioscia sturmi* (Vandel): syntype male. Dac dactylus of pereiopod 1 in rostral view; PE1-4 pereiopods 1 to 4 in caudal view, with detail of PE1 in rostral view.

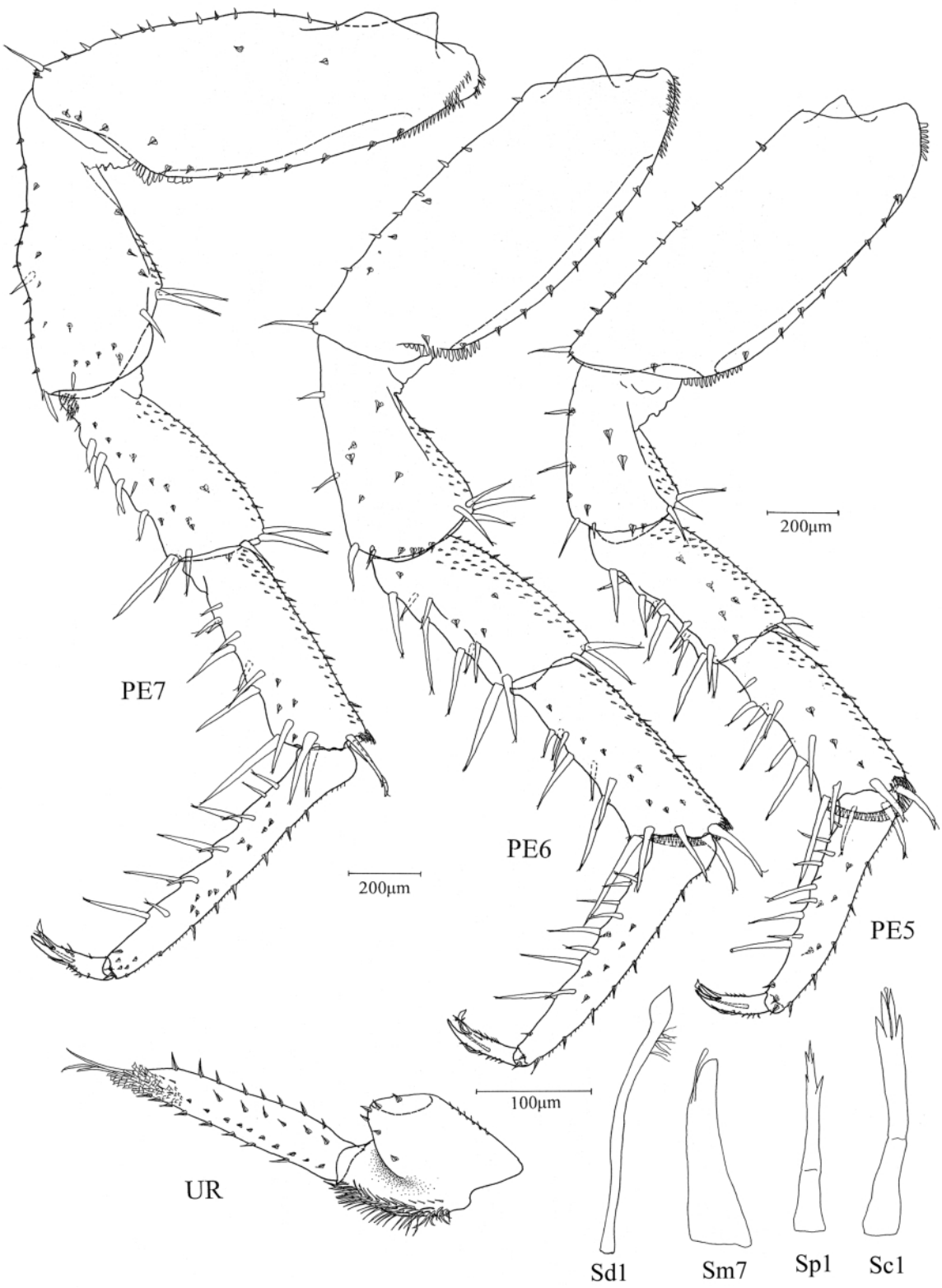


Fig. 14. *Ischioscia sturmi* (Vandel): syntype male. PE5-7 pereiopods 5 to 7 in caudal view; Sc1 ornamental sensory spine of carpus 1; Sd1 dactylar seta 1; Sm7 medial sensory spine of merus 7; Sp1 distal sensory spine of propus 1; UR uropod in rostral view.

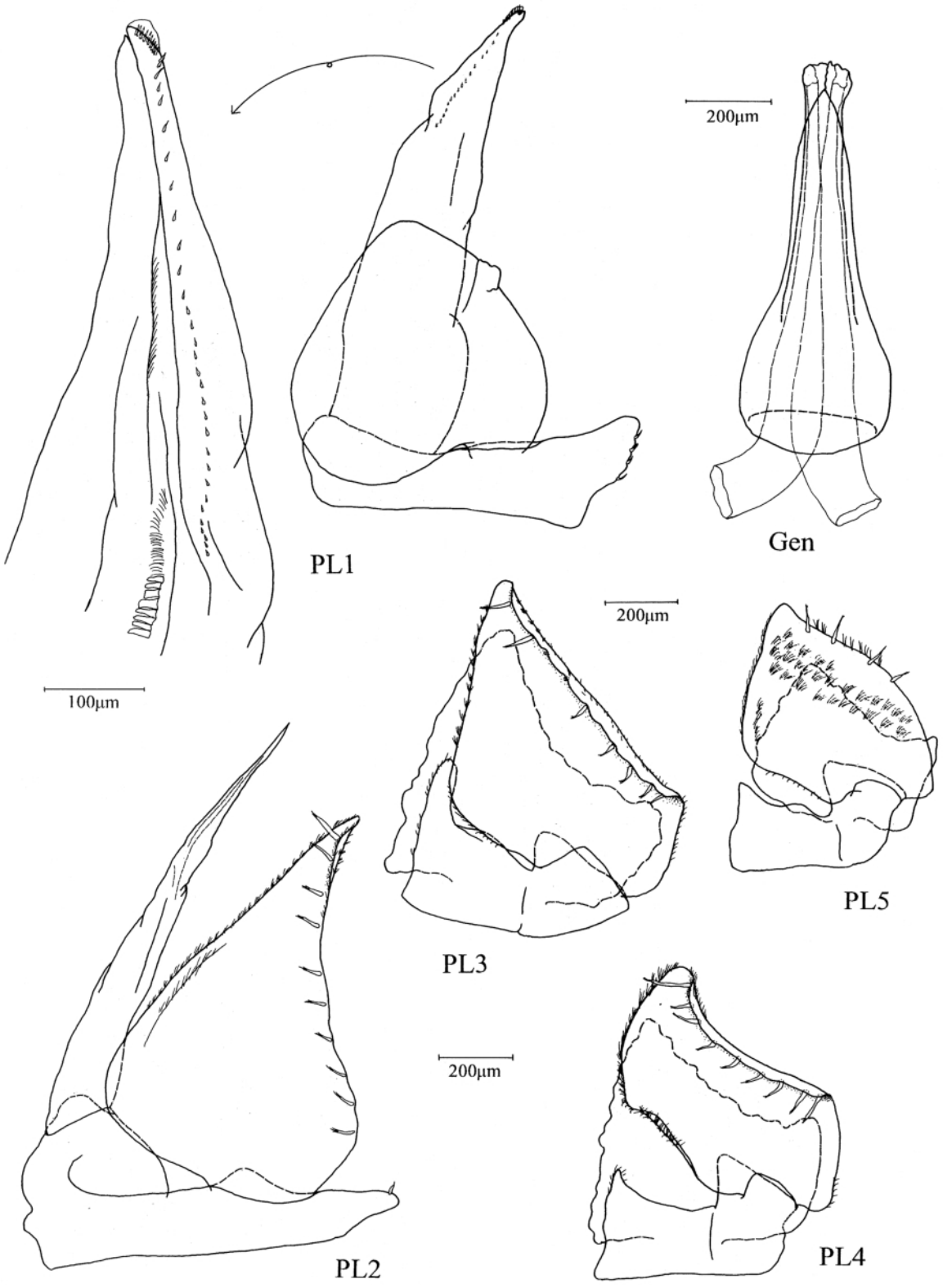


Fig. 15. *Ischioscia sturmi* (Vandel): syntype male. Gen genital papilla; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

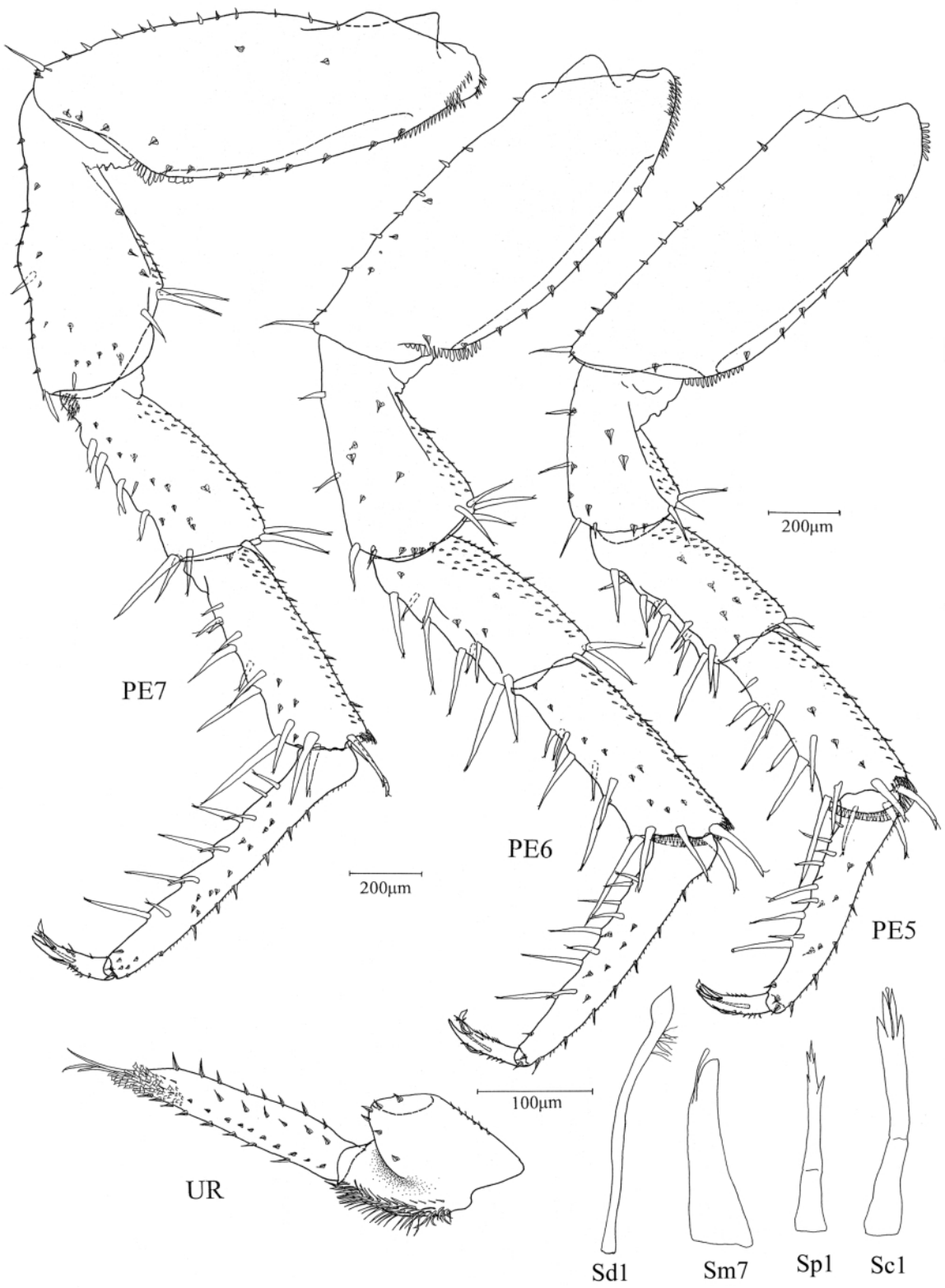


Fig. 16. *Ischioscia sturmi* (Vandel): syntype female. PE1, 2, 7 pereiopods in caudal view; with detail of PE1 rostrally; PL1, 2 pleopods 1 and 2 in rostral view.

Cephalothorax: linea frontalis, linea supra-antennalis and lamina frontalis present, linea supra-antennalis slightly bent between antennal sockets, vertex smooth, flattened, compound eyes prominent, with about 25 ommatidia in 4 rows (Fig. 11: Ctf).

Pereion: tegument smooth and shiny, coxal plates with sulcus marginalis, lacking gland pores and noduli laterales, coxal plates I to III caudally rounded, IV to VII caudally pointed.

Pleon: retracted from pereion, neopleurae of pleonites 3 to 5 prominent, pleotelson with lateral margins concave, ventrally with semicircular pit, apex at same level as distal end of uropod protopodites.

Antennula: composed of 3 articles, proximal joint stout, distal article coniform, bearing 3 aesthetascs apically and 4 medially (Fig. 11: An1).

Antenna: as in other members of the genus but rather short, flagellum 3-articulate with the distal joint slightly longer than articles 1 and 2, peduncular article 5 as long as flagellum, apical organ missing (broken off) in the examined specimens (Fig. 11: An2).

Mandible: pars intermedia covered with coniform setae, bearing 2 penicils on left and 1 on right mandible, distally with additional penicil, molar penicil simple (Fig. 12: Mdl/Mdr).

First maxilla: medial endite apically bearing 2 penicils and latero-distal point, lateral endite with prominent lateral setal fringe and 4+6 apical teeth, five of inner set cleft (Fig. 12: Mx1).

Maxilla: both lobes subequal in breadth, apically densely setose, laterally setae replaced by pectinate scales, medial lobe apically cuspidate (Fig. 12: Mx2).

Maxilliped: basipodite with sulcus lateralis, palp 3-articulate, distal article laterally bearing stout seta, medial setal tufts as in other members of *Ischioscia*, endite covered with trichiform setae, rostrally with setal tuft and knob-like penicil (Fig. 12: Mxp).

Pereiopods: resembling those of congeners (Figs 13, 14, 16: PE1-7), ornamental sensory spine of carpus 1 slender (Fig. 14: Sc1), scale field of propus 1 prominent, dactylus with long inner claw (Fig. 13: Dac) and dactylar seta with velum apically and some trichiform setae subapically (Fig. 14: Sd1). Sexual dimorphism: male pereiopods 1 to 3 with scale fields on rostral surface of carpus and merus, propus 1 to 2 also with scale fields; merus of pereiopods 4 and 7 medio-proximally with small hump, covered with short setae, ischium 7 medially with elongate hump, rostrally with sensory spine.

Pleopods: exopodites medially pointed, lateral margin with 9 sensory setae in pleopods 3 and 4, 4 in pleopod 5, exopodite 5 caudally with 3 rows of pectinate scales, endopodites pointed, bearing no setation, no respiratory areas visible in light microscope at 400× magnification (Fig. 15: PL1-5, Fig. 16: PL1-2). Sexual dimorphism: male pleopod 1 exopodite rounded to triangular, lateral margin bearing a groove and proximally a protrusion, endopodite acute, with small medial hyaline lobe, medio-caudal row of spines (Fig. 15: PL1); pleopod 2 exopodite pointed, endopodite apically flagelliform, much more slender than in other species of *Ischioscia* (Fig. 15: PL2).

Uropod: protopodite medially with long trichiform setae, endopodite inserting proximal of exopodite, apically with set of hyaline band-shaped scales (Fig. 14: UR).

Genital papilla: ventral shield slender with bulbous basis, terminal spatula truncate, surpassing apex of ventral shield (Fig. 15: Gen).

Remarks: *Ischioscia sturmi* is one of the species of its genus showing a linea frontalis. It shares with the groundpattern of the genus the lack of a deep incision of the male pleopod 1 exopodite. The scale field on pereiopod 7 ischium is reduced in this species, in contrast to *I. amazonica*. Additional characters separating *Ischioscia sturmi* from the species without linea frontalis: the molar penicil of the mandibles is simple instead of composed of about seven branches; the dactylar seta is terminated by a spatuliform velum, and subapically bears some fine hairs. The species differs from *I. andina* in the shape of the male pleopod 1 and has a more bent linea supra-antennalis; it can be distinguished from *I. amazonica* by the colour pattern and the shape of pleopod 1 of the male. In both *I. andina* and *I. amazonica* the endopodite of pleopod 1 is fairly truncate, whereas in *I. sturmi* the hyaline lobe is pointed.

Ischioscia amazonica Lemos de Castro, 1955

(Figs 17–21)

Material: Male (body length 7.5 mm, dissected): Brazil, Amazonas, Alto Itacoaí, MNRJ 7835; 1 male, 4 females: same data as dissected specimen.

Description: Colour: light chestnut with dark patches on coxal plates I to VI, medially on pereionites II and IV and a terminal band on pereionite VI, several light patches on pereionites and cephalothorax, pleon uniformly chestnut.

Cephalothorax: vertex flattened, lineae frontalis and supra-antennalis, and lamina frontalis present, compound eyes laterally protruding, 26 to 30 ommatidia arranged in 4 rows, no lateral lobes (Fig. 17: Ctf).

Pereion: dorsum arched, coxal plates prominent, tegument smooth, bearing scattered sensory setae, sulcus marginalis present, no noduli laterales discernible at 400× magnification.

Pleon: narrower than pereion, pleonites 3 to 5 with distinct neopleurae, pleotelson with concave lateral margins, semicircular pit at apex on ventral surface.

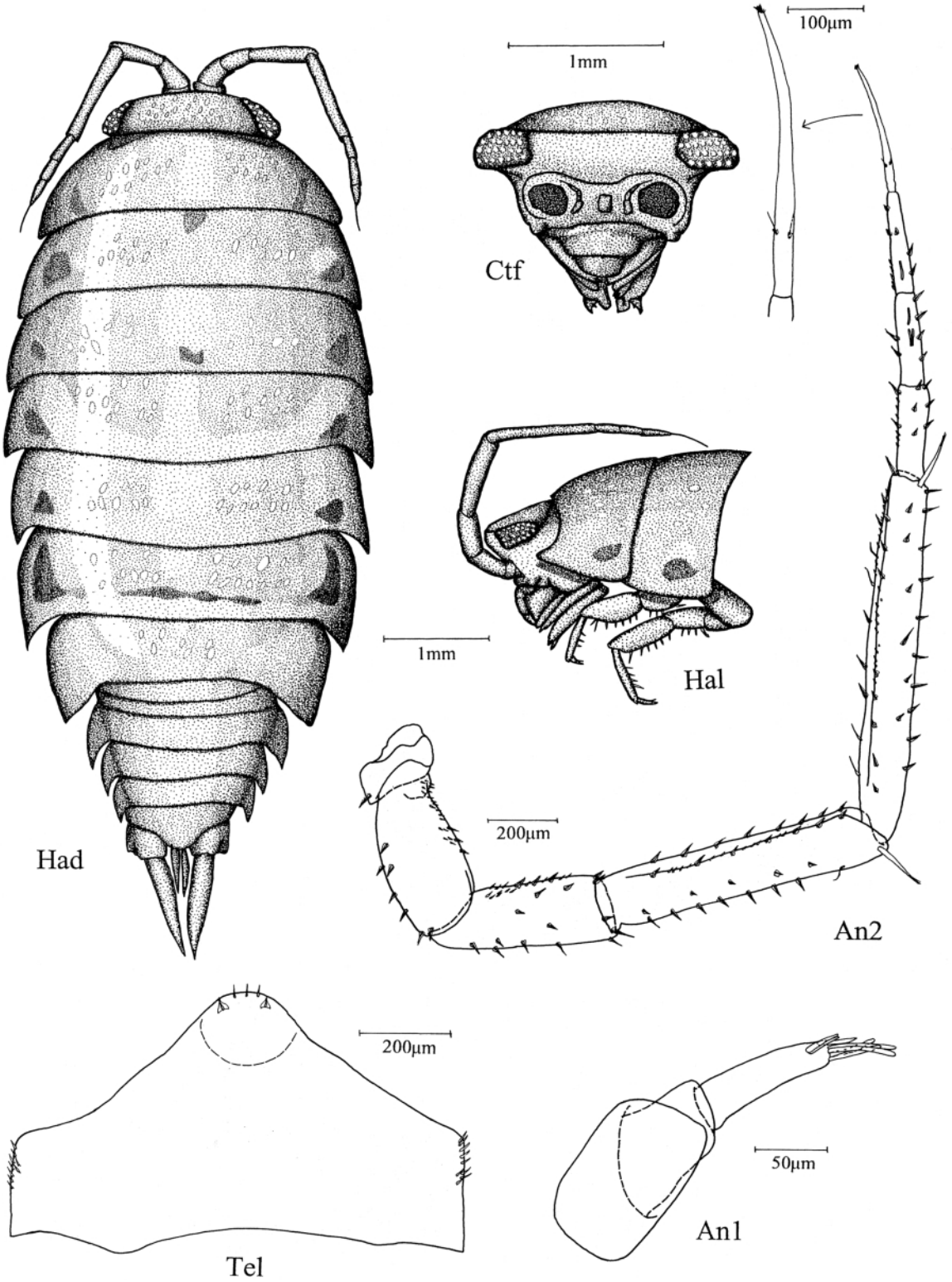


Fig. 17. *Ischioscia amazonica* Lemos de Castro: male, 7.5 mm. An1 antennula; An2 antenna, with detail of apical organ; Ctf cephalothorax in frontal view; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

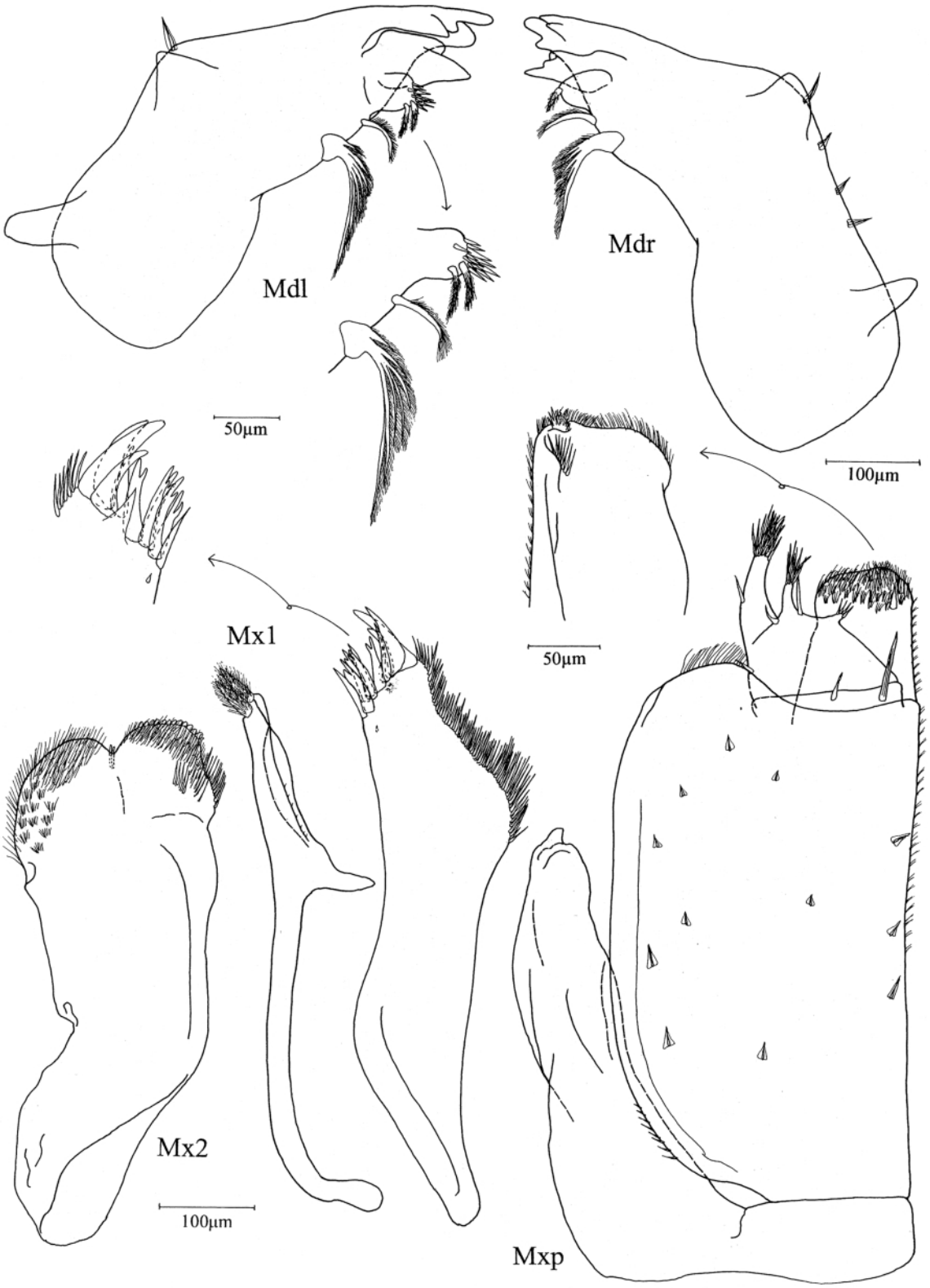


Fig. 18. *Ischioscia amazonica* Lemos de Castro: male. Mdl/Mdr left and right mandible, with detail of left pars intermedia; Mxp maxilliped, with detail of endite in rostral view; Mx1 first maxilla, with detail of apical lateral endite in rostral view; Mx2 maxilla.

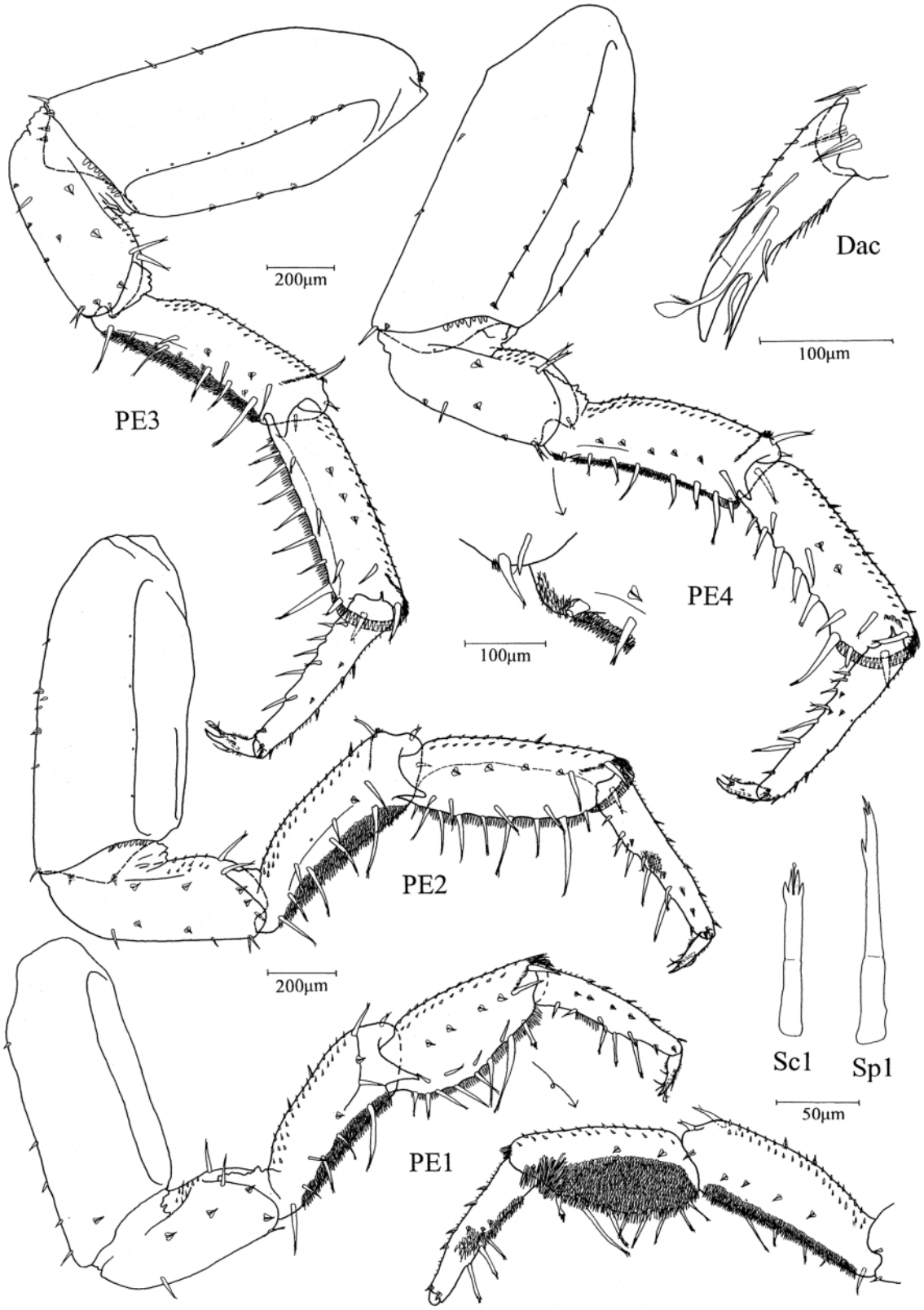


Fig. 19. *Ischioscia amazonica* Lemos de Castro: male. Dac dactylus of pereiopod 5 in rostral view; PE1-4 pereiopods 1 to 4 in caudal view, with details of PE1 rostrally and PE4 caudally; Sc1 ornamental sensory spine of carpus 1; Sp1 distal sensory spine of propus 1.

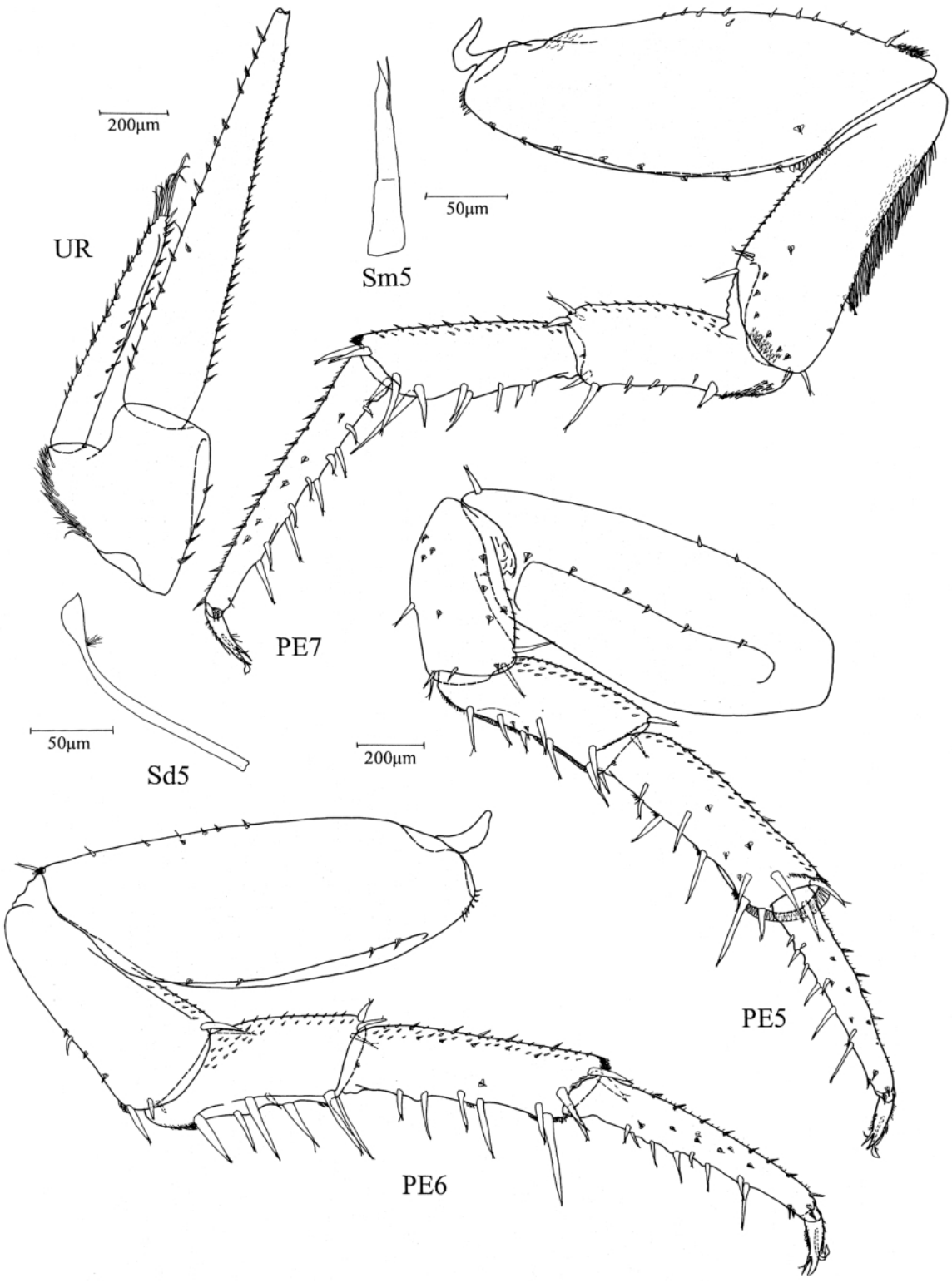


Fig. 20. *Ischioscia amazonica* Lemos de Castro: male. PE5-7 pereiopods 5 to 7 in caudal view; Sd5 dactylar seta 5; Sm5 medial sensory spine of merus 5; UR uropod in rostral view.

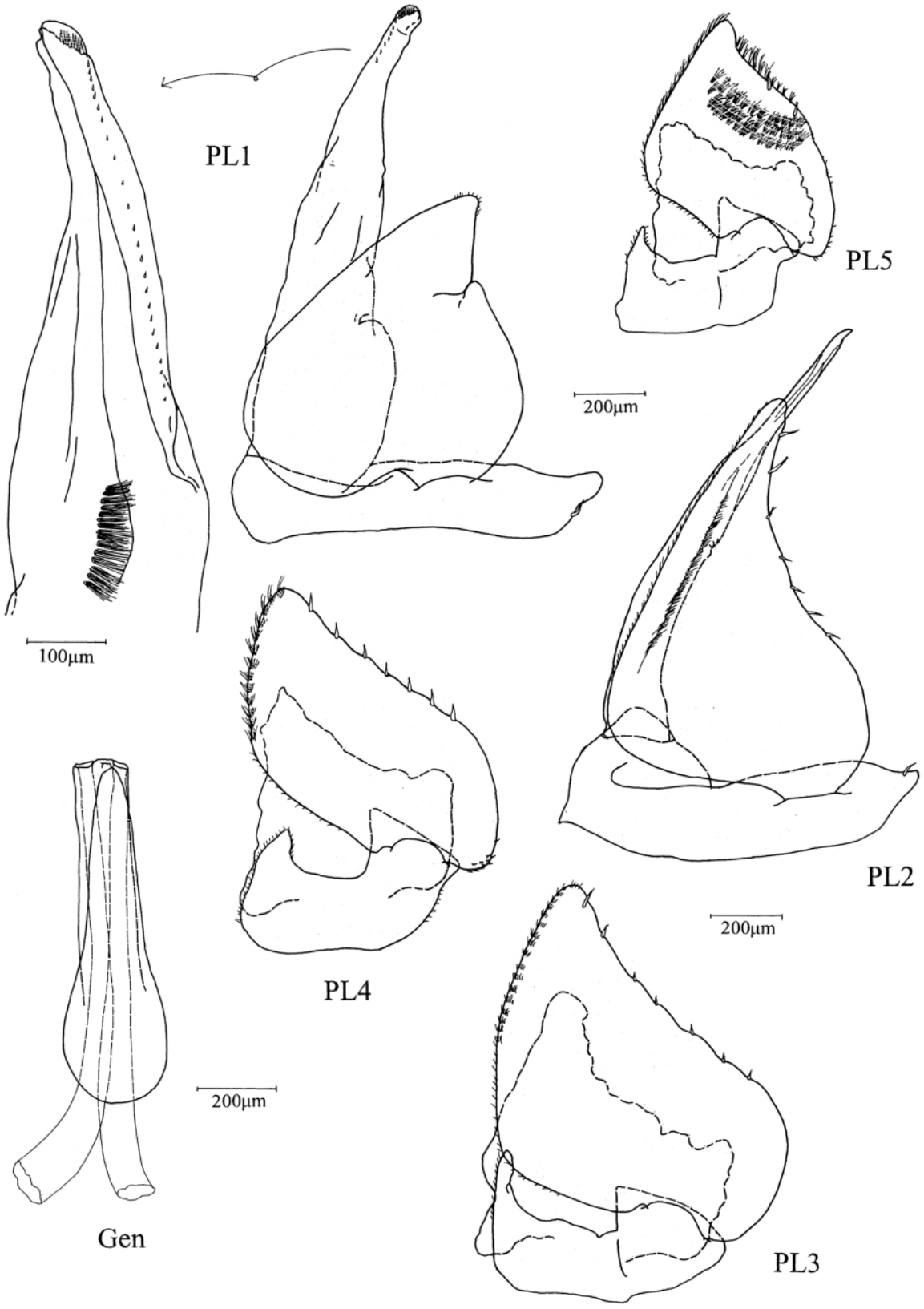


Fig. 21. *Ischioscia amazonica* Lemos de Castro: male. Gen genital papilla; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite1 in caudal view.

Antennula: rather slender, particularly distal article with sets of aesthetascs, proximal article with shield-like protrusion (Fig. 17: An1).

Antenna: slender with flagellum composed of 3 subequally long articles, distal one with apical organ of half the length of flagellum, proportions of first to fifth peduncular articles 1: 2: 2: 4: 5 (Fig. 17: An2).

Mandible: molar penicil composed of 7 branches, proximal one longest, distal one shortest, pars intermedia with few coniform setae, 1 penicil on right, 2 on left side, additional penicil proximal of pars intermedia (Fig. 18: Mdl/Mdr).

First maxilla: medial endite with 2 pointed penicils apically, lateral endite with 4+6 teeth apically, five of inner set cleft, 1 subapical tooth, hyaline lobe on rostral side (Fig. 18: Mx1).

Maxilla: both lobes subequal in breadth, densely setose, medial lobe with 12 cusps apically, sclerotized clasp present (Fig. 18: Mx2).

Maxilliped: basipodite with sulcus lateralis, few tricorn-like setae present, palp 3-articulate, medial setal tuft on stalk, proximal article with 2 setae, endite setose, with knob-like penicil on the frontal face (Fig. 18: Mxp).

Pereiopods: rather slender with scattered tricorn-like setae (Figs 19, 20: PE1-7), latero-distal setal tuft on carpus, carpus 1 with transverse antenna-grooming brush and ornamental sensory spine with hand-like apex (Fig. 19: Sc1), dactylus with long inner claw (Fig. 19: Dac), straight interungual seta, dactylar seta with spatuliform velum apically, few hairs subapically (Fig. 20: Sd5). Sexual dimorphism: male pereiopods 1 to 3 with carpal brushes on rostral surface of carpus, medially on merus 1 to 4, setose area medio-proximally on pereiopods 4 to 6 merus, ischium 7 with elongate medial scale field.

Pleopods: pleopod endopodites bilobate, exopodites rhomboid with up to 8 lateral sensory setae, medially with pectinate scales, no respiratory areas discernible, pleopod 5 with 3 rows of pectinate scales caudally (Fig. 21: PL1-5). Sexual dimorphism: male pleopod 1 exopodite triangular with wrinkled incision and slight lateral protrusion, endopodite with slightly bulbous apex, caudomedial row of spines present (Fig. 21: PL1); pleopod 2 exopodite pointed, laterally sinuous, endopodite longer than exopodite, with slightly hooked apex (Fig. 21: PL2).

Uropod: protopodite medially setose, laterally with groove, endo- and exopodites long, covered with tricorn-like setae (Fig. 20: UR).

Genital papilla: ventral shield pyriform, only slightly surpassed by truncate terminal spatula (Fig. 21: Gen).

Remarks: This interesting species was described by Lemos de Castro (1955) based on a male and some female specimens from the state of Amazonas. This species is closely related to *I. sturmi* with which it shares the structure of the dactylar seta which is apically spatuliform, a character more derived than the plumose seta of, e.g., *I. bolivari* as discussed below.

***Ischioscia bolivari* Vandel, 1968** (Figs 22–27)

Material: Male (syntype), body length 7 mm; female (syntype), 8 mm: Ecuador, Santo Domingo, IV.1965, leg. N. Leleup, MNHN (uncataloged).

Description: Colour: tergites maroon with yellowish brown patches, dark medial line lacking in pereionite 3, coxal plates with prominent yellowish patch bordered by dark brown area laterally, pleon without markings, ventral side light yellowish brown.

Cephalothorax: linea supra-antennalis and lamina frontalis conspicuous, linea frontalis lacking, traced by a slightly protruding area between eyes, vertex flattened, without setae, compound eyes consisting of about 20 ommatidia (Fig. 22: Ctf).

Pereion: tegument smooth, with scattered setae, coxal plates I to IV rounded, coxal plates V to VII pointed, with sulcus marginalis, gland pores and noduli laterales not perceptible at 400× magnification.

Pleon: set apart from pereion, neopleurae of pleonites 3 to 5 prominent, pleotelson pointed, lateral margins concave, bearing some tricorn-like setae.

Antennula: similar to other species of *Ischioscia* (Fig. 22: An1).

Antenna: flagellum 3-articulate with apical organ as long as proximal article, distal articles somewhat shorter, like peduncle covered with tricorn-like setae, proportions of first to fifth peduncular articles as 1:3:3:5:6 (Fig. 22: An2).

Mandible: pars intermedia with coniform setae, 2 penicils on left, 1 on right mandible, molar penicil composed of about 6 branches, between pars intermedia and molar penicil additional plumose seta (Fig. 23: Mdl/Mdr).

First maxilla: medial endite with 2 rather weak penicils, lateral endite with 4 + 6 teeth apically, five of inner set cleft, rostrally with hyaline triangular tooth and subapical coniform tooth, laterally bearing a fringe of trichiform setae (Fig. 23: Mx1).

Maxilla: medial lobe apically cuspidate, subapically setose, lateral lobe bearing even more setae, pectinate scales laterally, both lobes subequal in breadth (Fig. 23: Mx2).

Maxilliped: basipodite with sulcus lateralis, endite with knob-like penicil and setal tuft rostrally, palp 3-articulate, with prominent medial setal tufts, medial seta of proximal article fairly short, epipodite bearing some scattered hairs apically (Fig. 23: Mxp).

Pereiopods: rather slender with 2 rows of tricorn-like seta on basis (Figs 24, 25, 27: PE1-7), carpus with rostrodistal fringe of translucent dentation and setal tuft, dactylus with dactylar seta apically plumose (Fig. 24: Sc1), inner claw fairly short, interungual seta straight, twice as long as inner claw (Fig. 24: Dac). Sexual dimorphism: pereiopods 1, 2 and 7 sexually dimorphic, carpus

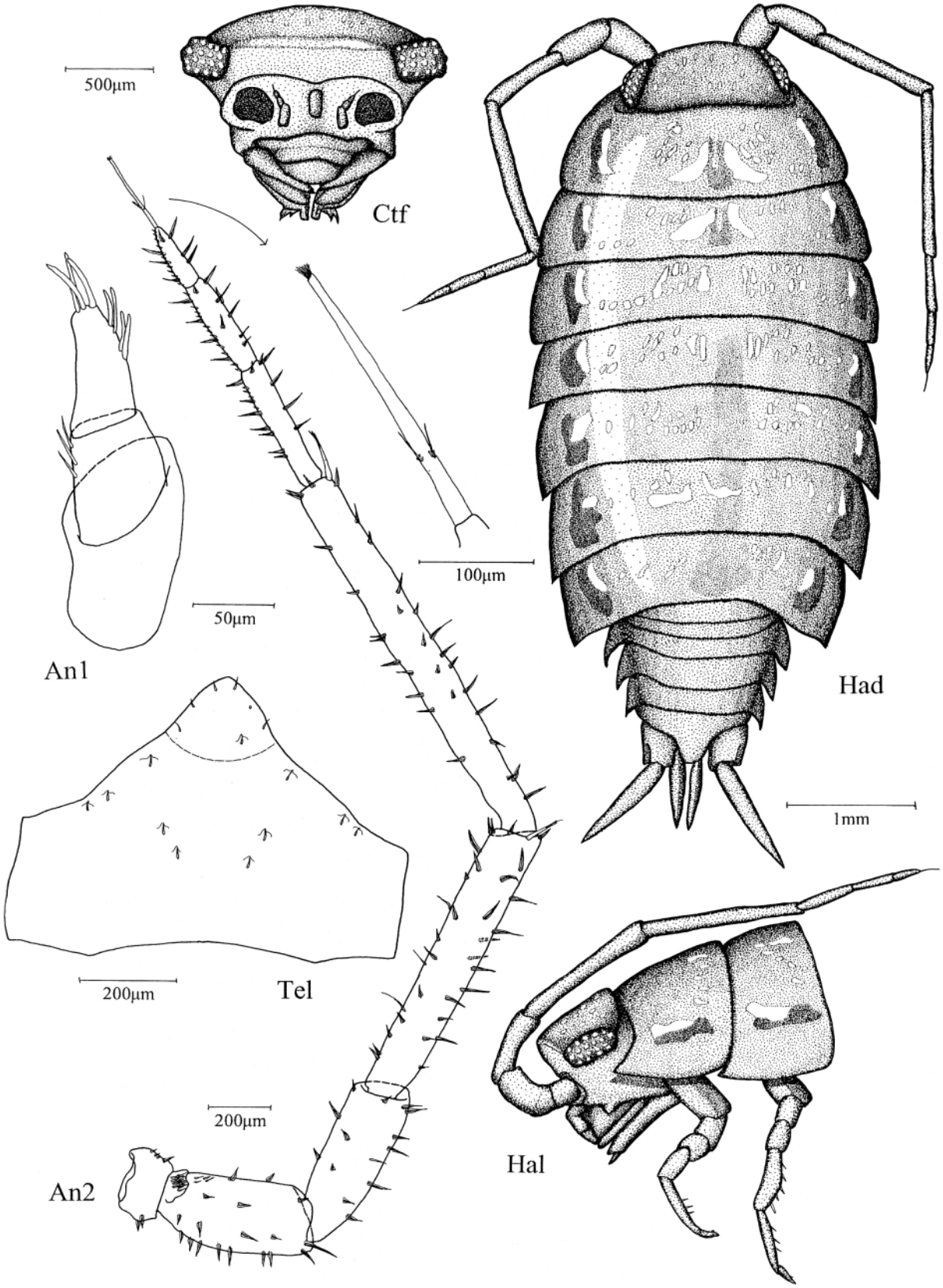


Fig. 22. *Ischioscia bolivari* Vandel: syntype male, 7 mm. An1 antennula; An2 antenna, with detail of apical organ; Ctf cephalothorax in frontal view; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

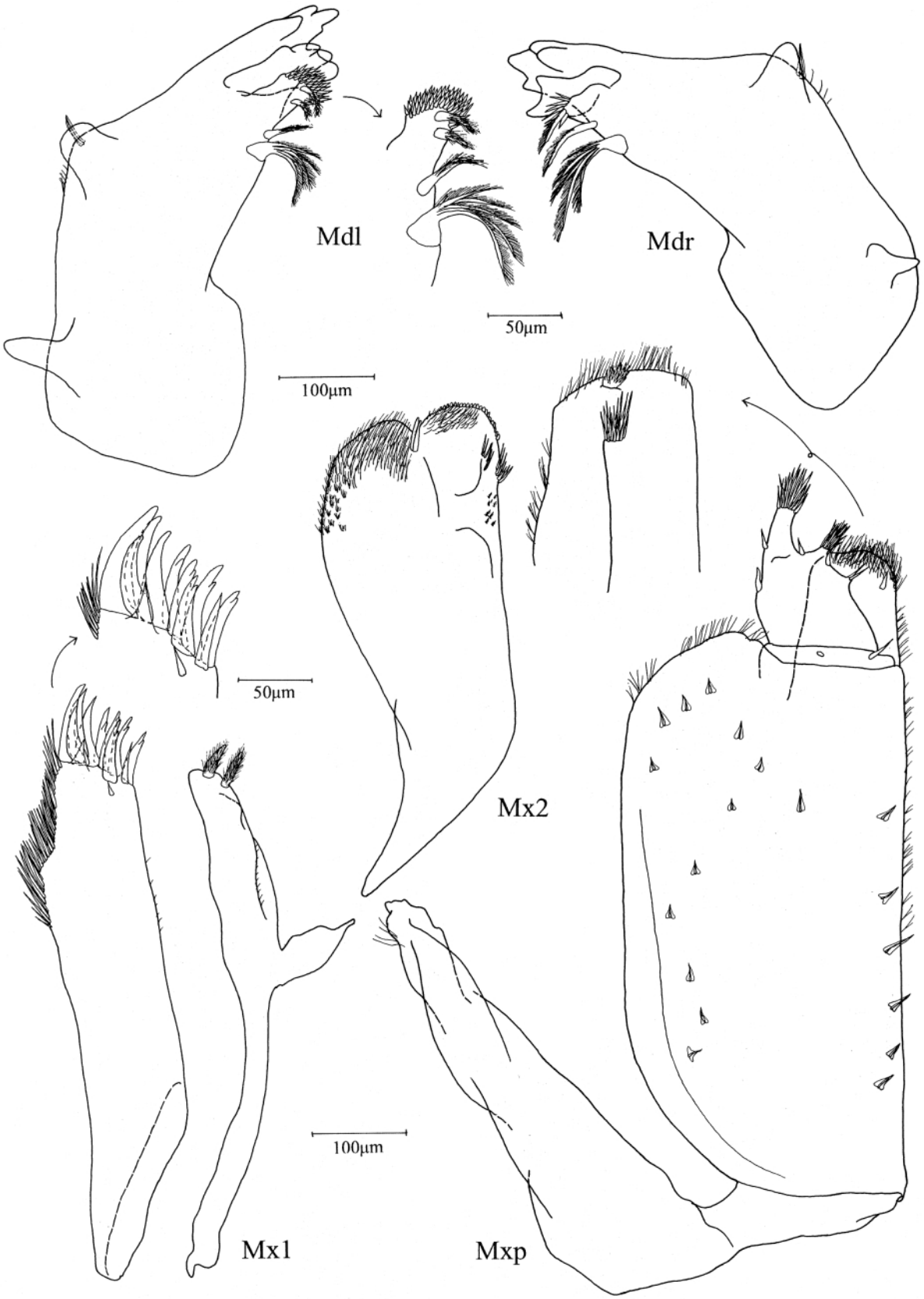


Fig. 23. *Ischioscia bolivari* Vandel: syntype male. Mdl/Mdr left and right mandible, with detail of left pars intermedia; Mxp maxilliped, with detail of endite in rostral view; Mx1 first maxilla, with detail of apical lateral endite in rostral view; Mx2 maxilla.

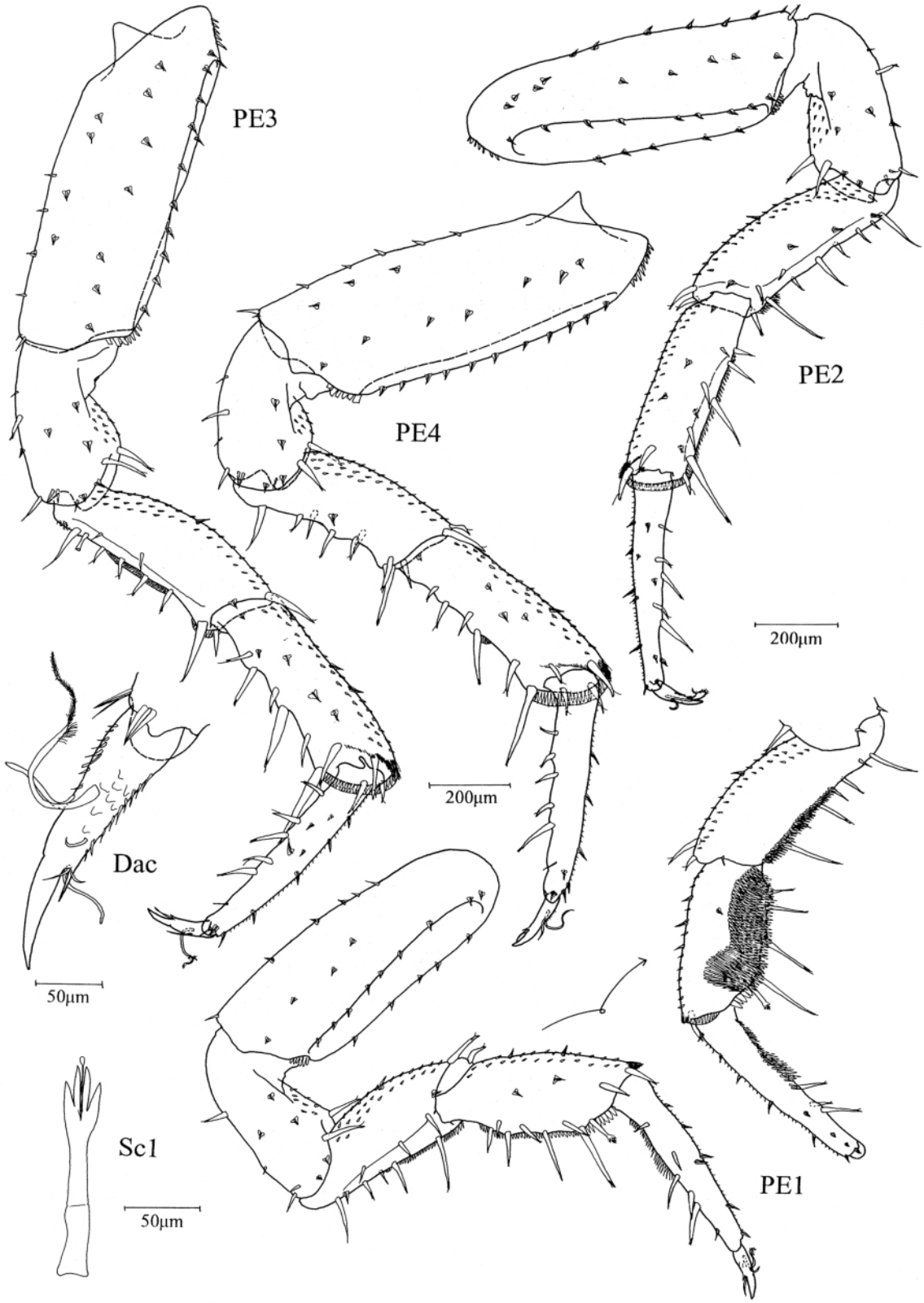


Fig. 24. *Ischioscia bolivari* Vandel: syntype male. Dac dactylus of pereiopod 5 in rostral view; PE1-4 pereiopods 1 to 4 in caudal view, with detail of PE1 rostrally; Sc1 ornamental sensory spine of carpus 1.

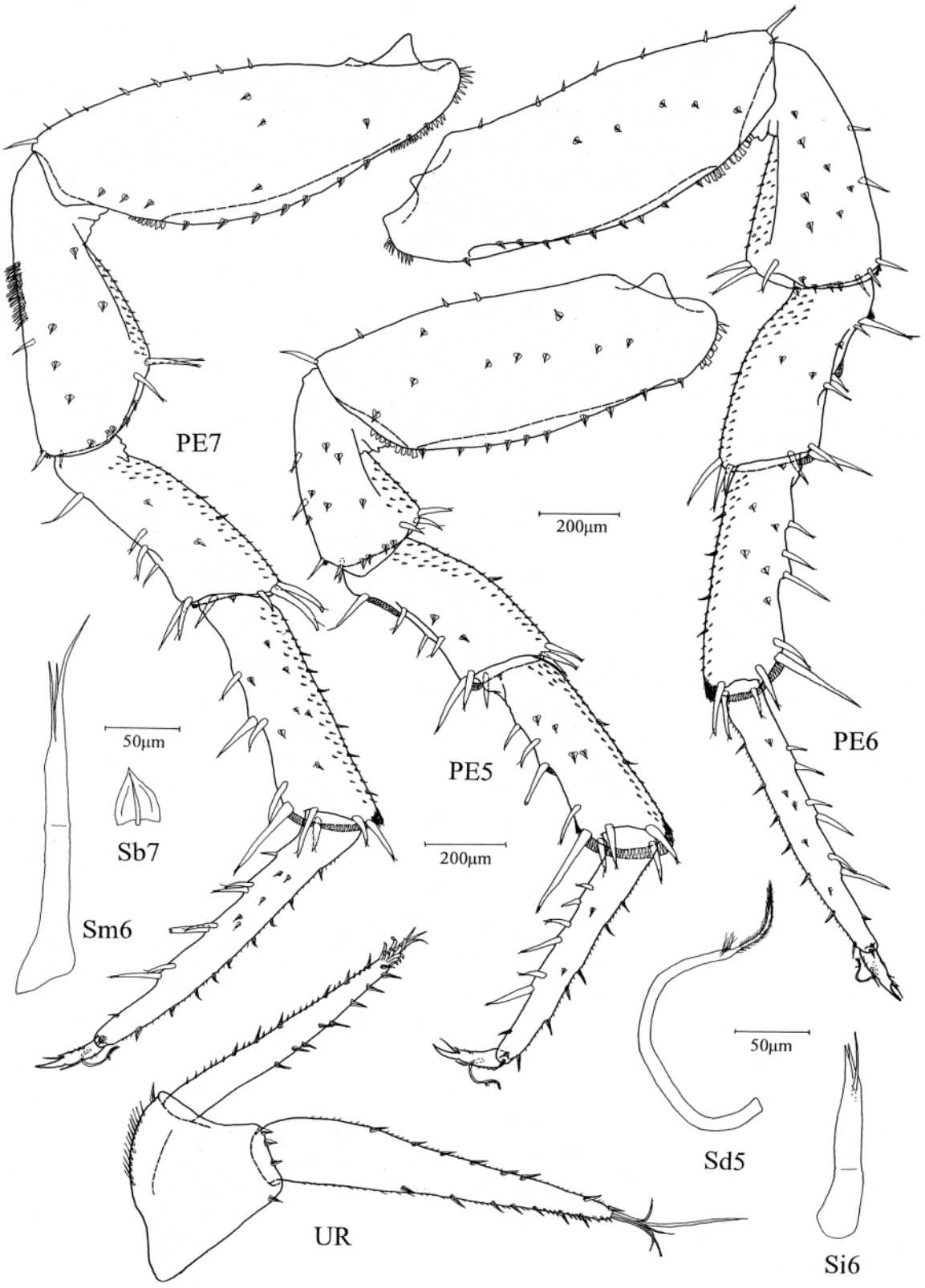


Fig. 25. *Ischioscia bolivari* Vandel: syntype male. PE5-7 pereiopods 5 to 7 in caudal view; Sb7 tricorn-like seta of basis 7; Sd5 dactylar seta 5; Si6 sensory spine of ischium 6; Sm6 medial sensory spine of merus 6; UR uropod in caudal view.

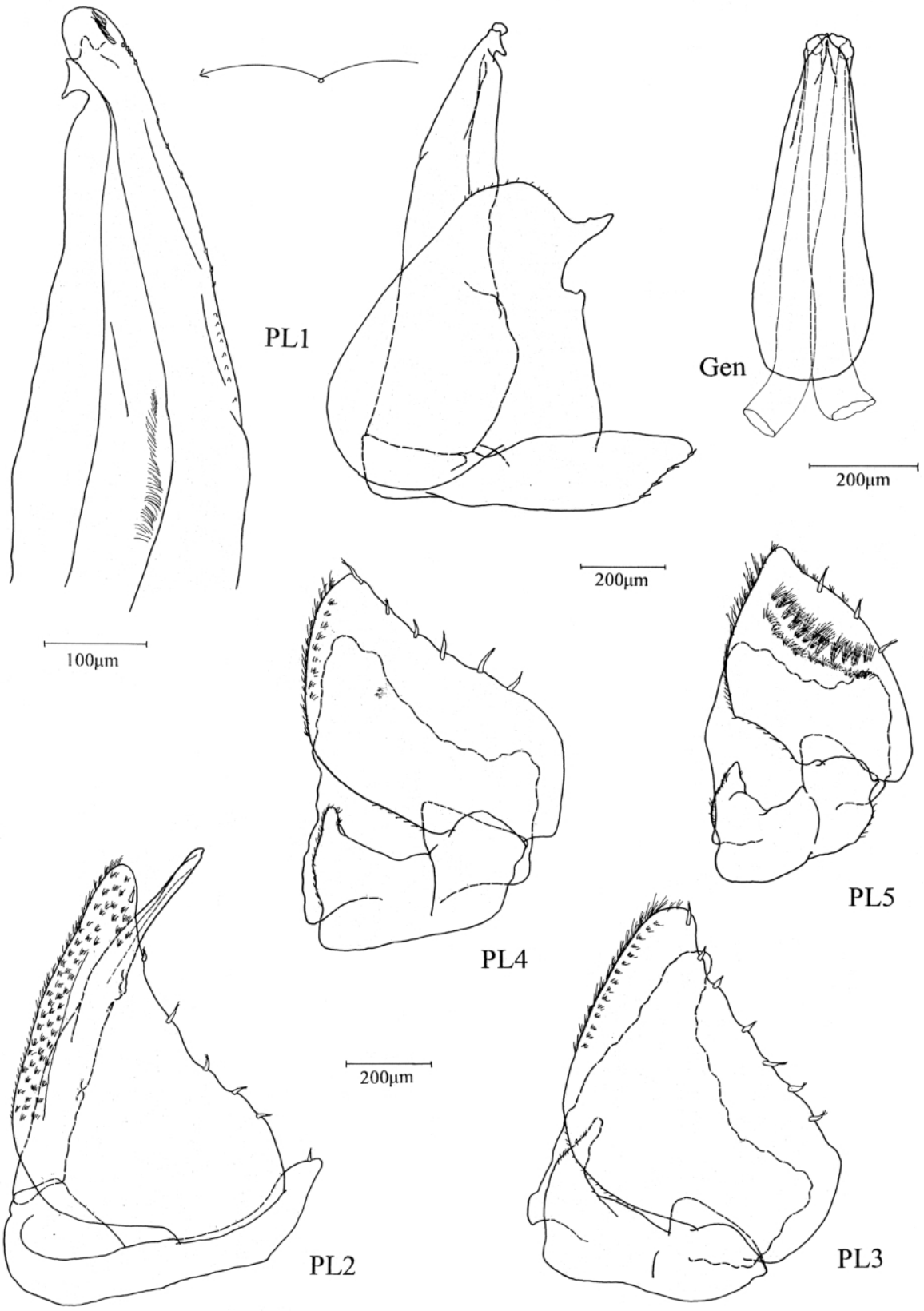


Fig. 26. *Ischioscia bolivari* Vandel: syntype male. Gen genital papilla; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite1 in caudal view.

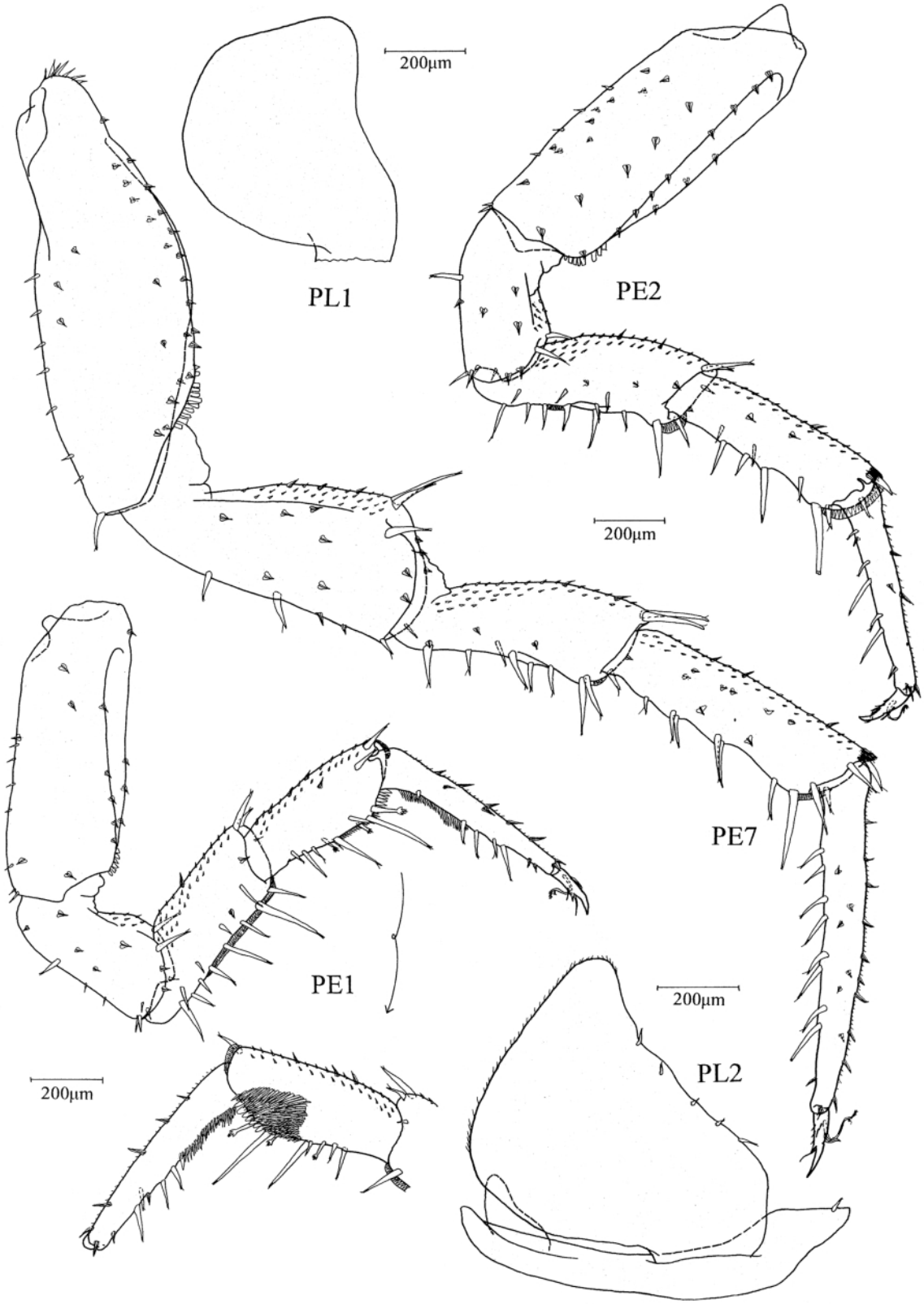


Fig. 27. *Ischioscia bolivari* Vandel: syntype female 8. PE1, 2, 7 pereiopods in caudal view, with detail of PE1 rostrally; PL1, 2 pleopods 1 and 2 in caudal view.

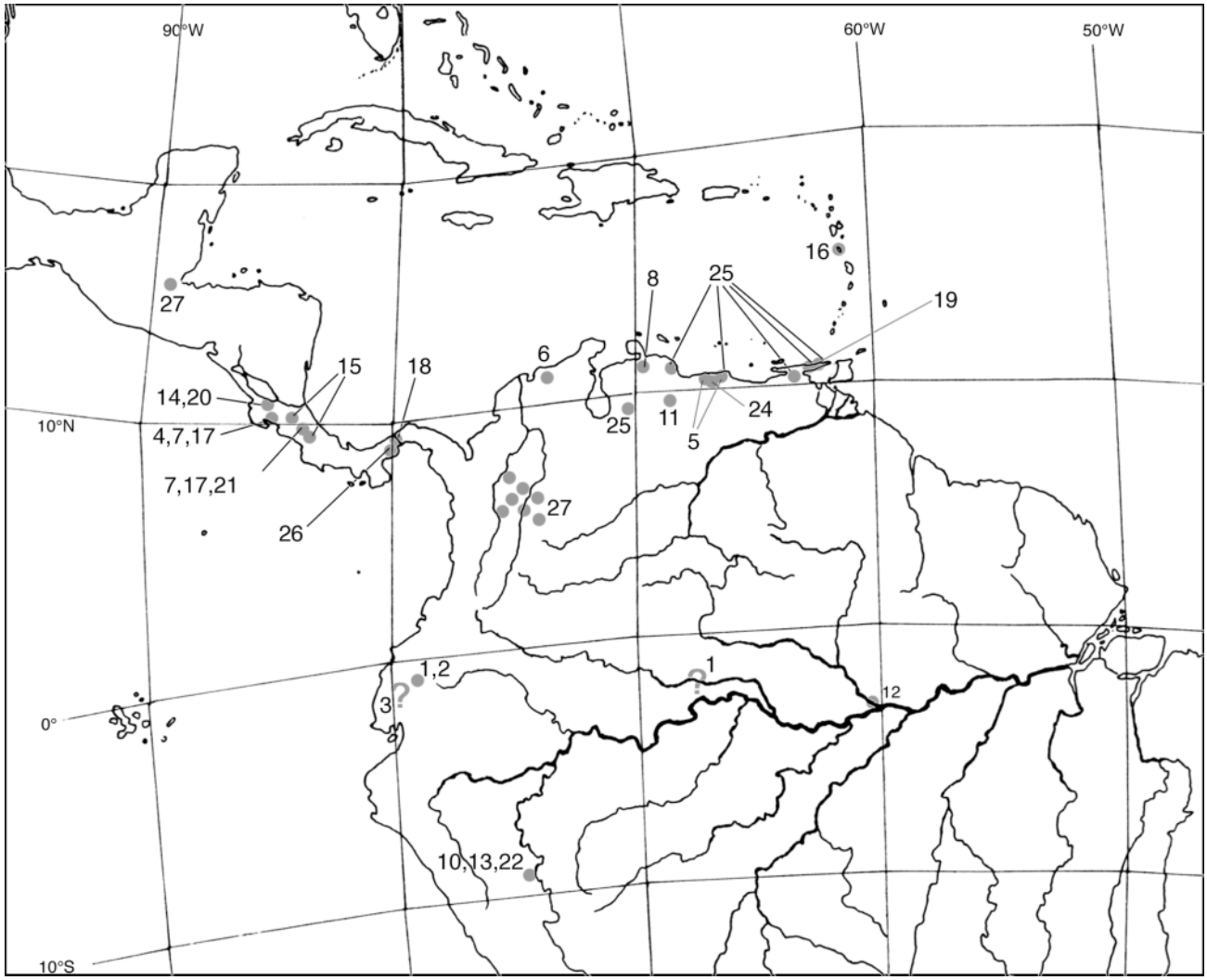


Fig. 28. Geographic distribution of *Ischioscia* species: 1 *amazonica*, 2 *andina*, 3 *bolivari*, 4 *cadoangelis*, 5 *colorata*, 6 *curvaculeus*, 7 *elongata*, 8 *fasciifrons*, 9 *guamae*, 10 *hanagarthi*, 11 *hirsuta*, 12 *irmleri*, 13 *longicauda*, 14 *marmorata*, 15 *martinae*, 16 *mineri*, 17 *muelleri*, 18 *panamensis*, 19 *pariae*, 20 *plurimaculata*, 21 *quadrispinis*, 22 *stenocarpa*, 23 *sturmi*, 24 *trifasciata*, 25 *variegata*, 26 *zebricolor*, 27 *Ischioscia* sp.

1 and 2 slightly enlarged with rostral scale fields, merus 1 and possibly 2 in adult male also with scale fields; ischium of male pereiopod 7 with 1 short sensory spine instead of 2 in the female, proximally with setose area.

Pleopods: pleopod exopodites rhomboid with sensory setae on lateral margin, medial margin bearing pectinate scales, pleopod 5 exopodite with 2 transverse rows of pectinate scales caudally, distal one with long hairs, proximal one with short hairs, endopodites medially pointed, pleopod 3 with most elongate endopodite (Fig. 26: PL1-5, Fig. 27: PL1-2). Sexual dimorphism: male pleopod 1 exopodite triangular with rounded edges, lateral margin bearing 2 acute protrusions separated by sinuous incision, endopodite pointed with pointed subapical lateral protrusion, latero-caudal row of spines reduced, spines very short, conspicuous only on apex (Fig. 26: PL1); pleopod 2 exopodite pointed with sinuous lateral margin bearing 6 sensory setae, medially with broad area bearing pectinate scales, endopodite slender, slightly surpassing exopodite (Fig. 26: PL2).

Uropod: protopodite with lateral groove, endopodite inserting proximally of exopodite, apically bearing some ribbon-shaped scales (Fig. 25: UR).

Genital papilla: ventral shield with almost parallel lateral margins, terminal spatula only slightly surpassing tip of ventral shield (Fig. 26: Gen).

Remarks: In several characters, *Ischioscia bolivari* agrees with the *martinae-variegata*-group from Venezuela and Central America, i.e. in the lack of the linea frontalis, the scale field of the male pereiopod 7 ischium, the shape of the male pleopod 1 exopodite with

its subapical lateral protrusion and deep incision, and in the laterally directed lobe at the apex of the male pleopod 1 endopodite (cf. Leistikow 1997). In contrast, the dactylus bears several characters not found in any other species examined. The inner claw is short, it can be discriminated from the surrounding setae only with difficulty. The dactylar seta has a prominent plumose apex, much longer than in other species and resembling the respective structure in some Scleropactidae, although it is most probably the plesiomorphic character state.

Ischioscia zebricolor Leistikow, 1999

Remarks: The species was originally described by Leistikow (1999b) based on three males from Panama, Gamboa. A recent survey of Oniscidea from Panama revealed new records of this interesting species. The material consists of 1 male and 12 females with a maximum body length of 5 mm. They were collected at Cerro Campana, 850 m a.s.l. (Bouchon, pers. comm.). The new sample corroborates the assumption in Leistikow (1999b) that the specimens examined are adults.

Ischioscia species

Material: Several females of an *Ischioscia* species were collected in Guatemala, at several localities representing undisturbed primary forest of the Sierra de las Minas (e.g., 1 female on hilltop above the Finca de Los Irrayoles, 700 m a.s.l., 17.X.1998, leg. A. Leistikow) as well as rural areas (several females in the southern zonas of Ciudad de Guatemala, in coll. Universidad del Valle de Guatemala).

Remarks: An exact specific determination of females is not yet possible. The records are interesting in the light of the remarkable shift of the northern border of the known geographic range of the genus to a latitude from 9°N to now 15°N.

Discussion

The genus *Ischioscia* Verhoeff is one of the most diverse taxa of the Crinocheta of the philosciid facies in the Neotropics. It occupies an area from the central Amazonian region northwest to the mountains of Guatemala. Most of the species are described from Costa Rica and Venezuela, where considerable research has been done in the last years (Leistikow 1997, 1999b, 2000, 2001b).

The numerous species of *Ischioscia* are all very similar to each other. The characters in which they differ are mainly the sexually dimorphic structures of the males. For most characters, several parallelisms and/or reversals must be assumed, because otherwise they support conflicting splits. Thus, the cladogram represents a phylogeny hypothesis that is comparatively weakly founded, and changes are likely when more species will be added. However, this hypothesis is useful as a basis for considerations on biogeography, ecology, and for further investigations.

In the evolution of *Ischioscia*, there are several adaptations to the copulatory behaviour of these species. Particularly the male pereiopods 1 to 3 and 7 have become complex structures which might play an important role in the mounting behaviour of the male. As stated above, the dorsal tegument of the females is rather smooth, the males can cling more effectively on the females when there are structures which support better contact to the female. These structures are the carpal brushes and ischial brushes, the extensions of the pereiopod 1 (to 3) carpus, and lobes on the pereiopod 7 found in several species.

Interestingly, the shape of the male pleopod 1 endopodites is rather uniform compared to other taxa of the philosciid facies, such as *Androdeloscia* or the oriental *Burmoniscus* Collinge, 1904. The uniformity of the pleopod 1 endopodites resembles the case of several other taxa of the Crinocheta, e.g. *Trachelipus* (Schmidt 1997). The explanation of similarity or diversity of the male pleopod 1 endopodites is hardly possible at the moment because of a lack of investigations on their functional morphology.

From the biogeographic point of view, the genus *Ischioscia* is of particular interest since it is a characteristic taxon of the Amazonian-Caribbean region. The species have dispersed in this region (Fig. 28) and can be found in both lowland and montane forests. Dispersion must have been channelled by the high ranges of the Andes, with the valleys acting as dispersion routes from the Andean Amazon region, where their closest relatives occur, to the Central American land bridge. A detailed discussion of the distributional patterns was given in Leistikow (2001c). Finally it should be noted that within most of its range the taxon *Ischioscia* is the only "philosciid" taxon with representatives of considerable size, i.e. more than 10 mm body length. It is apparently very successful in competing with similar taxa such as *Balloniscus* Budde-Lund and *Benthana* Budde-Lund, with at least the latter found in tropical areas of eastern South America.

Acknowledgements

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Appendix

Data matrix for PAUP

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Characters ..................................          1 11111 11112 22222 22222 3333
.............................................  12345 67890 12345 67890 12345 67890 1234
Ligia baudiniana ............................  00000 00000 00000 00000 00000 00000 0000
Deto echinata ...............................  01000 00000 00000 00000 00000 00000 0000
Philoscia muscorum ..........................  01000 01000 00000 00000 00000 01000 0000
Androdeloscia ferrarai.......................  01010 10000 00000 00000 00000 10000 0000
Prosekia rutilans ...........................  00010 00000 00000 00000 01000 00000 0000
Tropiscia flagellata.........................  10110 00000 00000 00000 010?0 10000 0000
I. zebricolor ...............................  10111 11010 01000 10000 00011 1?000 1000
I. variegata ................................  11111 00111 11110 11011 10000 11111 0111
I. marmorata ................................  11111 10111 11110 00111 00000 11111 01?0
I. hirsuta ..................................  11111 00111 11111 11111 10000 11111 1001
I. colorata..................................  11111 00111 11111 11111 10000 11111 1101
I. trifasciata ..............................  11111 00111 11110 11001 10000 11011 0001
I. pariae....................................  11111 11111 11110 11111 10000 11111 0011
I. quadrispinis .............................  11111 00111 11110 11011 10000 11111 11?1
I. martinae..................................  11111 00111 11010 11010 00000 11111 0100
I. mineri....................................  11111 00111 11110 11001 00000 11011 100?
I. bolivari..................................  11111 00110 01000 11000 00000 11111 0100
I. fasciifrons ..............................  11111 00111 11010 00100 00000 11010 1000
I. cadoangelis ..............................  11111 00111 11000 11010 01000 11111 01?0
I. elongata..................................  11111 00111 11011 10010 00000 11111 10??
I. muelleri..................................  11111 00111 11011 00010 00000 11111 10??
I. plurimaculata ............................  11111 00111 01010 11100 00000 11011 00?0
I. guamae....................................  11111 00111 11010 11001 10000 11111 1001
I. sturmi....................................  10111 11111 11010 00000 00111 10000 00?0
I. panamensis ...............................  10111 00111 11110 11011 10000 11111 1101
I. amazonica ................................  10111 11110 11011 10010 00111 11000 00?0
I. curvaculeus ..............................  11111 00110 01000 10000 00000 11011 00?0
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