

specific variability, as follows. (A) The merus is trapezoidal in all species of Trichodactylinae and in some species of other genera; in two species of this group, *Dilocarcinus truncatus* and *D. bulbifer*, the antero-mesial angle is produced into a triangular tooth located near the articulation of the palp (Fig. 8G, H; a); the distal external spine is considerably reduced (r), particularly in the Trichodactylinae (Fig. 6B, D, E), but also in *Forsteria venezuelensis* (Fig. 8A) and in some species of *Sylviocarcinus* (Fig. 7A). (B) The merus is conspicuously narrow in some species of *Valdivia*, *Sylviocarcinus*, and *Dilocarcinus*; this reduction of the merus is accompanied in some species of *Dilocarcinus* by a conspicuous slenderness of the exognath. (4) The ischium is unusually wide in *Zilchiopsis emarginatus*.

Peristomial spinulation, orbits and basal antennal articles

Some freshwater crabs, in particular the Pseudothelphusidae, are capable of aerial respiration (DÍAZ & RODRÍGUEZ, 1977), but, in the Trichodactylidae, respiration takes place only under water and the orientation of the water coming through the efferent channels, away from the inhaling orifices at the base of the chelipeds, is achieved by several spinuous borders, ridges and hairy areas. The peristomial spinulation in Trichodactylidae comprises the lower orbital margin and the buccal angle, and both varies from smooth ridges, as in *Avotrichodactylus constrictus* (Fig. 2A), to ridges provided with strong hooked spines, as in *Dilocarcinus dentatus* and *Fredilocarcinus musmuschiae* (Fig. 2D, F).

In most species of Portunidae and Trichodactylidae the access of the water currents is kept away from the orbits by means of a lateral expansion of the antennal basal article; this expansion is usually interpreted as the exopod of this appendage. In the Portunidae the expansion is well developed and directly in contact with the lower orbital margin (Fig. 9A); in the Trichodactylidae an occlusor tooth is interposed between the expansion and the orbital margin, but both antennal expansion and occlusive tooth display considerable variability.

In the genera *Sylviocarcinus* (Fig. 9B-G) and *Zilchiopsis* (Fig. 9I, J) the lobe is conspicuously developed. All the species of *Valdivia* present a lobe moderately reduced, but the species of Trichodactylinae could be arranged in a series (Fig. 10D-I) which displays a progressive reduction of this lobe, beginning with *Trichodactylus fluviatilis* and *T. petropolitanus*, and ending in *T. kensleyi*. In *Dilocarcinus* and *Fredilocarcinus* the lobe is completely absent (Fig. 10J-L).

The reduction of the basal antennal expansion is accompanied by an increase in size of the occlusor tooth. In *Sylviocarcinus devillei* and *S. piriformis* (Fig. 10B, C) the tooth is fused to the external orbital angle. This tooth is progressively detached in the species of *Sylviocarcinus* and other genera; it becomes obsolescent in *Zilchiopsis sattleri* (Fig. 9J), and even disappears in *Trichodactylus petropolitanus* (Fig. 10E).

The internal orbital angle is the third element closing the orbit on its inner angle. In most species it is well developed, either spiniform or blunt, and directed upwards. However, in *Fredilocarcinus musmuschiae* and in some *Dilocarcinus* (Fig. 2D-F), in addition to the reduction of the occlusive orbital tooth and the basal antennal expansion, the outer orbital angle and the spines following it laterally are bent downwards, and thus the floor of the orbital cavity is continuous with the epistome. In this particular case the orbits are very large in the vertical direction and eyes very small, disproportionate to orbital cavity.

REPRODUCTIVE STRUCTURES

Penial groove

As discussed above, the male opening of Trichodactylidae is located in the coxa of the 5th pereopod, reaching the base of the first gonopod through a penial groove. This groove, however, does not show the same degree of development in all species. In the most rudimentary condition found in *Sylviocarcinus* (Fig. 13) the

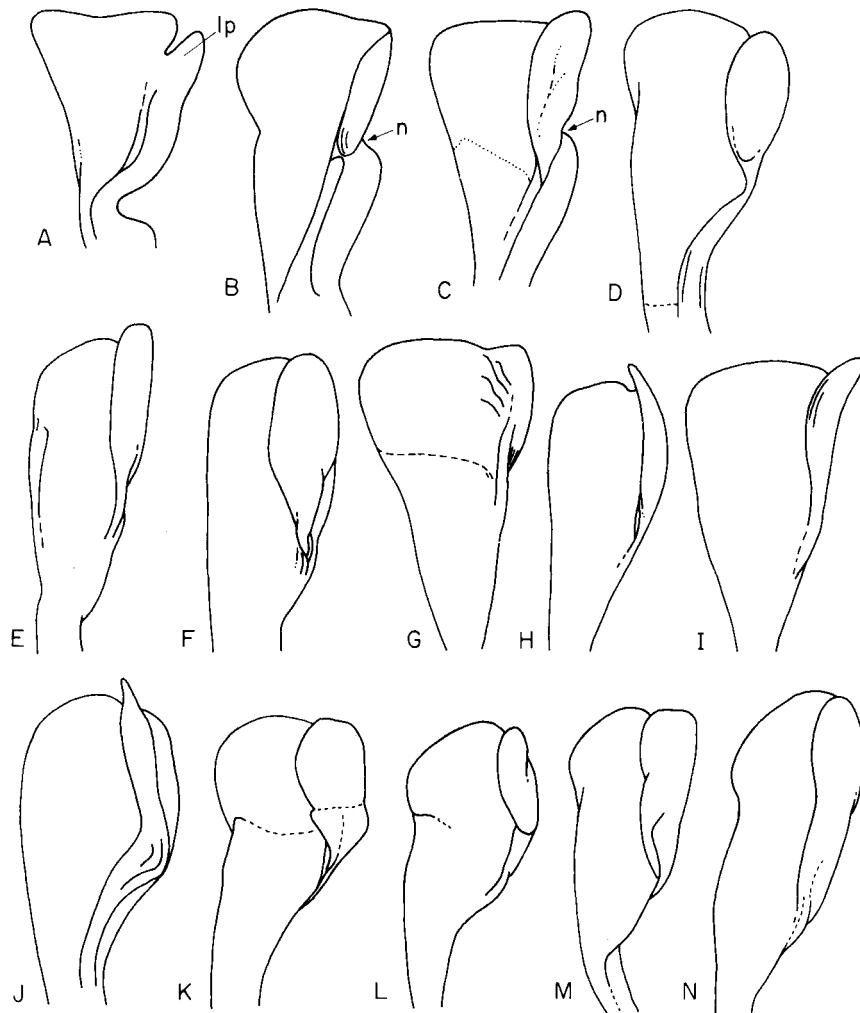


FIGURE 5

Endopod of 1st maxilliped, cephalic (anterior) view: A, *Lupella forceps* (Portunidae); B, *Sylviocarcinus piriformis*; C, *S. devillei*; D, *S. pictus*; E, *Valdivia serrata*; F, *V. camerani*; G, *Forsteria venezuelensis*; H, *V. barttii*; I, *Zilchiopsis sattleri*; J, *Trichodactylus quinquedentatus*; K, *T. fluviatilis*; L, *Fredilocarcinus musmuschiaae*; M, *Z. emarginatus*; N, *Dilocarcinus dentatus*. lp, portunid lobe; n, incision.

penial groove is a shallow depression and the surface of the sternite is not folded over it; consequently the sternal lobe is rudimentary. The 7th episternite can be elongated and narrow (Fig. 13A-F), or short and wide (Fig. 13G-J), but it is not projected over the groove.

In the species of *Trichodactylus*, *Mikrotrichodactylus* and *Avotrichodactylus* (Fig. 12), the caudal portion of the 7th episternite is narrow and displaced backwards, forming a spur which, together with the sternal lobe (r), partially covers the penial groove. These species can be serialized according to the progressive elongation of the 7th episternite, from the condition found in *Trichodactylus fluviatilis* and *T. kensleyi* (Fig. 12A, C) in which the caudal spur is narrow and almost straight, to the spur strongly bent inwards of *T. quinquedentatus* (E), and widened as in *Avotrichodactylus oaxensis* (G).

Male abdomen

A narrowing of the abdomen in many groups of Brachyura is associated with the displacement of the male opening from a coxal to a sternal position. In the Trichodactylidae, although the male apertures are always coxal, this trend is manifest in several species. *Mikrotrichodactylus* has a triangular abdomen, very short and wide; but in *Trichodactylus* some species have a similar triangular abdomen, while others, like *T. fluviatilis*, have a trapezoidal, narrower one, with the margins concave. Some species of *Dilocarcinus* possess a wide, rounded abdomen. In all other species the abdomen is more or less trapezoidal.

In many groups of Brachyura there is a trend to the stenosis of the abdominal segments, which eventually may end in the obsolescence of the abdominal sutures. Within the Trichodactylidae, only in the members of the subfamily Trichodactylinae all abdominal sutures are clearly visible. In *Sylviocarcinus piriformis* all sutures are partially visible. In *S. devillei*, *S. maldonadoensis*, the genus *Avotrichodactylus*, and the species of *Valdivia*, only the sutures 6/7 and 7/8 are visible. In *S. pictus*, *S. sp.* and all the species of other genera only the 6/7 suture is visible and mobile.

First male gonopod

As stated before, the conical shape of the first male gonopod is a plesiomorphic state. The Trichodactylinae depart from this form and, in all of them, there are angular lobes on the mesial and lateral sides of the first gonopod, giving to this appendage a flask-shaped appearance. On the other hand, the V-shaped apical opening (gonopore) found also in the Trichodactylinae and in *Sylviocarcinus*, is a plesiomorphic state. All other species have a terminal, slit-like gonopore, usually flanked by corneous processes (Fig. 15). The apical setae present in some Trichodactylinae (with the exception of *Avotrichodactylus*, Fig. 15C) are small, scattered on the cephalic surface (Fig. 15B) whereas in other species they are very long, conspicuous and grouped as a brush in the lateral surface (Fig. 15).

Notwithstanding the diversity of form displayed by the gonopods inside each genus, it is possible to dispose them in series according to postulated homologies, as shown for *Dilocarcinus* (Fig. 14). The gonopod which depart most from the general morphology found in the family is that of *Fredilocarcinus musmuschiae*, but even here it is possible to place it in the last stages of the series of *Dilocarcinus*.

Second male gonopod

Three types of male second gonopod are found within the Trichodactylidae, (1) very short, (2) S-shaped, of equal length or slightly longer than first, and (3) very long, rolled up as a crosier. The second type possibly corresponds to the apomorphic state found in the Carcininae. The Trichodactylidae do not possess the specializations found in some species of Liocarcininae, particularly in *Macropipus* and other genera, in which the apex of the second gonopod ends in a pseudochela due to the reduction of the terminal flagellum

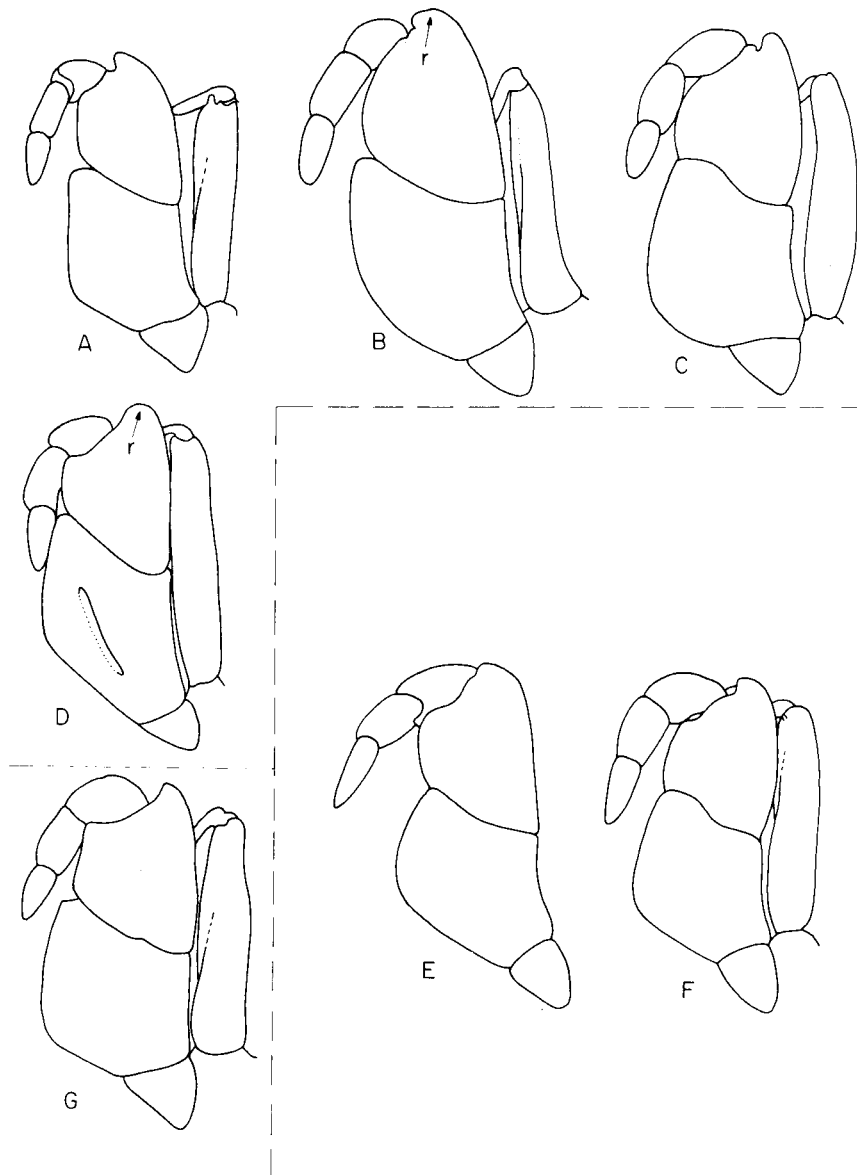


FIGURE 6

Left third maxilliped in Trichodactylidae: A, *Trichodactylus fluviatilis*; B, *T. petropolitanus*; C, *T. kensleyi*; D, *T. quinquedentatus*; E, *Mikrotrichodactylus borellianus*; F, *M. panoplus*; G, *Avotrichodactylus oaxensis*. r, distal external spine.

(ZARIQUEY, 1968, Fig. 124, 126), but in the very short appendage of *Rodriguezia* and *Avotrichodactylus*, a similar reduction is achieved (Fig. 23E, H; 24E).

PEREIOPODS

In the generalized condition the walking legs are stout, with the propodus widened (length/width = 1.2-1.8), the dactylus lanceolate, and the lower margin of dactylus and propodus densely covered by long setae. In a few species the legs are more slender (length/width of propodus = 2, or more; length/width of merus >4). The two cave species found in the family have, of course, extremely long pereopods. The setation is also different in some Trichodactylinae: the long setae are replaced by sparse short hairs, or are totally absent, and the sides of the dactylus are covered by a felt-like tomentum (Fig. 17I; Fig. 22I).

In most species the chelipeds are stout and conspicuously unequal in size, but in *Valdivia gila* this inequality reaches its maximum, with a cheliped considerably larger than the carapace. In many species the chelipeds possess longitudinal grooves along the external surfaces of the fingers. This condition is reminiscent of the grooved chelipeds of Portunidae, and is more manifest in the smaller cheliped. In a few species, the grooves are obsolescent.

Data Analysis

In contrast with the Pseudothelphusidae in which most reliable characters for the cladistic analysis are found in the first gonopod (RODRÍGUEZ & CAMPOS, 1989), in the Trichodactylidae there are many somatic characters available. Of all the characters discussed before, 40 were selected for the cladistic analysis (table I). Several were rejected because of their continuous distribution and others were not used because of their intraspecific variability. Only two characters from those of the first male gonopod were selected due to the difficulties encountered in homologating the characters in conical and flask-shaped types of gonopods. The species included in the phylogenetic analysis are listed in table II. *Dilocarcinus castelnaui*, *D. argentinianus* and *D. spinifer* were excluded because the carapace morphology in the genus *Dilocarcinus* is rather uniform and the excluded species did not contribute new information to the analysis. A few other species in other genera were also excluded because some of the morphological data required for the matrix of characters were not available.

The phylogenetic programs used were Phylip (Phylogeny Inference Program) 3.0 (FELSENSTEIN, 1984) routings MIX, and PAUP (Phylogenetic Analysis Using Parsimony) 2.2 routing BAND B that guarantee the finding of all the most parsimonious trees. A strict consensus was obtained by using the program CONTREE included in PAUP.

Five and 18 more parsimonious trees with 108 steps and Consistency Index of 0.37 were found with programs Phylip and PAUP, respectively. An individual tree with character changes is shown in Fig. 16A. The strict consensus tree in Fig. 16B summarizes the point of agreement in all trees. The species of *Trichodactylus*, *Valdivia* and *Sylviocarcinus* forms well-defined monophyletic groups. *Rodriguezia* appears nested in *Trichodactylus* and the three species of *Avotrichodactylus* form three distinct clades closely associated, but *A. constrictus* and *A. oaxensis* forms a dichotomy in the strict consensus tree which is readily resolved by the diagnostic characters of both species. The species *Sylviocarcinus* and *Valdivia* form two well differentiated

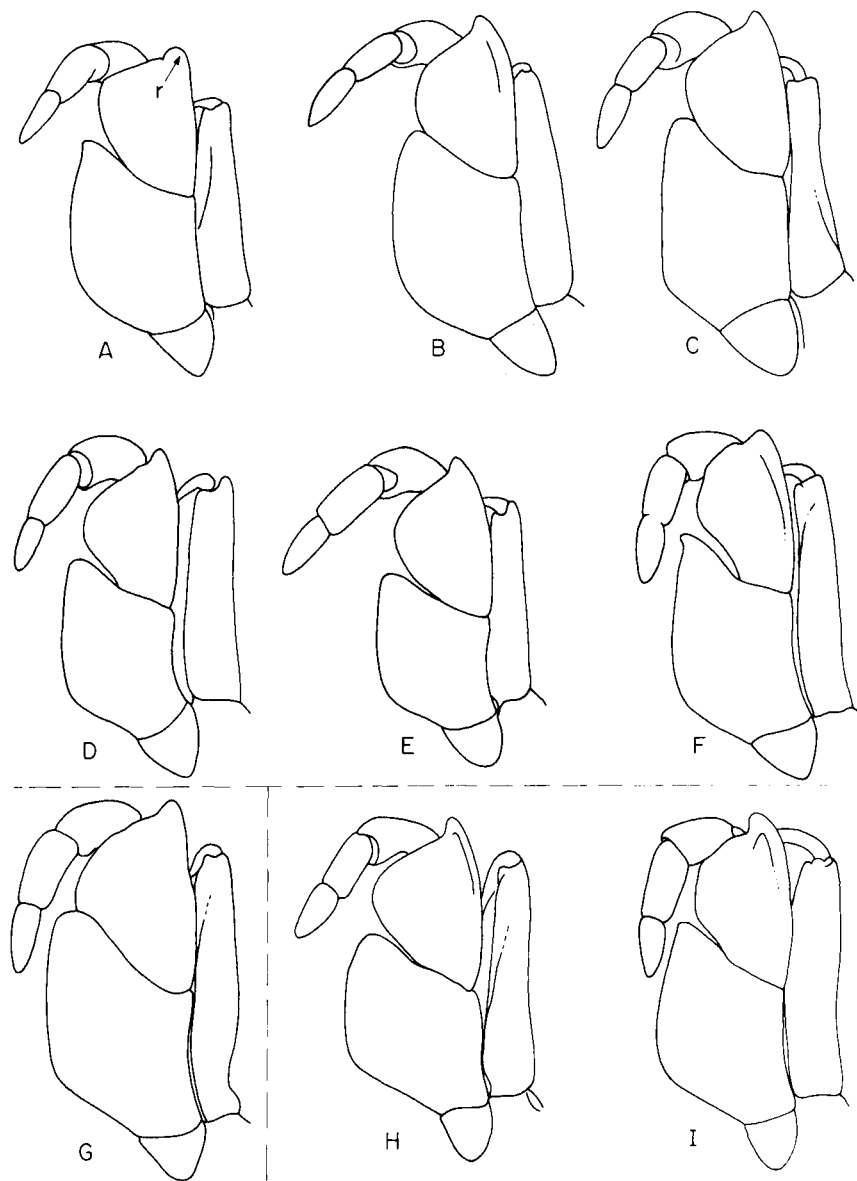


FIGURE 7
 Left third maxilliped in Trichodactylidae: A, *Sylviocarcinus piriformis* (Magdalena Valley); B, *S. maldonadoensis*; C, *S. piriformis*; D, *S. sp.*; E, *S. pictus*; F, *S. devillei*; G, *Fredilocarcinus musmuscbiae*; H, *Zilchiopsis emarginatus*; I, *Z. sattleri*. r, distal external spine.

clades. In *Dilocarcinus* there is an unresolved trichotomy with *D. dentatus*, *D. medemi*, and *D. niceforei* explainable for the exclusion of most gonopodal characters in the present analysis. *Forsteria venezuelensis* and *Fredilocarcinus musmuschiae* appear as basal clades for the species of *Sylviocarcinus* and *Dilocarcinus* respectively. The two species of *Zilchiopsis* are widely separated in the cladogram.

The tree shown in Fig. 16A agrees with our tentative biogeographical model for the evolution of the group as will be discussed further in the biogeographical section. All trees agree on reversal to plesiomorphic conditions in characters 3, 6, 7, 9, 10, 13, 17, 19, 21, 24, 25, 32, 36, and 38 as the most parsimonious explanation, and independent development of the derived states in characters 1, 2, 4, 5, 6, 9, 11, 14, 15, 17, 18, 20, 26, 28, 30, 39, and 40.

This cladistic analysis can be translated into the following taxonomic arrangement:

Subfamily TRICHODACTYLINAE H. Milne Edwards, 1853

Genus *Trichodactylus* Latreille, 1828

Genus *Mikrotrichodactylus* Pretzmann, 1968

Genus *Rodriguezia* Bott, 1969

Genus *Avotrichodactylus* Pretzmann, 1968

Subfamily DILOCARCININAE Pretzmann, 1978

Tribe HOLTHUISIINI Pretzmann, 1978

Genus *Sylviocarcinus* H. Milne Edwards, 1853

Tribe VALDIVIINI Pretzmann, 1978

Genus *Valdivia* White, 1847

Genus *Forsteria* Bott, 1969

Tribe DILOCARCININI Pretzmann, 1978

Genus *Zilchiopsis* Bott, 1969

Genus *Fredilocarcinus* Pretzmann, 1978

Genus *Dilocarcinus* H. Milne Edwards, 1853

The major divergence between the cladogram and this classification is in the validation of the genus *Zilchiopsis*. As will be explained further in the systematic section, the species grouped under this genus are transitional between the Valdiviini and the Dilocarcinini. However, to avoid an excessive generic splitting, the four species are kept in one genus inside the Tribe Dilocarcinini.

This taxonomic arrangement differs in several respects from the classifications used by other authors. RATHBUN (1906) gave generic status only to *Trichodactylus*, reduced *Valdivia* and *Dilocarcinus* to subgenera of the first, and discarded *Sylviocarcinus*. This simple arrangement was used by all latter authors until PRETZMANN (1968b) and BOTT (1969) proposed two alternative systems, with little in common between themselves (Appendix 1). BOTT (1969) recognized *Trichodactylus*, *Valdivia*, *Dilocarcinus* and *Sylviocarcinus* as distinct genera (the first three with different subgeneric divisions), and created *Zilchiopsis* and *Poppiana* as new genera. PRETZMANN's system is more elaborate. In a first version (PRETZMANN, 1968b), he divided *Trichodactylus* into new subgenera, considered *Valdivia* (with the subgenera *Valdivia* and *Rotundovaldivia*) and *Dilocarcinus* as separate genera, omitted *Sylviocarcinus*, and created *Holthuisia* (also spelled *Holthuisisia* by the author) as a new genus. In a further version of his system PRETZMANN (1978a) elevated *Rotundovaldivia* to generic rank, created *Fredilocarcinus* as a new subgenus within *Dilocarcinus*, and admitted BOTT's genus *Zilchiopsis*. He arranged these genera into a single subfamily, Trichodactylinae, with four tribes, Trichodactylini, Holthuisiini, Dilocarcinini and Valdiviini.

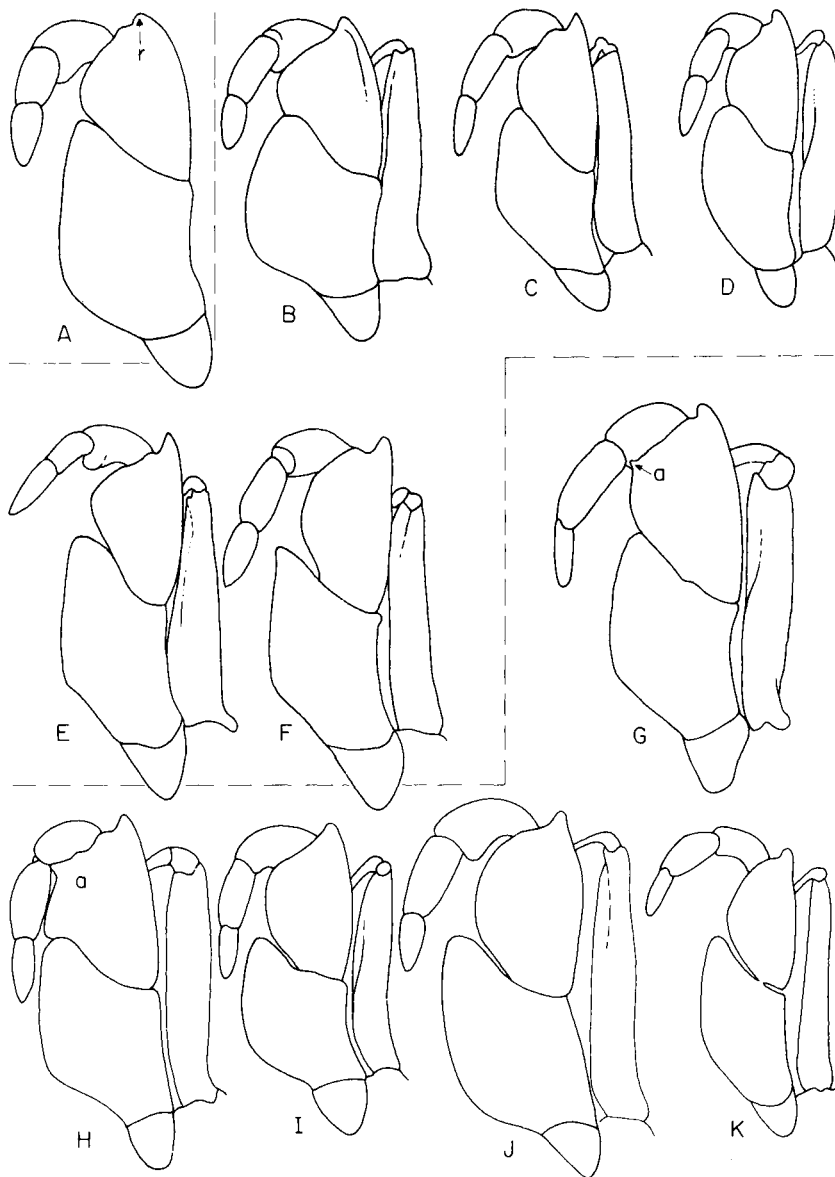


FIGURE 8

Left third maxilliped in Trichodactylidae: A, *Forsteria venezuelensis*; B, *Zilchiopsis emarginatus*, young; C, *Valdivia serrata*; D, *V. camerani*; E, *V. haritii*; F, *V. gila*; G, *Dilocarcinus truncatus*; H, *D. bulbifer*; I, *D. pagei*; J, *D. dentatus*; K, *D. niceforei*. a, antero-mesial tooth; r, distal external spine.

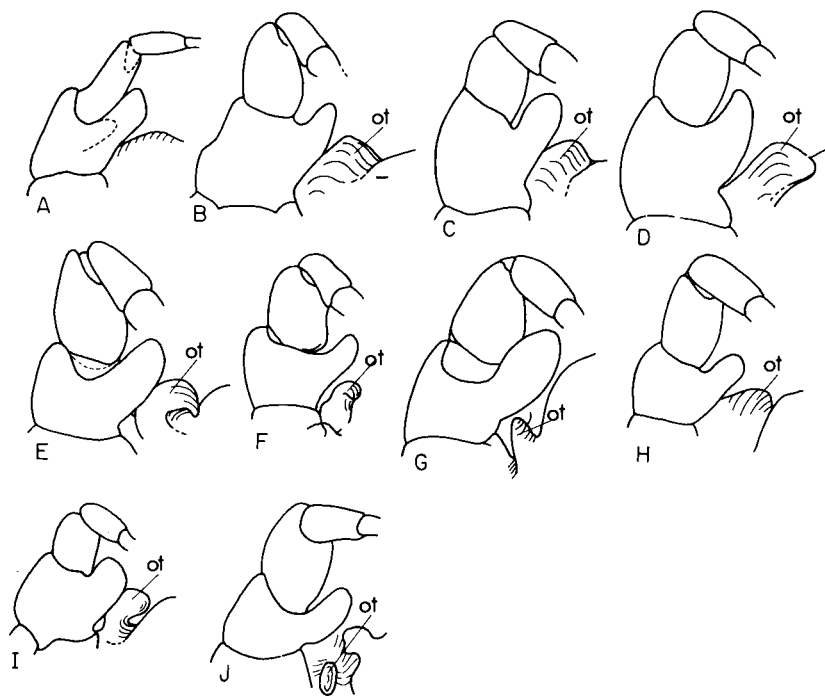


FIGURE 9

Basal article of left antenna, species with a lateral expansion: A, *Lupella forceps* (Portunidae); B, *Sylviocarcinus devillei*; C, *S. piriformis* (Maracaibo basin); D, *S. maldonadoensis*; E, *S. sp.*; F, *S. pictus*; G, *S. piriformis* (Magdalena Valley); H, *Forsteria venezuelensis*; I, *Zilchiopsis emarginatus*; J, *Z. sattleri*. ot, occlusive tooth.

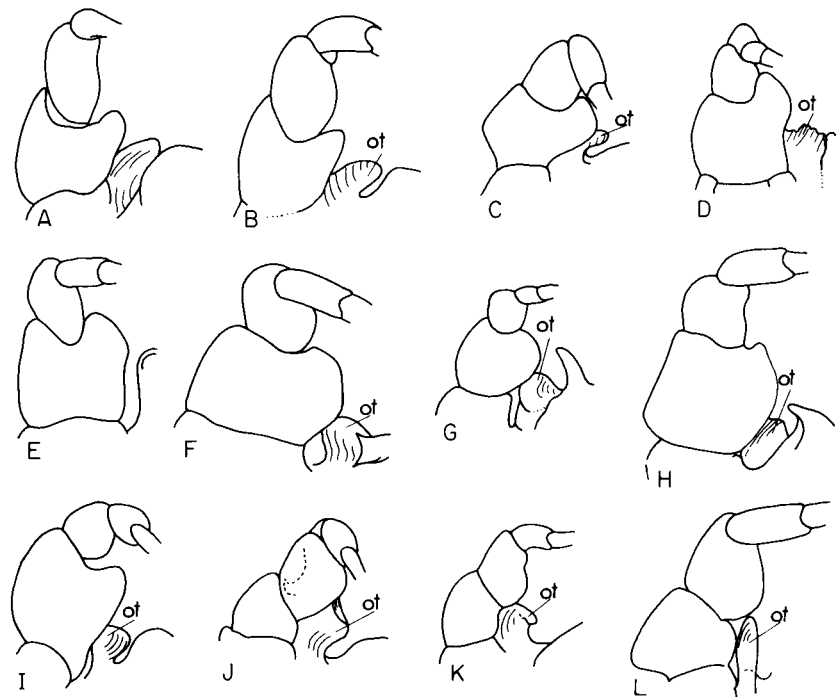


FIGURE 10

Basal article of antenna, species with exopodite reduced: A, *Valdivia gila*; B, *V. serrata*; C, *Zilchiopsis emarginatus*, young; D, *Trichodactylus fluviatilis*; E, *T. petropolitanus*; F, *T. quinquedentatus*; G, *T. kensleyi*; H, *Mikrotrichodactylus panoplus*; I, *Avotrichodactylus constrictus*; J, *Fredilocarcinus musmuschiai*; K, *Dilocarcinus bulbifer*; L, *D. dentatus*. ot, occlusive tooth.

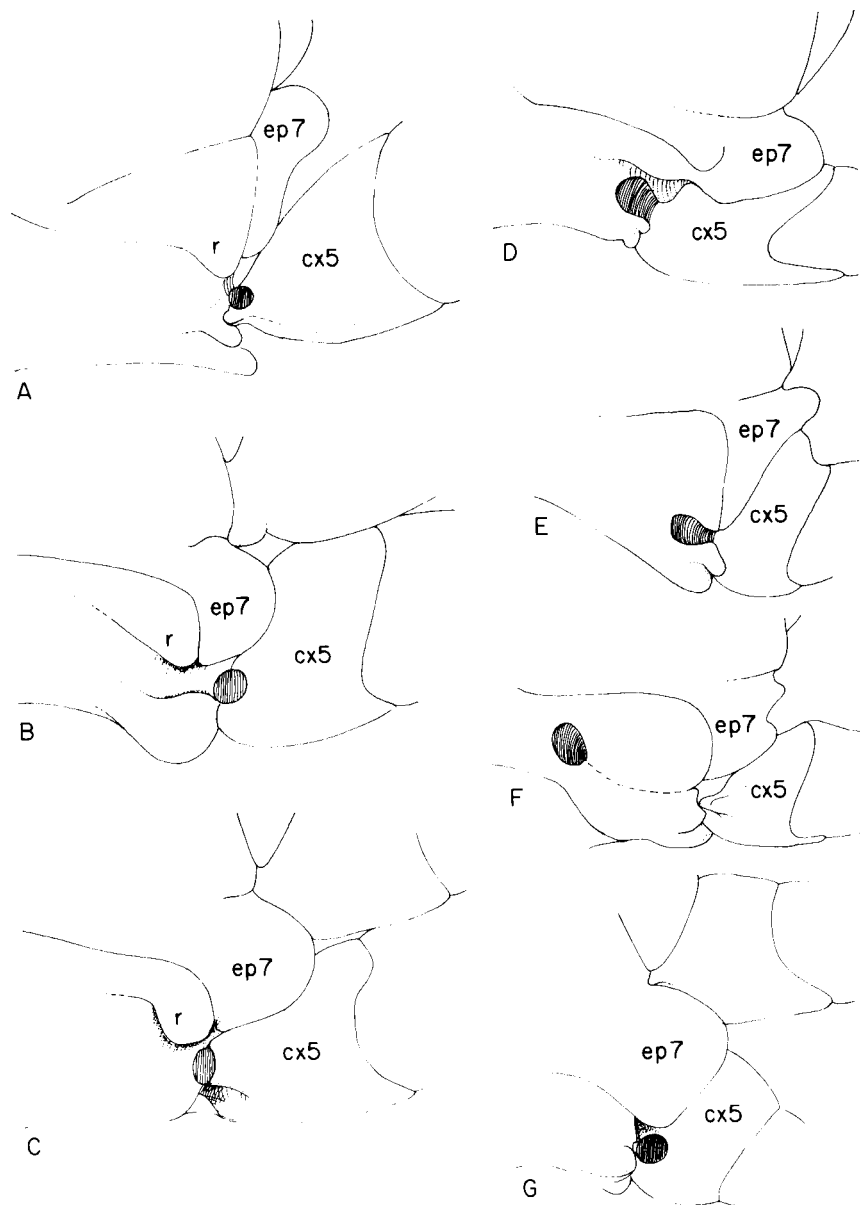


FIGURE 11

Relative position of genital aperture in different species of Brachyura: A, *Callinectes bocourti* (Portunidae); B, *Mikrotrichodactylus borellianus* (Trichodactylidae); C, *Sommaniathelphusa sexpunctata* (Parathelphusidae); D, *Geograpsus lividus* (Grapsidae); E, *Percnon gibbesi* (Grapsidae); F, *Cyclograpsus integer* (Grapsidae); G, *Eudaniela garmani* (Pseudothelphusidae). cx5, fifth coxa; ep7, 7th episternite; r, lobe of 8th sternite. Penis removed to expose genital aperture.

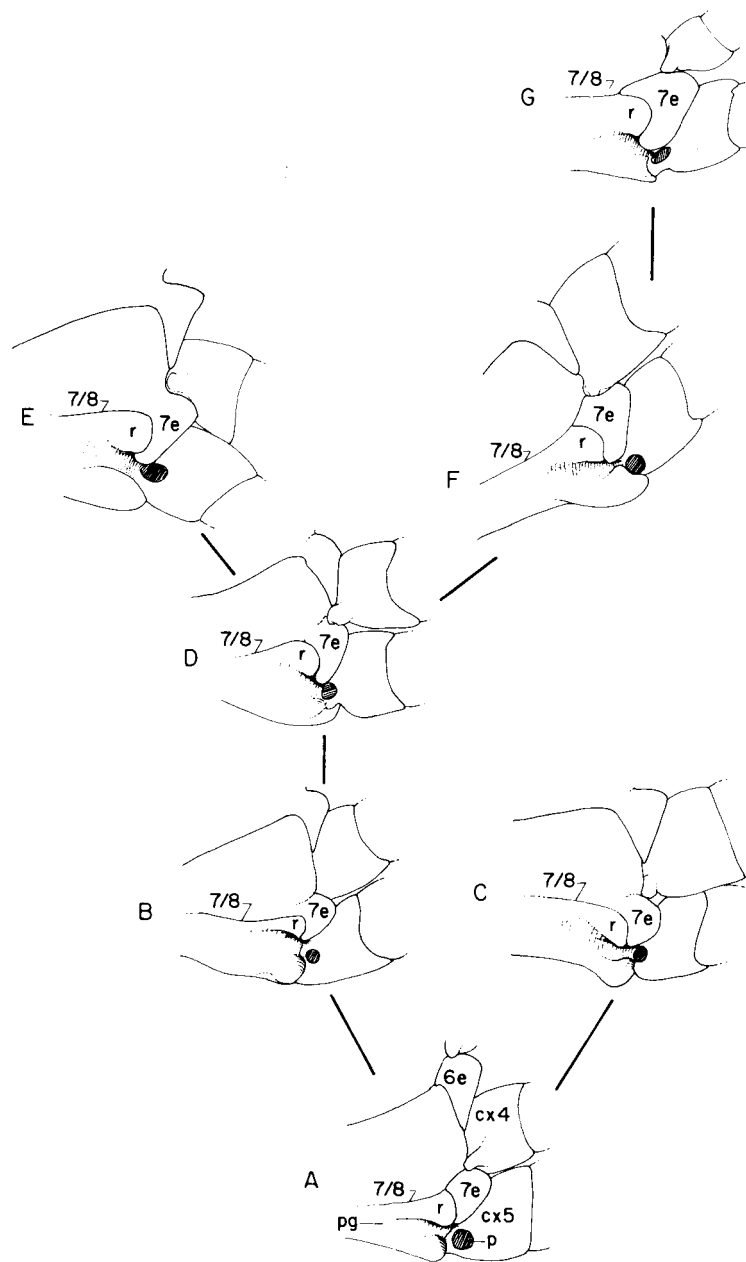


FIGURE 12

Homologies in the penial groove of Trichodactylinae: A, *Trichodactylus fluviatilis*; B, *T. petropolitanus*; C, *Mikrotrichodactylus borellianus*; D, *T. kensleyi*; E, *T. quinquedentatus*; F, *Avotrichodactylus constrictus*; G, *A. oaxensis*. cx4, fourth coxa; cx5, fifth coxa; 6e, 6th episternite; 7e, 7th episternite; p, foramen; pg, penial groove; r, lobe of 8th sternite; 7/8, suture between 7th and 8th sternite.

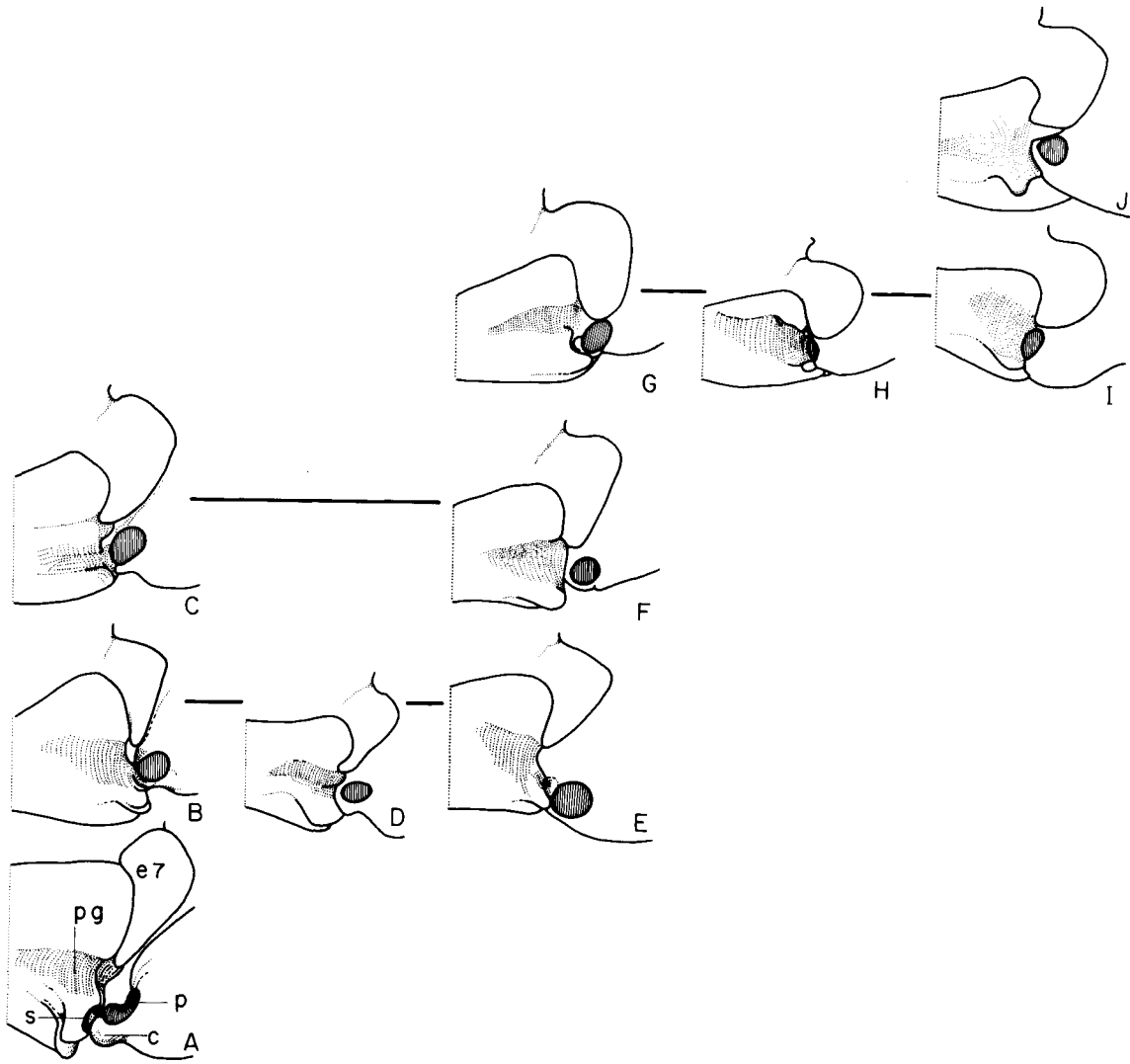


FIGURE 13

Homologies in the penial groove of Dilocarcininae. A, *Sylviocarcinus devillei*; B, *S. piriformis*; C, *S. pictus*, *S. sp.*; D, *Forsteria venezuelensis*; E, *Valdivia barttii*; F, *V. camerani*, *V. gila*, *V. serrata*; G, *Zilchiopsis emarginatus*, young; H, *Z. emarginatus*, *Z. sattleri*, *Fredilocarcinus musmuschiae*; I, *Dilocarcinus truncatus*, *D. bulbifer*, *D. niceforei*; J, *D. dentatus*, *D. pagei*. c, condylus; e7, 7th episternite; p, foramen; pg, penial groove; s, socket.

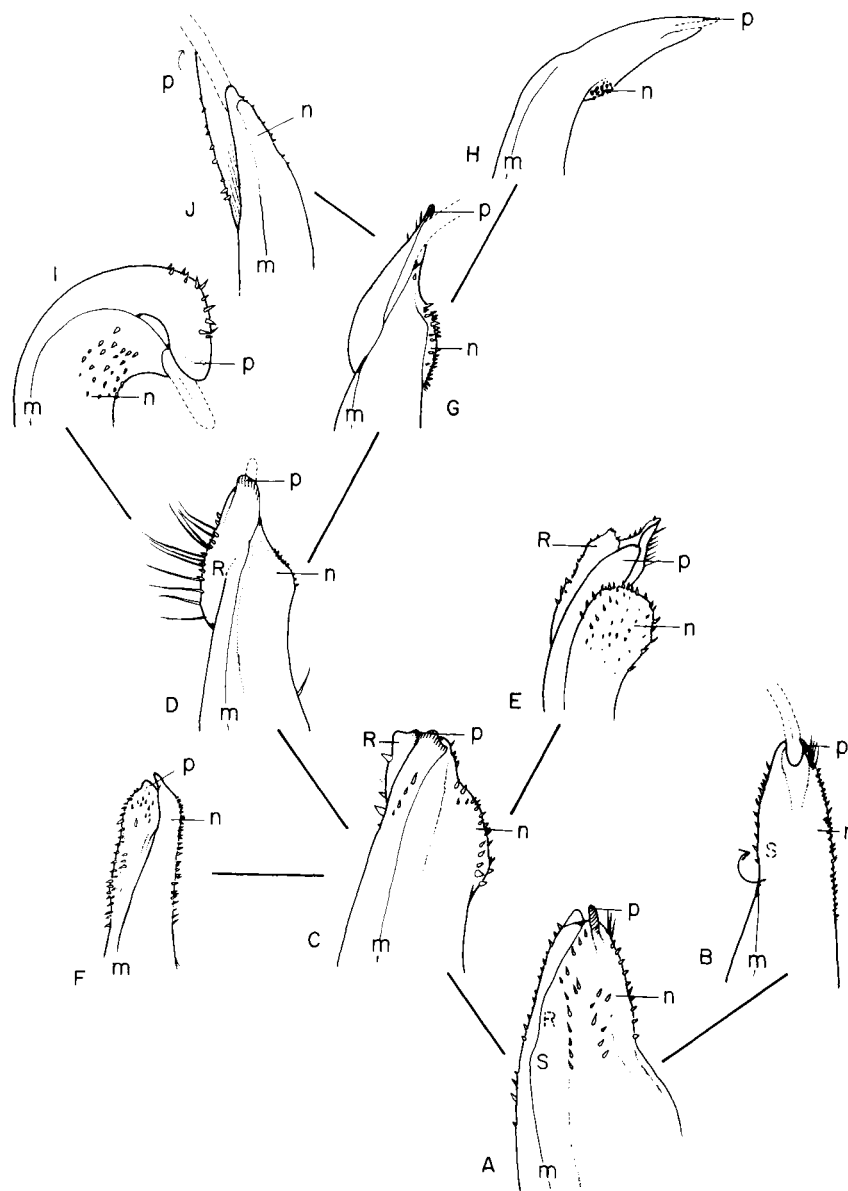


FIGURE 14

Homologies in the gonopods of *Dilocarcinus*. A, *D. argentinianus*; B, *D. dentatus*; C, *D. truncatus*; D, *D. pagei*; E, *D. bulbifer*; F, *D. medemi*; G, *D. spinifer*; H, *D. septemdentatus*; I, *D. niceforei*; J, *D. castelnaui*. m, margin; n, lateral process; p, distal process; R, cephalic surface; S, caudal surface. Appendages drawn in caudal view.

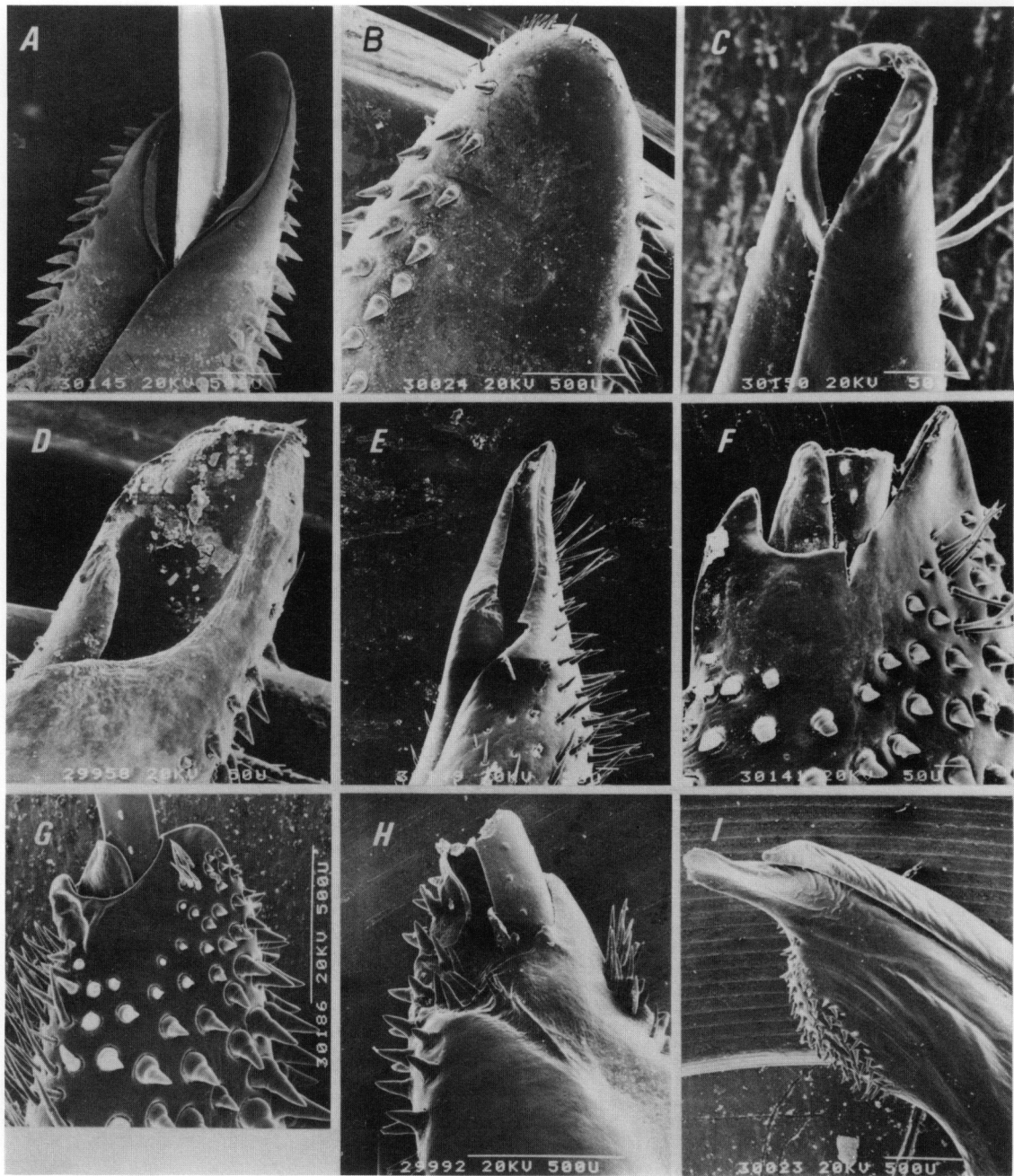


FIGURE 15

Detail of the apex of first gonopod: A, *Trichodactylus petropolitanus*; B, *T. fluviatilis*; C, *Avotrichodactylus oaxensis*; D, *Sylviocarcinus piriformis*; E, *Valdivia camerani*; F, *V. serrata*; G, *V. gila*; H, *Dilocarcinus dentatus*; I, *Forsteria venezuelensis*. A, C-G, caudal; B, H, cephalic; I, latero-cephalic; second gonopod broken in F, H.

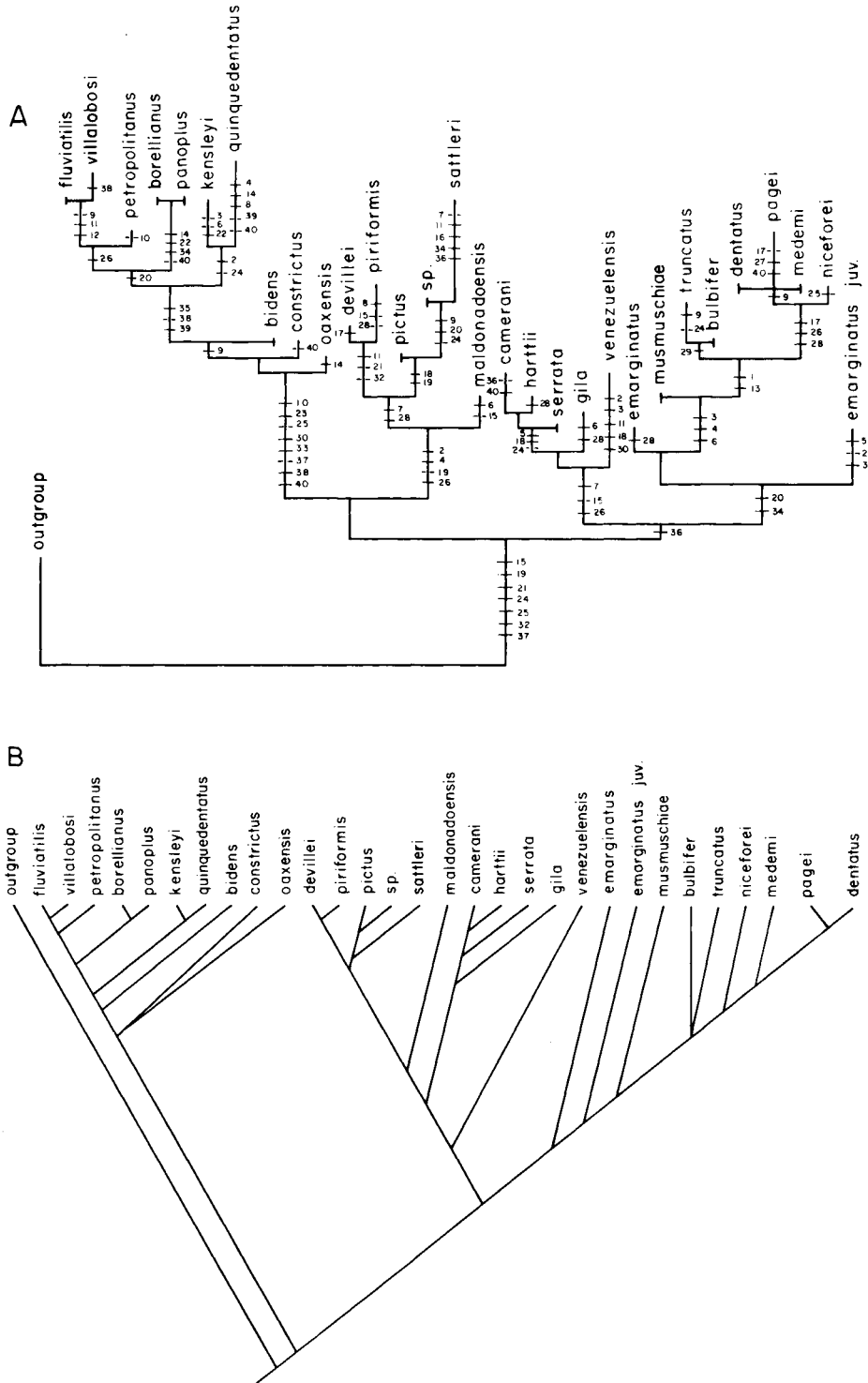


FIGURE 16
 A, One of the most parsimonious cladograms obtained, with indication of the changes in character states (solid horizontal lines); B, strict consensus tree.

TABLE I
Characters used to compare the Trichodactilidae species
The first alternative listed for each character is considered to be plesiomorphic

- 1 Carapace, outline (0) hexagonal, (1) suborbicular
- 2 Carapace, upper surface (0) moderately arched, (1) strongly arched
- 3 Carapace, (0) uneven, (1) smooth
- 4 Carapace with transbranchial ridge (0) present, (1) absent
- 5 A pair of lunulated protogastric lobes (0) absent, (1) present
- 6 Carapace, median grooves (H depression) (0) deep, (1) shallow or obsolete
- 7 Carapace, posterior margin (0) with a high carina, (1) without a high carina
- 8 Carapace, (0) always wider anteriorly, (1) becoming wider posteriorly with age
- 9 Carapace, at least in immatures, (0) wider on anterior third, (1) wider near middle
- 10 Postero-lateral margin (0) straight or slightly arcuate, (1) strongly arcuate
- 11 Lateral teeth of carapace (0) not obsolete in large males, (1) present in young, obsolete in large males.
- 12 Lateral teeth of carapace (0) present at least in juveniles, (1) absent or only represented by small notches even in young specimens
- 13 Lateral teeth in young specimens (0) 0-5, (1) >5
- 14 Lateral teeth (0) not beyond middle of carapace, (1) beyond middle of carapace
- 15 Front (0) straight, (1) bilobed
- 16 Front, (0) very advanced, concealing epistome, (1) partially or completely retracted, exposing epistome
- 17 Margin of front (0) unarmed, (1) armed with spines or large granules
- 18 Lower orbital border (0) without a recess, (1) with a recess next to external orbital angle
- 19 Orbit, occlusive tooth (0) continuous with, (1) distinct from inner orbital angle
- 20 Lower orbital margin (0) directed upwards at inner orbital angle, (1) directed downwards
- 21 Middle gutter of epistome (0) ending in a single point, (1) ending in two separate points
- 22 Aperture of efferent channels, lateral yugal lobe (0) absent, (1) present
- 23 Postgastric pits (0) present, (1) absent
- 24 Sternum (0) with a deep depression on somite 1 and one on each side of somites 2+3, (1) without conspicuous depressions
- 25 Abdominal segments, (0) all sutures visible, (1) at least sutures 3/4 and 4/5 obsolete
- 26 Abdomen (0) triangular, (1) trapezoidal
- 27 Third abdominal segment (0) without a carina, (1) with a distal carina
- 28 Third maxilliped, merus (0) trapezoidal, (1) conspicuously narrow
- 29 Third maxilliped, antero-mesial angle of merus (0) rounded, (1) produced into a triangular tooth located near articulation of palp
- 30 Third maxilliped, distal external spine (0) triangular, acute, (1) reduced
- 31 Third maxilliped, ischium (0) not unusually wide, (1) unusually wide
- 32 Endopodite of 1st maxilliped (0) with a notch, (1) without a notch on mesial border
- 33 Penial groove (0) open cephalad, (1) overlapped by 8th tergite and sternal lobe
- 34 Eighth episternite (0) narrow, (1) expanded laterally
- 35 First gonopod (0) conical-elongate, (1) flask-shaped
- 36 Gonopore (0) V-shaped, open caudal, (1) slit-like, open cephalic
- 37 First gonopod apical setae (0) if present, small, located on cephalic surface, (1) very long, on lateral surface
- 38 Second gonopod (0) of equal length or longer than first, (1) considerably shorter
- 39 Pereiopods 2-5, (0) lower margin of propodous and dactylus with rows of long setae, (1) without long setae
- 40 Fifth pereiopods, propodous (0) wide (length/width < 1.8) (1) slender (length/width = 2 or more)

TABLE II
Data matrix of 40 characters of the Trichodactylidae

<i>Trichodactylus fluviatilis</i>	1010000001110010001110110100010110100011
<i>T. kensleyi</i>	1100010011000010001011100000010110100011
<i>T. petropolitanus</i>	1010000010000010001110110100010110100011
<i>T. quinquedentatus</i>	1111000011000110011010100000010110100000
<i>Mikrotrichodactylus borellianus</i>	1010000011000110001111110000010111100010
<i>M. panoplus</i>	1010000011000110001111110000010111100010
<i>Rodriguezia villalobosi</i>	1010000001110010001110110100010110100111
<i>Avotrichodactylus bidens</i>	1010000011000010001010110000010110000101
<i>A. constrictus</i>	1010000001000010001010110000010110000100
<i>A. oaxensis</i>	1010000001000110001010110000000110000101
<i>Sylviocarcinus devillei</i>	1111001000100010100000011101000000001000
<i>S. maldonadoensis</i>	1111010000000000000010011100000100001000
<i>S. pictus</i>	11110010000000010011010011101000100001000
<i>S. piriformis</i>	1111001100100000000000011100000000001000
<i>S. sp.</i>	1111001010000010011110001101000100001000
<i>Valdivia camerani</i>	0000101000000000011010001100000100001001
<i>V. gila</i>	0000111000000000001010011101000100011000
<i>V. hartii</i>	0000101000000000011010001101000100011000
<i>V. serrata</i>	0000101000000000001010001100000100011000
<i>Forsteria venezuelensis</i>	0110001000100000011010011100010100011000
<i>Zilchiopsis emarginatus</i>	01000000000000011001110011001000101011000
<i>Z. emarginatus, juvenile</i>	0000100000000010001100011000001101011000
<i>Z. sattleri</i>	1111000010100011011110001101000101011001
<i>Dilocarcinus truncatus</i>	1111010010001011001110001000100101011000
<i>D. bulbifer</i>	1111010000001011001110011000100101011000
<i>D. dentatus</i>	1111010010001011101110011101000101011000
<i>D. medemi</i>	1111010010001011101110011101000101011000
<i>D. niceforei</i>	1111010000001011101110010101000101011000
<i>D. pagei</i>	1111010010001011001110011111000101011001
<i>Fredilocarcinus musmuschiae</i>	0111010000000011001110011000000101011000

II - SYSTEMATIC STUDY

Family TRICHODACTYLIDAE H. Milne Edwards, 1853

Trichodactylacea H. Milne Edwards, 1853, p. 213.

Trichodactylidae Smith, 1870, p. 152.- RATHBUN, 1893, p. 660.- PRETZMANN, 1968a, p. 1.- PRETZMANN, 1968b, p. 70.- BOTT, 1969, p. 12.- SMALLEY & RODRÍGUEZ, 1972, p. 41.- LOPRETTO, 1976, p. 67.- MANNING & HOBBS, 1977, p. 159.- PRETZMANN, 1980, p. 661.- PRETZMANN & MAYTA, 1980, p. 5.- RODRÍGUEZ, 1981, p. 47.- BOWMANN & ABELE, 1982, p. 24.- PRETZMANN, 1983a, p. 307.- PRETZMANN, 1983b, p. 317.

Thelphusidae (Trichodactylinae), ORTMANN, 1893, p. 486.- YOUNG, 1900, p. 202.

Potamonidae (Trichodactylinae), ORTMANN, 1896, p. 445.- ORTMANN, 1897, p. 296.- MOREIRA, 1901, p. 42.- ORTMANN, 1903, p. 310.- RATHBUN, 1906, p. 30.- RINGUELET, 1949, p. 99.- HOLTHUIS, 1959, p. 210.

Trichodactylinae, COLOSI, 1920, p. 9.- BOTT, 1955, p. 319.

Heterotremata sensu Guinot (1977), in which penis is lodged in penial groove located across middle of 8th sternite. First male gonopod conical or flask shaped, with distal portion armed with strong conical spines; gonopore large V-shaped, open caudally, or narrow, slit-like, open distally and flanked by one or two corneous lamellae. Second male gonopod of equal length, or much longer than first gonopod, exceptionally reduced to short flagellum. Efferent openings large, restricted below only by endopod of first maxilliped. Endopod of first maxilliped with inner ("portunoid") lobe. Exopod of third maxilliped, including flagellum, always well developed. Antennae usually with the basal article expanded into outer lobe which, together with occlusive tooth, closes orbit near yugal angle. Podomeres of walking legs flattened, without spines, with rows of long hairs on upper and lower margins of propodus and dactylus, propodus of fifth pair widened. Carapace subcircular or subhexagonal, moderately wider than long ($cb/cl = 1.05-1.25$), with 1 to 12 lateral teeth relatively large; cervical grooves absent.

Type genus.- *Trichodactylus* Latreille, 1828.

Key to the subfamilies and tribes of TRICHODACTYLIDAE

1. Postgastric pits absent, abdominal segments with all sutures visible, or partially visible, penial groove overlapped by 8th tergite and sternal lobe, first gonopod flask-shaped (or when elongated then second gonopod very reduced), gonopore V-shaped, caudalSubfamily TRICHODACTYLINAE

- Postgastric pits present, abdominal segments with sutures 3-5 obsolete, penial groove not overlapped by 8th tergite and sternal lobe, first gonopod conical, elongate (Subfamily DILOCARCININAE).....2
- 2. Carapace hexagonal, upper surface moderately arched, (exceptionally strongly arched), with regions well marked, 2-6 lateral teeth, first gonopod with a strong lateral lobe on proximal half, gonopore terminalTribe VALDIVIINI
- Carapace suborbicular, strongly arched, surface smooth, 3-11 lateral teeth3
- 3. Front advanced, epistome not visible in dorsal view, gonopore V-shaped, open caudal, second gonopod much longer than first, rolled-overTribe HOLTUISIINI
- Front bilobed, partially or completely retracted, exposing the epistome, gonopore terminal, apical, second gonopod moderately longer than first.....Tribe DILOCARCININI

Subfamily TRICHODACTYLINAE H. Milne Edwards, 1853

Carapace suborbicular, with 0-5 lateral teeth; front bilobed; postgastric pits absent; abdominal segments with all sutures visible, or partially visible; third maxilliped with merus trapezoidal, not conspicuously narrow, its distal external spine reduced (except in *Avotrichodactylus oaxensis*); penial groove overlapped by 8th tergite and sternal lobe; first gonopod flask-shaped (except in *Avotrichodactylus*); gonopore V-shaped, open caudal, apical setae, if present, small, located on cephalic surface; second gonopod of equal length or considerably shorter than first.

Key to the genera of Trichodactylinae

- 1. Gonopod flask-shaped2
- Gonopod conical, progressively tapering to a narrow tip.....*Avotrichodactylus*
- 2. Second male gonopod considerably shorter than first (approximately 1/2), the terminal article considerably shorter (approximately 1/2) than first, acuminate.....*Rodriguezia*
- Second male gonopod considerably longer than first, sinuous or sickle-shaped; terminal article slightly longer (1.2-1.5) than first.....3
- 3. First male gonopods in normal position placed along longitudinal axis of body; apex not bent mesiad*Trichodactylus*
- First male gonopods in normal position folded diagonally under abdomen; apex bent mesiad.....*Mikrotrichodactylus*

Type genus.- *Trichodactylus* Latreille, 1828.

Trichodactylus Latreille, 1828

Trichodactylus Latreille, 1828, p. 705.

Trichodactylus (*Trichodactylus*), RATHBUN, 1906, p. 35.- BOTT, 1969, p. 13 (part.).- PRETZMANN, 1968b, p. 70 (part.).

Trichodactylus (*Rodriguezia*), BOTT, 1969, p. 25 (part.).

Trichodactylus (*Mikrotrichodactylus*), PRETZMANN, 1968b, p. 71 (part.).

Antero-lateral margin of carapace with 2-5 teeth behind external orbital angle which may be well developed, but more frequently, minute, reduced to blunt protuberances or absent; front moderately bilobed; postgastric pits absent; abdominal segments with all sutures visible; third maxilliped with merus trapezoidal, not conspicuously narrow, its distal external spine reduced; dactylus and propodus of legs covered by felt-like pubescence; penial groove overlapped by 8th tergite and sternal lobe; first gonopod short, straight in dorsal and lateral views, divided into two portions by strong middle constriction as observed in caudal view, basal portion expanded in meso-lateral direction, with strong conical spines over distal portion, apical setae, if present, small, located on cephalic surface; gonopore V-shaped, open caudal; second male gonopod longer than first, sinuous, terminal article longer (1.2-1.5) than first.

Type species.- *Trichodactylus fluviatilis* Latreille, 1828, p. 705.

Key to the species of *Trichodactylus*

1. Lateral margin of carapace with 2-3 teeth, or completely devoided of teeth2
 - Carapace with 5 lateral teeth or prominences behind external orbital angle5
2. Lateral margins of carapace sharp, with 2 notches which define 2 rudimentary teeth, rarely a third notch more spaced than the other, or lateral margin rounded off, completely devoided of teeth3
 - Lateral margins angled, armed with 3 prominent teeth4
3. Basal portion of gonopod expanded in mesial and lateral directions, mesial border ending distally in rounded angle more advanced than the lateral border*fluviatilis*
 - Basal portion of gonopod not expanded in mesial directions*maytai*
4. Inner orbital angle with strong hooked spine directed mesially; occlusive orbital tooth small, molariform, completely filling gap between orbital angle and antennal lobe*kensleyi*
 - Inner orbital angle pyramidal, prominent, acute or more or less rounded off; occlusive orbital tooth absent....*petropolitanus*
5. Distal portion of gonopod tubular, with parallel sides; apical margin rounded in caudal view*quinquedentatus*
 - Distal portion of gonopod oval shaped in caudal view, apical margin directed mesially*ehrharti*

Trichodactylus fluviatilis Latreille, 1828

Fig. 1D, E; 3A; 4A; 5K; 6A; 10D; 12A; 15B; 17A-K

Trichodactylus fluviatilis Latreille, 1828, p. 705.- WHITE, 1847a, p. 31.- LUCAS, 1857, p. 8.- ORTMANN, 1897, p. 325.- NOBILI, 1899a, p. 2.- MOREIRA, 1901, p. 45, 107.- PRETZMANN, 1968b, p. 70.- RODRÍGUEZ, 1981, p. 48.

Trichodactylus (Trichodactylus) fluviatilis, RATHBUN, 1906, p. 25, pl. xv, fig. 11.

Trichodactylus (Trichodactylus) fluviatilis fluviatilis, BOTT, 1969, p. 15, pl. 1, fig. 1a, b, pl. 18, fig. 33.- BOTT, 1970, p. 333.- MANNING & HOBBS, 1977, p. 159.

?*Thelphusa quadrata* Latreille, 1825, p. 269 (*nomen nudum*).

Trichodactylus quadrata, H. MILNE EDWARDS, 1837, p. 16.

Trichodactylus quadratus, H. MILNE EDWARDS, 1839, p. 60, pl. xv, fig. 2 (see H. MILNE EDWARDS, 1836-1844).- H. MILNE EDWARDS, 1853, p. 214.- HELLER, 1865, p. 171.- VON MARTENS, 1869a, p. 2.- VON MARTENS 1869b, p. 515.- SMITH, 1869, p. 36 (part.).- GÖLDI, 1885, p. 662.- GÖLDI, 1886, p. 25, pl. ii, fig. 2.- THALLWITZ, 1891, p. 53.- YOUNG, 1900, p. 228 - 229.

Trichodactylus punctatus Eydoux & Souleyet, 1842, p. 237, pl. iii, fig. 1, 2.- (?)DANA, 1852, p. 294.- H. MILNE EDWARDS, 1853, p. 214.- SMITH, 1869, p. 36.- RATHBUN, 1893, p. 660.

Trichodactylus dentatus H. Milne Edwards, 1853, p. 214.- LUCAS, 1857, p. 8.- A. MILNE EDWARDS, 1869, p. 173.- ORTMANN, 1897,

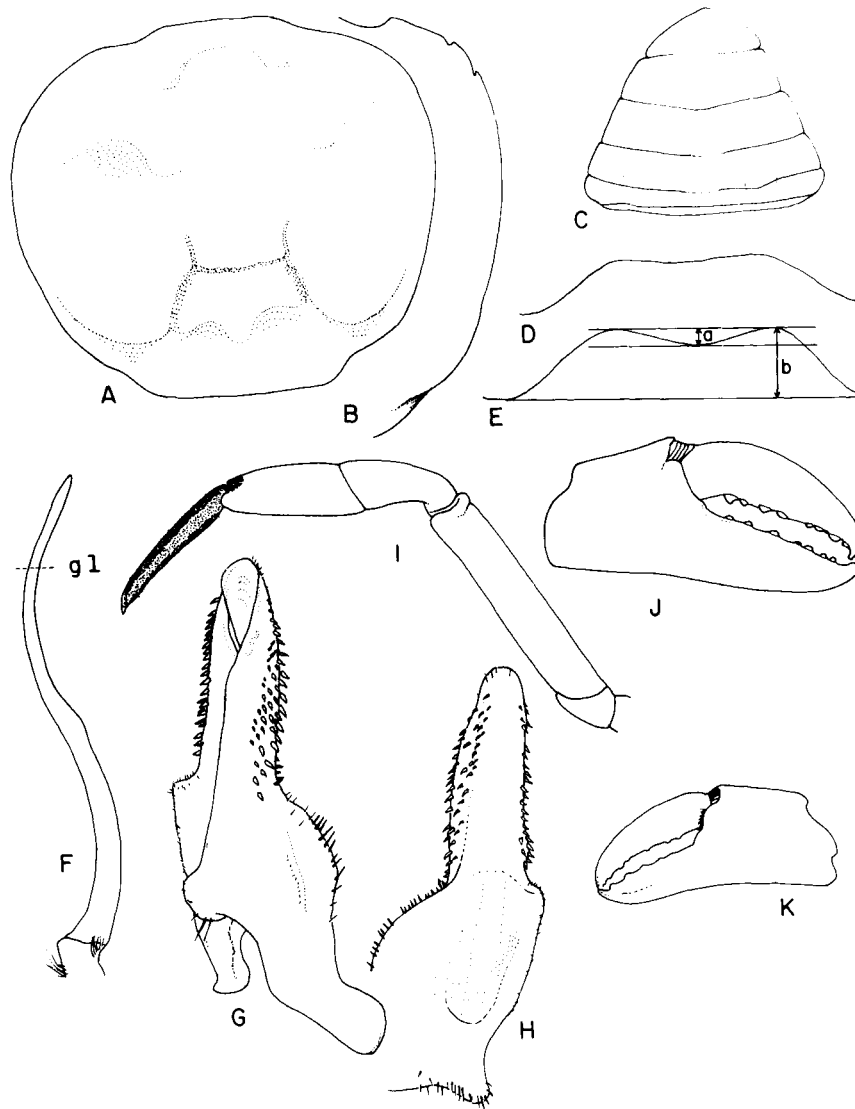


FIGURE 17

Trichodactylus fluviatilis Latreille, A, C, D, F-K, male from Rio Parahiba do Sul, cl 31.3 mm; B, E, male from Tijuca (USU 202), cl 34.9 mm: A, B, outline of carapace; C, abdomen; D, E, front; F, second male gonopod, left; G, first male gonopod, left, caudal; H, same, cephalic view; I, third pereopod, left; J, larger chela; K, smaller chela. a, depth of frontal sinus; b, total depth of front; gl, level of gonopore of first gonopod.

p. 325, 326.- NOBILI, 1899a, p. 2.- YOUNG, 1900, p. 228, 229.- MOREIRA, 1901, p. 46, 108.
Trichodactylus (Trichodactylus) fluviatilis dentatus, BOTT, 1969, p. 18, pl. 24, fig. 64.- MANNING & HOBBS, 1977, p. 159.
Trichodactylus (Trichodactylus) edwardsi Rathbun, 1906, p. 40, pl. xix, fig. 3 [*nomen novum pro Trichodactylus dentatus* H. Milne Edwards, 1853, non *Orthostoma dentata* Randall, 1839 = *Dilocarcinus dentatus* (Randall, 1839)].- PRETZMANN, 1968b, p. 70.
Uca cunninghami Bate, 1868, p. 447, pl. xxi, fig 3.- VON MARTENS 1869b, p. 515.- *Trichodactylus cunninghami*, A. MILNE EDWARDS, 1869, p. 172.- (?)SMITH, 1869, p. 36.
Trichodactylus dentatus var. *cunninghami*, NOBILI, 1899a, p. 1.- NOBILI, 1897, p. 3.
Trichodactylus crassus A. Milne Edwards, 1869, p. 172.- ORTMANN, 1897, p. 325.- MOREIRA, 1901, p. 45, 107.
Trichodactylus (Trichodactylus) crassus, RATHBUN, 1906, p. 41, pl. xv, fig. 9, 10.- PRETZMANN, 1968b, p. 70.
Trichodactylus (Trichodactylus) fluviatilis crassus, BOTT, 1969, p. 17, pl. 18, fig. 34.
Trichodactylus (Trichodactylus) fluviatilis rionovoensis Bott, 1969, p. 17, pl. 1, fig. 2a, b, pl. 18, fig. 35.- MANNING & HOBBS, 1977, p. 159.

Description

Carapace suborbicular, generally wider in old specimens; upper surface irregular; epi- and mesogastric regions prominent, cardiac and intestinal depressed, meso- and metabranchial either flat or moderately prominent, frontal region either flat or strongly concave; well marked branchio-cardiac, branchio-urogastric and urogastric grooves; wide depression on each side of the intestinal region, and another on each side between hepatic and epibranchial regions which defines a transverse, crescent-shaped ridge that runs across epibranchial region. Postgastric pits absent. Lateral margins angled or more or less rounded; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace; antero-lateral margin devoided of teeth, or with 3 notches which define 3 more or less evident teeth; when present, never project from outline of carapace, last weaker than other two, placed further apart from second than second is from first. Front slightly bilobed, more or less inclined downwards, visible or not visible in dorsal view. Orbits suborbicular; orbital suture absent; lower orbital margin with small rounded papillae, smothered or well defined; inner orbital angle pyramidal, sometimes with a papillae on apex; occlusive orbital tooth rounded, small; outer orbital angle smooth, not projected; buccal angle smooth or faintly papillated, not armed. Front advanced, hiding epistome in dorsal view; anterior surface of front high in the middle, thin on sides; 2 distinct middle pillars separated by U-shaped sinus, but without deep recess; antennular septum sunken; epistome high and directed forward. Eyes small, eye-stalk wide at base, tapering to cornea.

All abdominal segments distinct in male and female; male abdomen triangular, variable; outer margin slightly concave, last segment widely rounded, approximately 0.56 as long as broad.

A shallow transverse depression across ischium of third maxilliped. Chelipeds strongly unequal, largest strongly developed in old males, fingers widely gaping, high particularly at base, or dactylus slender; lower margin of movable finger sinuous; teeth small, subequal, regularly placed along fingers. Carpus with internal margin triangular or spiniform; merus with or without apical spine on upper border and large triangular tooth on distal angle of latero-inferior margin. Legs long and slender, devoided of long hairs; merus of 3rd pereopod 3.0 to 4.5 times as long as broad; propodus of 5th pereopod flattened and broad, 1.9-2.3 times as long as wide; dactylus falciform, covered by felt-like pubescence.

First gonopod short, straight in dorsal and lateral views; divided into two portions by strong middle constriction as observed in caudal view; basal portion expanded in mesial and lateral directions, flattened in caudal and cephalic directions, lateral border rounded or transverse, mesial border ending distally in a rounded angle more advanced than lateral border; distal portion is a narrow tube with subparallel sides, mesial border straight, lateral border slightly arched, apical margin rounded in caudal view, gonopore long, oval; strong conical spines arranged over distal portion as follow: mesial surface with a band of spines arranged in approximately 3 irregular sinuous rows; lateral surface with wide band of spines arranged in approximately 4

irregular rows directed transversely towards base and towards caudal surface, and second narrower band of spines, more cephalad and parallel to former, arranged in approximately 2 irregular rows and continued over lateral expansion of base by slenderer spines; caudal and cephalic surfaces devoided of spines; patch of spinules over basal mesial angle. Second gonopod considerably longer than first, sinuous or broadly S-shaped; terminal article slightly longer (1.2) than first, basal incurved laterally, terminal incurved mesially; apex flat and acuminate.

Material examined

Brazil. Floresta do Horto, Rio de Janeiro State; 8 June 1984; L. de O. SALLE; 1 male, 3 females (USU 125). Rio dos Macacos, Serra da Carioca, Rio de Janeiro State; 21 November 1984; M. A. TAVARES; 4 males, 1 female (USU 229). Serra da Carioca, Covanca, Tijuca, Rio de Janeiro State; 3 males, 4 females (USU 202). Rio Parahiba do Sul, Valenca, Rio de Janeiro State; D. A. MACHADO FILHO; 1 male (USU 138).

Type and distribution

Type locality Brazil. Type not extant. Aside from doubtful records, i. e. Guiana (possibly French Guiana since it is one of LEPRIEUR's collections), Tefé (Central Brazil), Rio Negro (the affluent of the Amazon where the Thayer Expedition made collections, not Rio Negro, between the states of Paraná and Santa Catarina, near the area of distribution of the species, but draining to the Rio Iguassú), Chile and "Sandwich islands" (RATHBUN, 1906), and Peru (NOBILI, 1899a), the identifiable localities mentioned in the literature are the following: Brazil. Rio de Janeiro State: Rio de Janeiro (RATHBUN, 1906; BOTT, 1969; GÖLDI, 1886); Rio de Janeiro (*edwardsi*, RATHBUN, 1906); Tijuca (BATE, 1868; MOREIRA, 1901); Teresópolis (BOTT, 1969); Nova Friburgo (BOTT, 1969). Minas Geraes State: Rio Angu, tributary of Rio Parahiba (GÖLDI, 1886); Sacutenga (BOTT, 1969); Serra da Bisca (Bicas?) (GÖLDI, 1886). Sao Paulo State: Ilha do Puzios (BOTT, 1969); Sao Paulo, 1,000 m alt; Sao Sebastian (*dentatus*, BOTT, 1969). Santa Catarina State: Rio Negro (RATHBUN, 1906); Joinville, between Rio Nova y Rio Humboldt (BOTT, 1969); Rio Itapoca, Jaraguá District (BOTT, 1969); Punta do Pharol, Sao Francisco do Sul (MOREIRA, 1901); Rio Novo basin (type of *riovovoensis*, BOTT, 1969). Rio Grande do Sul State (GÖLDI, 1886). Bahia State: Bahia (type of *crassus*, A. MILNE EDWARDS, 1869; RATHBUN, 1906); Bahia (Salvador) (BOTT, 1970). Espiritu Santo State: Santa Cruz (=Aracruz, *dentatus*, RATHBUN, 1906).

Remarks

Specimens can be separated into two distinct groups, as was first pointed out by GÖLDI (1885, 1886) who divided them into two separate species, *T. quadrata* and *T. cunninghami*, and by RATHBUN (1906) who included all specimens under *T. fluviatilis*.

Group a. The carapace more square; lateral margins sharp, with 2 notches which define 2 rudimentary teeth, rarely a third notch more spaced than the other 2; frontal margin visible in dorsal view; lower orbital margin with distinct granules; carapace surface more flattened and irregular; the branchial area flattened or concave.

Group b. Carapace more orbicular; lateral margins rounded off and smooth, devoided of teeth; frontal margin sharply inclined downwards and consequently not visible in dorsal view; papillae of lower orbital margin relatively smaller, less conspicuous; carapace surface less irregular, branchial region clearly convex.

In several species of Trichodactylidae the lateral spines become worn out with age, and the lateral margin correspondingly rounded off. In *T. fluviatilis* mature and immature specimens are found in both groups.

All specimens recorded under Material examined belong to group a, with the exception of the male specimen from Rio Parahiba (USU 138).

Further variability is observed within group a. RATHBUN (1906) already recorded specimens with 1 to 3 lateral teeth and with margins either rounded or acute. Two of the subspecies proposed by BOTT (1969) partly reflect this intra-group variability, as follows:

(1) *T. f. crassus*. Carapace strongly arched, but still the frontal margin visible in dorsal view; 1-2 lateral teeth. All specimens under this name are from Bahia (Sao Salvador) (LATREILLE, 1828; RATHBUN, 1906).

(2) *T. f. dentatus*. Carapace convex in the anterior posterior direction; grooves scarcely marked; front not visible dorsally, margins acute; third lateral tooth not rudimentary, developed, sharp, slightly bent outwards; first interdental space shorter (0.50-0.75) than second space, sinus in front of teeth U-shaped; the type locality is undetermined; additional material from Rio de Janeiro (RATHBUN, 1906) and Sao Paulo (BOTT, 1969).

(3) *T. f. rionovoensis*. Smaller than *fluviatilis sensu stricto* (cb 20 vs 40 mm), carapace convex, only the H depression marked, no teeth or notches on margin of carapace; basal portion of first gonopod not very expanded. All specimens come from Rio Novo, Santa Catarina State (near Joinville).

After examining supplementary material of *crassus* from the type locality, BOTT (1970) synonymized it with *fluviatilis sensu stricto*. The distribution of the 2 remaining subspecies do not make sense from a biogeographical point of view, since their localities are nested inside the range of *fluviatilis sensu stricto*. It is almost certain than *dentatus* is a variation of group a and *rionovoensis* young specimens of group b.

Trichodactylus maytai Pretzmann, 1978

Trichodactylus (Trichodactylus) maytai Pretzmann, 1978a, p. 165, fig. 8.- PRETZMANN, 1983a, p. 307, pl. 1, fig. 1, pl. 2, fig. 7, pl. 3, fig. 11, pl. 4, fig. 15, pl. 5, fig. 19.- PRETZMANN, 1983b, p. 320.

Description

Carapace suborbicular; upper surface completely smooth; central grooves of carapace only slightly marked. Lateral margins angled, completely devoided of teeth; exorbital angle with depression behind it, followed by inconspicuous papillae. Front moderately bilobed, the margin somewhat irregular; lower orbital margin with a lobe followed by small granules; inner orbital angle with blunt spine.

All abdominal segments distinct in male (unknown in female); male abdomen subtriangular, wide, outer margin straight; last segment wide, triangular-rounded, the proximal margin narrower than distal margin of penultimate segment; distal outer angles of penultimate segment projected forwards.

Chelipeds strongly unequal; larger chela swollen, fingers moderately gaping, teeth only slightly defined; smaller chela with longitudinal carinae on the external surface; carpus with a long, acute spine. P2-P5 long and slender.

First gonopod with basal portion expanded in the meso-lateral direction, distal portion a narrow straight tube, slightly reduced distally, with strong and numerous conical spines.

The species is well differentiated by its unarmed lateral margin. The preceding description is based on PRETZMANN's (1978a, 1983a) description of the holotype and only specimen known.

Type and distribution

The species is only known from the type specimen, a small male cl 16.1 mm from Tingo Maria, Huanuco Department, Perú (PRETZMANN, 1978a).

Fig. 3D; 4B; 10G; 12D; 18A-G

Description

Carapace suborbicular; upper surface irregular; protogastric region more prominent than rest; hepatic, epibranchial and intestinal depressed; meso- and metabranchial moderately prominent; frontal region concave; branchio-cardiac and branchio-urogastric grooves represented by deep and wide depressions; urogastric grooves less conspicuous; area between mesobranchial, meso- and urogastric regions elevated, forming subtriangular or Y-shaped lobe. Postgastric pits absent. Lateral margins angled, with 3 prominent acute spines behind external orbital angle; first and second closer than second and third; third more prominent, directed transversely laterad; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace. Front moderately bilobed, margin somewhat irregular, slightly convex in frontal view. Orbits small, suborbicular, orbital suture absent; lower orbital margin smooth; inner orbital angle with strong hooked spine directed mesially; occlusive orbital tooth small, molariform, completely filling gap between inner orbital angle and lateral lobe of antenna; outer orbital angle rounded, not projected; buccal angle rounded, smooth or with minute papillae. Front advanced, hiding epistome in dorsal view; anterior surface of front high in middle, moderately thin on sides; middle pillars distinct; antennular septum sunken; epistome high and directed backwards, with thin transverse ridge in middle portion. Eyes small, but filling orbital cavity, eyestalk wide at base, tapering to cornea.

All abdominal segments distinct in male and female, but ankylosed, except for 7th in male which is movable; male abdomen subtriangular, wide, outer margin slightly concave, last segment triangular-rounded, approximately 0.58 as long as broad, with proximal margin narrower than distal margin of penultimate segment.

Shallow transverse depression across ischium of 3rd maxilliped. Chelipeds moderately unequal; lower margin of fixed finger sinuous, teeth small, subequal, spaced and regularly placed over fingers; a longitudinal carina on external surface of each finger. Carpus with strong hooked spine on inner margin. Legs long and slender, with scattered hairs; merus of 3rd pereopod 3.2 times as long as wide; propodus of 5th pereopod narrow, approximately 3.8 times as long as wide; dactylus falciform, long and narrow, covered by felt-like pubescence and short hairs irregularly placed.

First gonopod short, straight in dorsal and lateral views; divided into two portions by strong middle constriction as observed in caudal view; basal portion expanded in meso-lateral direction, flattened in caudal-cephalic direction, lateral border expanded into sinuous lobe, mesial border convex; distal portion a narrow tube with mesial border almost straight, lateral border slightly more convex, apical margin rounded in caudal view, gonopore long, oval; strong conical spines arranged over distal portion as follow: mesial surface with a band of spines arranged in approximately 3 irregular sinuous rows; lateral surface with a wide band of spines arranged in approximately 4 irregular rows directed transversely towards base and towards caudal surface, and second narrower band of spines, more cephalad and parallel to former, arranged in approximately 2 irregular rows and continued over lateral expansion of base by slenderer spines; caudal and cephalic surfaces devoided of spines; few long subapical spinules on cephalic surface. Second gonopod slightly longer than first, sinuous or broadly S-shaped; terminal article longer (1.5) than first, basal incurved laterally, terminal incurved mesially; apex flat and acuminate.

Material examined

Paraguay. Canendiyu, Rio Carapa at bridge on dirt highway 45.1 km WSW of Salto del Guáira; Rio Parana drainage; 14 July 1979; J. N. TAYLOR & T. W. GRIMSHAW; Lat/Long: 24° 10' 54" S - 54° 41' 42" W; Field

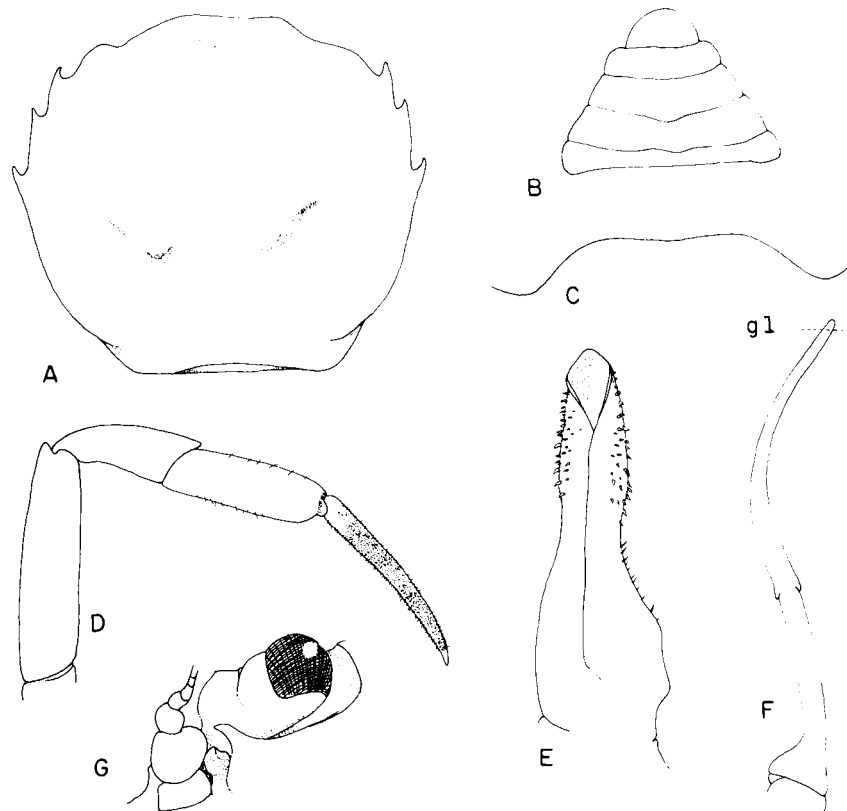


FIGURE 18

Trichodactylus kensleyi, new species, male holotype from Rio Paraguay, cl 14.3 mm: A, outline of carapace; B, abdomen; C, front; D, third pereiopod, left; E, first male gonopod, left, caudal; F, second male gonopod; G, orbital area. gl, level of gonopore of first gonopod.

Number P79-49 (USNM Accession No. 341275); 1 male holotype, cl 14.3 mm, cb 15.7 mm, 1 spent female paratype, cl 19.8 mm, cb 23.1 mm, 1 mature female paratype, cl 16.4 mm, cb 17.7 mm.

Remarks

The species resembles *T. petropolitanus* in the spinulation of the lateral borders and other details of the carapace. However, in addition to the differences in the first male gonopod, the inner orbital angle with the strong spine and the occlusive tooth closing the orbital cavity are characteristic of *T. kensleyi*.

Etymology

The species is named after the distinguished carcinologist Dr Bryan KENSLEY who kindly made available the freshwater crabs collected by the University of Michigan expedition to Paraguay in 1979.

Trichodactylus petropolitanus (Göldi, 1886)

Fig. 4C: 6B; 10E; 12B; 15A; 19A-I

Sylviocarcinus petropolitanus Göldi, 1885, p. 663 (*nomen nudum*).- GÖLDI, 1886, p. 33, pl. 3, fig. 18-23.

Trichodactylus petropolitanus, MOREIRA 1901, p. 46, 108.- RODRÍGUEZ, 1981, p. 48.

Trichodactylus (Trichodactylus) petropolitanus, PRETZMANN, 1968b, p. 70.

Trichodactylus (Valdivia) petropolitanus, RATHBUN, 1906, p. 46.

Trichodactylus (Trichodactylus) petropolitanus petropolitanus, BOTT, 1969, p. 19, pl. 2, fig. 3a, b, pl. 18, fig. 36.- BOTT, 1970, p. 335.- MANNING & HOBBS, 1977, p. 160.

Trichodactylus (Valdivia) thayeri Rathbun, 1906, p. 45, pl. 16, fig. 11.

Trichodactylus (Valdivia) thayeri glaber Pretzmann, 1968a, p. 4.

Trichodactylus (Trichodactylus) thayeri, PRETZMANN, 1968b, p.70.

Trichodactylus (Valdivia) tifucanus Rathbun, 1906, p. 47, pl. 17, fig. 3.

Trichodactylus (Valdivia) tifucanus acutidens Pretzmann 1968a, p. 4.

Trichodactylus (Trichodactylus) tifucanus, PRETZMANN, 1968b, p. 70.

Trichodactylus (Trichodactylus) tifucanus theresiopoliensis Pretzmann, 1968b, p. 70.

Description

Carapace suborbicular. Upper surface irregular; proto-and mesogastric regions considerably more prominent than rest; hepatic, epibranchial and intestinal depressed; meso- and metabranchial slightly prominent; frontal region concave; well marked and wide branchio-cardiac and branchio-urogastric grooves; urogastric grooves less conspicuous; separation between epi- and mesobranchial regions defined by transverse, recurved ridge. Postgastric pits absent. Lateral margins angled, armed with 3 prominent teeth behind external orbital angle; first and second spiniform, prominent, directed forward, third smaller, directed transversely laterad; postero-lateral ridge of carapace bent mesially in its posterior end, ending in an elongated swelling over postero-lateral angles of carapace. Front moderately bilobed, margin somewhat recurved upwards and clearly visible dorsally. Orbits suborbicular, orbital suture rudimentary, marked only by small notch on orbital margin; lower orbital margin with small rounded papillae; inner orbital angle pyramidal, prominent, acute or more or less rounded off; occlusive orbital tooth absent; outer orbital angle rounded, not projected; buccal angle rounded, smooth or with minute papillae. Front advanced, hiding epistome in dorsal view; anterior surface of front high in middle, moderately thin on sides; middle pillars not distinct; antennular septum sunken; epistome high and directed forward. Eyes small, eyestalk wide at base, tapering to cornea.

All abdominal segments distinct in male and female; male abdomen subtriangular, variable, outer margin slightly concave, last segment triangular, pointed, approximately 0.5 as long as broad.

Shallow transverse depression across ischium of 3rd maxilliped. Chelipeds strongly unequal, largest strongly developed in old males, fingers widely gaping; lower margin of fixed finger sinuous, teeth small, subequal, widely spaced and regularly placed over fingers. Carpus with internal margin triangular or spiniform; merus with distal spine on the upper border and large triangular tooth on distal angle of latero-inferior margin. Legs long and slender, devoided of long hairs; merus of 3rd pereopod approximately 4 times as long as wide; propodus of 5th pereopod narrow, approximately 2.7 times as long as wide; dactylus falciform, long and narrow, covered by felt-like pubescence.

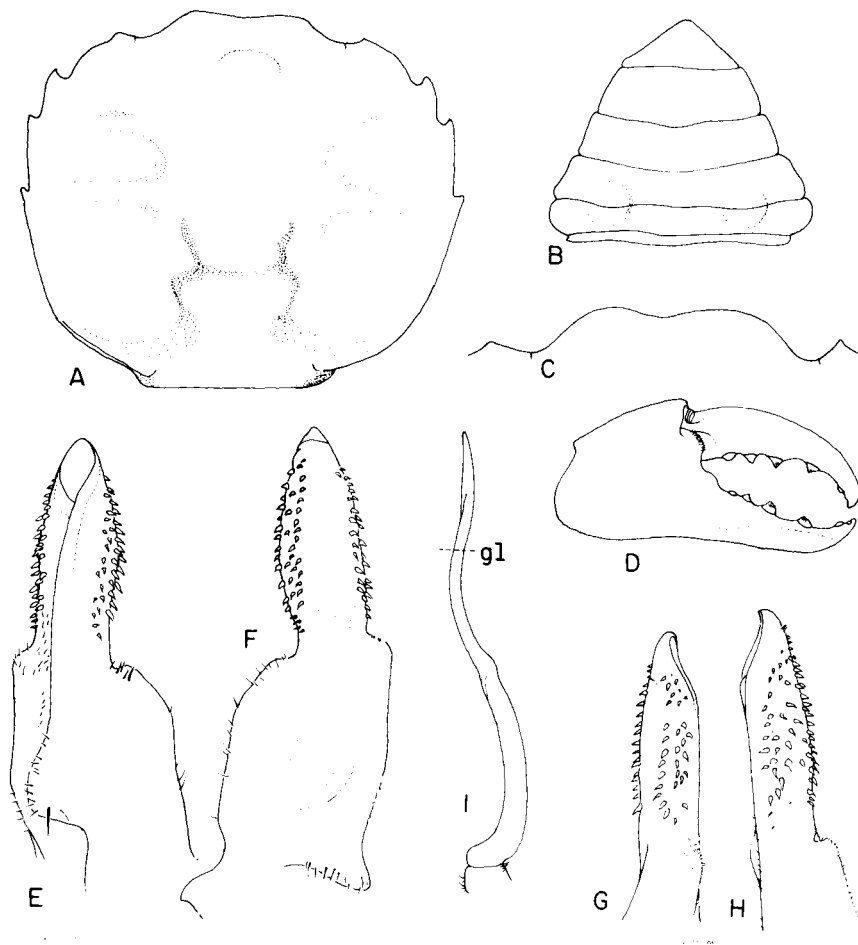


FIGURE 19

Trichodactylus petropolitanus (Göldi), male from Barao de Vassouras, cl 30.5 mm: A, outline of carapace; B, abdomen; C, front; D, larger cheliped; E, first male gonopod, left, caudal; F, same, cephalic view; G, same, mesial view; H, same, lateral view; I, second male gonopod. gl, level of gonopore of first gonopod.

First gonopod short, straight in dorsal and lateral views; divided into two portions by strong middle constriction as observed in caudal view; basal portion expanded in meso-lateral direction, flattened in caudal-cephalic direction, lateral border rounded, mesial border ending distally in rounded angle more advanced than lateral border; distal portion a narrow tube with parallel sides, mesial border straight, lateral border slightly arched, apical margin rounded in caudal view, gonopore long, oval; strong conical spines arranged over distal portion as follow: mesial surface with band of spines arranged in approximately 3 irregular sinuous rows; lateral surface with wide band of spines arranged approximately in 4 irregular rows directed transversely towards base and towards caudal surface, and second narrower band of spines, more cephalad and parallel to former, arranged in approximately 2 irregular rows and continued over lateral expansion of base by slenderer spines; caudal and cephalic surfaces devoided of spines; a patch of spinules over basal mesial angle. Second gonopod considerably longer than first, sinuous or broadly S-shaped; terminal article slightly longer (1.3) than first, basal incurved laterally, terminal incurved mesially; apex flat, acuminate.

Material examined

Brazil. Barao de Vassouras, Rio Parahiba do Sul, Rio de Janeiro State; 13 November 1979; D. A. MACHADO FILHO; 1 male (USU 134). Rio Parahiba do Sul, Rio de Janeiro State; 15 May 1979; D. A. MACHADO FILHO; 1 male (USU 138).-

Type and distribution

Brazil. Rio de Janeiro State: Petropolis (GÖLDI, 1886, type of *petropolitanus*); Mount Tijuca (type of *tifucanus*), and Macacos (RATHBUN, 1906). Santa Catarina State: Joinville and Rio Novo (BOTT, 1969, 1970). Espiritu Santo State (?): Santa Cruz (=Aracruz ?, RATHBUN, 1906, type of *thayeri*).

Trichodactylus quinquedentatus Rathbun, 1893

Fig. 1C; 3B; 4C; 5J; 6D; 10F; 12E; 20A-H

Trichodactylus quinquedentatus Rathbun, 1893, p. 660, pl. 77, fig. 7.- NOBILI, 1896, p. 2.- ORTMANN, 1897, p. 325, 326.- NOBILI, 1899, p. 1.- DOFLEIN, 1899b, p. 188.- YOUNG, 1900, p. 228.- ZIMMER, 1912, p. 7.- RODRÍGUEZ & MANRIQUE, 1967, p. 183.- RODRÍGUEZ, 1981, p. 47.

Trichodactylus (Trichodactylus) quinquedentatus, RATHBUN, 1906, p. 42, pl. 15, fig. 3.- PRETZMANN, 1968b, p. 70.

Trichodactylus (Rodríguezia) quinquedentatus, BOTT, 1969, p. 27.- SMALLEY & RODRÍGUEZ, 1972, p. 43, fig. 1, 2.- COTTARELLI & ARGANO, 1977, p. 210.

Description

Carapace suborbicular; upper surface forms regular arch; only urogastric and cardiac regions distinct, set-off by deep and wide branchio-cardiac and branchio-urogastric grooves; urogastric groove forms flat depression; cardiac region convex, intestinal region depressed, not separated from others by grooves. Postgastric pits absent. Lateral margins angled; postero-lateral margins defined by thin ridge whose distal half runs transversely inwards, close to ridge over 5th coxa, and ends away from postero-lateral angles; antero-lateral margins armed with 5 small but acute teeth behind external orbital angle, first 3 well developed, last 2 reduced, last pair implanted behind middle of carapace. Front slightly bilobed, upper surface flat. Orbits suborbicular; orbital suture absent, position indicated by flat depression; lower orbital margin entire; inner orbital angle with strong

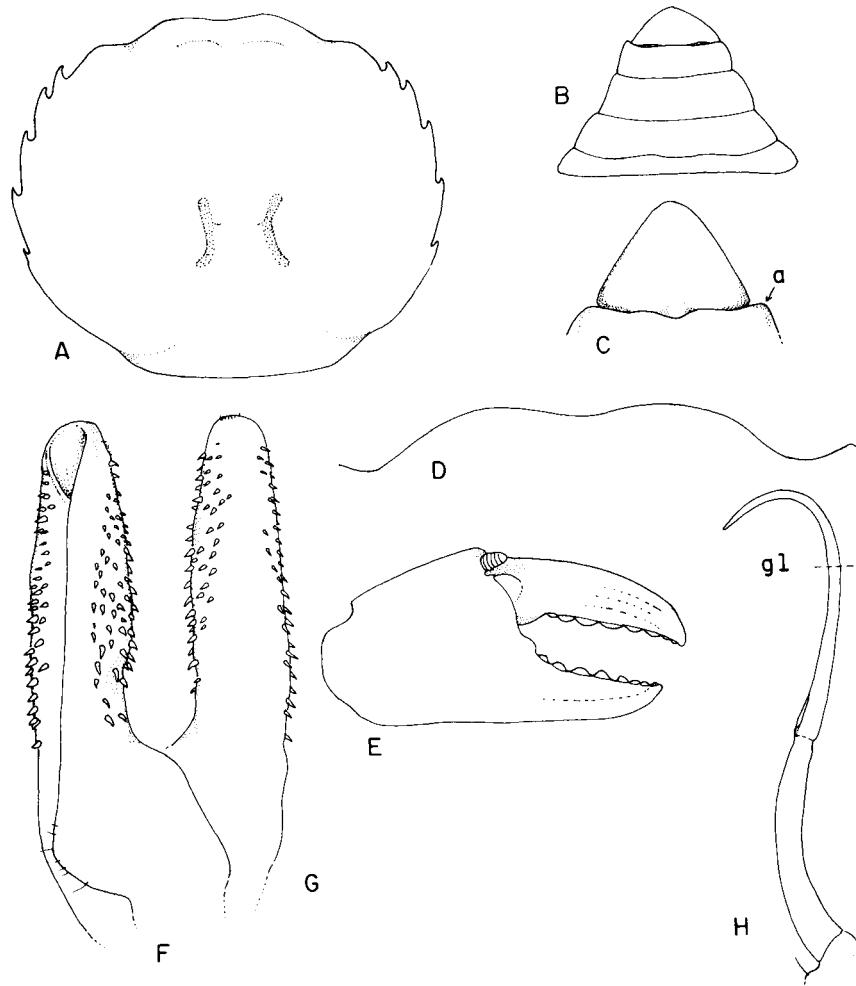


FIGURE 20

Trichodactylus quinquedentatus Rathbun, male from Rio Fundación, cl 20.4 mm: A, outline of carapace; B, abdomen; C, 7th abdominal segment; D, front; E, larger chela; F, first male gonopod, left, caudal; G, same, cephalic; H, second male gonopod. a, latero-distal lobe of 6th segment; gl, level of gonopore of first gonopod.

sharp spine, sometimes followed laterally by recess and second spine or strong tubercle; external orbital angle not armed, in some specimens lateral margin not in contact with orbit in this area, but separated from it by small recess; buccal angle smooth, not armed. Front little advanced, epistome partially visible in dorsal view; anterior surface of front not high, with a thin ridge over each antennular fossa; 2 middle pillars separated by U-shaped recess; interantennular septum moderately sunken, epistome not very high, directed forwards. Eyes normal.

All abdominal segments distinct in male and female; male abdomen triangular, wide at base; outer margin slightly concave; last segment widely rounded, approximately 0.7 as long as broad, its base conspicuously narrower than margin of the last segment.

Conspicuous transverse groove across ischium of 3rd maxilliped. Chelipeds strongly unequal, largest strongly developed in males, fingers moderately gaping; lower margin of fixed finger slightly sinuous; teeth small subequal in proximal half, diminishing in size towards tip on distal half, widely spaced and regularly placed over cutting surfaces. Carpus with strong hooked spine on internal margin; merus with small sharp spine on upper border and larger one at middle of each lower margin, distal angle of latero-inferior margin not strongly produced. Legs long and slender, lower and upper margins of dactylus and lower margin of propodus covered with long hairs, lateral sides of dactylus and propodus, and distal part of carpus covered by a felt-like pubescence; long hairs scattered elsewhere over the leg; merus of third pereopod approximately 4 times as long as broad; propodus of 5th pereopod broad, approximately 1.6 as long as wide; dactylus falciform, moderately long.

First gonopod short, straight in dorsal and lateral views, divided into two portions as observed in caudal view, basal portion with lateral border expanded, sinuous, mesial border straight, not advanced; distal portion forming narrow tube, with parallel sides, mesial border straight, lateral border slightly arched, apical margin rounded in caudal view, gonopore subtriangular; strong conical spines arranged over distal portion as follows: mesial surface with band of spines arranged in approximately 3 irregular rows; lateral surface with band of spines arranged approximately in 6 irregular rows directed transversely towards base and towards caudal surface; caudal and cephalic surfaces devoided of spines. Second gonopod considerably longer than first, sinuous, apical article 1.5 longer than basal, basal incurved laterally, terminal bent mesially; apex rounded, acuminate.

Material examined

Colombia. Rio Fundacion, near Santa Marta, 15 November 1967; A. ZAMORA; 1 male, 1 female (Ivic). Rio Gaira, near Santa Marta; 15 November 1967; A. Zamora; 1 male, 1 female (Ivic). Rio Sevilla, near Santa Marta; 15 November 1967; A. ZAMORA; 1 male, 2 females (Ivic). Rio Aracataca, near Santa Marta; 15 November 1967; A. ZAMORA; 1 male, 4 females (Ivic). Rio Cesar, 10 km south of Valledupar; 2 January 1968; A. ZAMORA; 4 males, 3 females (Ivic).

Type and distribution

Nicaragua. Rio Escondido, 50 miles from Bluefields (type locality, RATHBUN, 1906). Colombia. Magdalena Department: Santa Marta (PEARSE, 1915) and rivers up to 80 km south of this city (SMALLEY & RODRÍGUEZ, 1972); Cesar Department: 10 km South of Valledupar (SMALLEY & RODRÍGUEZ, 1972); Atlantico Department: Barranquilla (ZIMMER, 1912). Bolivar Department: Cartagena (SMALLEY & RODRÍGUEZ, 1972). Of the disjunct distribution of this species in Nicaragua and Colombia, SMALLEY & RODRÍGUEZ (1972), said: it "*is unusual when compared with distribution of other species of the family. Unfortunately, the only known Nicaraguan specimen is a female; however, the suborbital margin is very distinctive in this species, and in our opinion the similarity of the Nicaraguan holotype to the Colombian specimens is sufficiently close to confirm the conclusion of previous workers that they are the same species*".

Trichodactylus ehrhardti (Bott, 1969)

Trichodactylus (Trichodactylus) panoplus ehrhardti Bott, 1969, p. 22, pl. 4, fig. 7a, b, pl. 18, fig. 38.

Type and distribution

The male holotype, with a cb of 9.5 mm, a female paratype, and several other specimens, come from Lago Manacapuru, near Manaus, Brazil. BOTT (1969) also reports specimens from Rio Negro, 80 km from Manaus.

Remarks

This species resembles *Trichodactylus (Valdivia) faxoni* Rathbun, 1906, also reported from the Amazon (see under "Species incertae sedis"), in the reduction of the teeth, particularly the last two which are "very small, blunt, near each other, difficult to see" (RATHBUN, 1906).

Mikrotrichodactylus Pretzmann, 1968

Trichodactylus (Mikrotrichodactylus) Pretzmann, 1968b, p. 71

Very small species, carapace length usually under 20 mm at maturity, front bilobed, lateral margin with a series of 5 lateral teeth behind external orbital angle, which reach level of cardiac region; postgastric pits absent; all abdominal segments distinct in male and female, male abdomen very wide; third maxilliped with merus trapezoidal, not conspicuously narrow, distal external spine reduced; dactylus and propodus of legs covered by felt-like pubescence; first male gonopods in normal position folded diagonally under abdomen; basal portion expanded laterally into wide thin lobe, distal portion with bulbous expansion, apex awl-shaped, strongly bent mesiad; gonopore V-shaped, large, open caudally; second male gonopod considerably longer than first, sickle-shaped; terminal article longer (1.35) than first.

Type species.- *Trichodactylus borellianus* Nobili, 1896

The lateral margin with 5 spines reaching postero-lateral margin of carapace is a character only found outside this group in *Trichodactylus quinquedentatus* and *T. ehrhardti*. These species also present the small size and several morphological traits (i. e., shape of chela) of *Mikrotrichodactylus*, or characters intermediate between both genera (i. e. length of second male gonopod), but with the first gonopod typical of *Trichodactylus*. The small body size of the species of *Mikrotrichodactylus* is found also in *Trichodactylus maytai*, *T. kensleyi* and the species of *Avotrichodactylus* and *Rodriguezia* within the family. Notwithstanding this overlap of characters, *M. panoplus* and *M. borellianus* possess a very distinctive first gonopod which justifies the erection of *Mikrotrichodactylus* Pretzmann, 1968b, as a separate taxa, to receive them.

Key to the species of *Mikrotrichodactylus*

1. Carapace convex, with regions slightly marked. Lateral teeth subequal, equidistant. Last abdominal article of male triangular, length/width = 0.5. Bulbous expansion of distal portion of first gonopod with a single lobe on lateral side*panoplus*

- Carapace flattened, with regions more marked and covered by gibbositities. Last abdominal article of male suboval, length/width = 0.3. Bulbous expansion of distal portion of gonopod formed by two longitudinally subparallel lobes
*borellianus*

Mikrotrichodactylus borellianus (Nobili, 1896)

Fig. 2B; 3E; 4E; 6E; 11B; 12C; 21A-H

Trichodactylus borellianus Nobili, 1896, p. 2.- NOBILI, 1898, p. 12.- NOBILI, 1899a, p. 3.- NOBILI, 1901, p. 11.- RODRÍGUEZ, 1981, p. 48.

Trichodactylus (Valdivia) borellianus, RATHBUN, 1906, p. 5, pl. 17, fig. 6, text-fig. 115.

Trichodactylus (Dilocarcinus) borellianus, RINGUELET, 1949, p. 104, pl. 8, fig. 2.

Trichodactylus (Trichodactylus) borellianus, BOTT, 1969, p. 23, pl. 5, fig. 8a, b, pl. 18, fig. 39.- LOPRETTO, 1976, p. 74, fig. 6-9.- MANNING & HOBBS, 1977, p. 159.

Trichodactylus (Mikrotrichodactylus) borellianus brasiliensis Pretzmann, 1968b, p. 71.

?*Trichodactylus (Trichodactylus) parvus* Moreira, 1912, p. 151, pl. 6, fig. 12, 13, text-fig. 2, 3.

Description

Carapace suborbicular; upper surface moderately convex, irregular; protogastric region vaulted and, together with mesobranchial, more elevated than others; frontal, hepatic and epibranchial regions depressed, flat, or slightly concave; area between cardiac and intestinal regions forming concave depression; branchio-urogastric groove deep and thin, well marked, forming semicircle. Postgastric pits absent. Lateral margins angled, irregular; postero-lateral ridge of carapace not bent abruptly inwards, but ends near margin of carapace above 5th pereopod; spinulation of lateral margin consists of strong sinuous postorbital lobe, followed by two tiny spines placed very close to each other on hepatic margin, these followed by concavity of margin and then three large equidistant hooked spines, last placed at level of cardiac region. Front very wide, in the form of spatulated lamella, squarish due to right-angled orientation of inner orbital margin; surface of these margins arched; frontal lobes widely spaced by shallow notch. Orbits rounded, small, shallow, eyes completely fill orbits; orbital suture absent; lower orbital margin smooth; inner orbital angle with strong blunt spine directed mesially; occlusive orbital tooth small, attached to external orbital angle; expanded lobe of antenna, occlusive tooth and inner orbital angle applied to each other to form continuous closure of orbit near yugal angle; outer orbital angle smooth, not projected, with a conspicuous constriction behind it; buccal angle smooth, with frontal angle retracted. Front advanced, hiding epistome in dorsal view; anterior surface of front retracted, very high in middle, oblique laterally; 2 distinct but very close middle pillars, without deep recess; antennular septum sunk; epistome high and directed backwards, with very faint transverse ridge across it.

All abdominal sutures distinct in both male and female, but only last segment freely movable, segments 3-5 ankylosed; male abdomen wide, triangular; lateral margins of segments 3-6 form lobes over general outline of abdomen; last segment widely rounded, approximately 0.3 as long as broad.

Thin transverse depression across ischium of 3rd maxilliped. Chelipeds strongly unequal, largest strongly developed in mature males, fingers short and curved, widely gaping, lower margin of movable finger sinuous; teeth small, subequal, regularly placed along fingers; palm and fingers smooth, smaller chela with longitudinal ridge on each finger and covered by felt-like pubescence. Carpus with strong hooked spine; merus without spines. Legs long and slender; dactyli long, falciform, with short felt-like pubescence on sides and short hairs on upper and lower margins, claws short without conspicuous carinae; lower margin of propodus with patches of short hairs.

First male gonopods in normal position fold diagonally under abdomen. Basal portion expanded laterally into wide thin lobe, with border turned cephalad, mesial border thin, straight; distal portion with bulbous expansion,

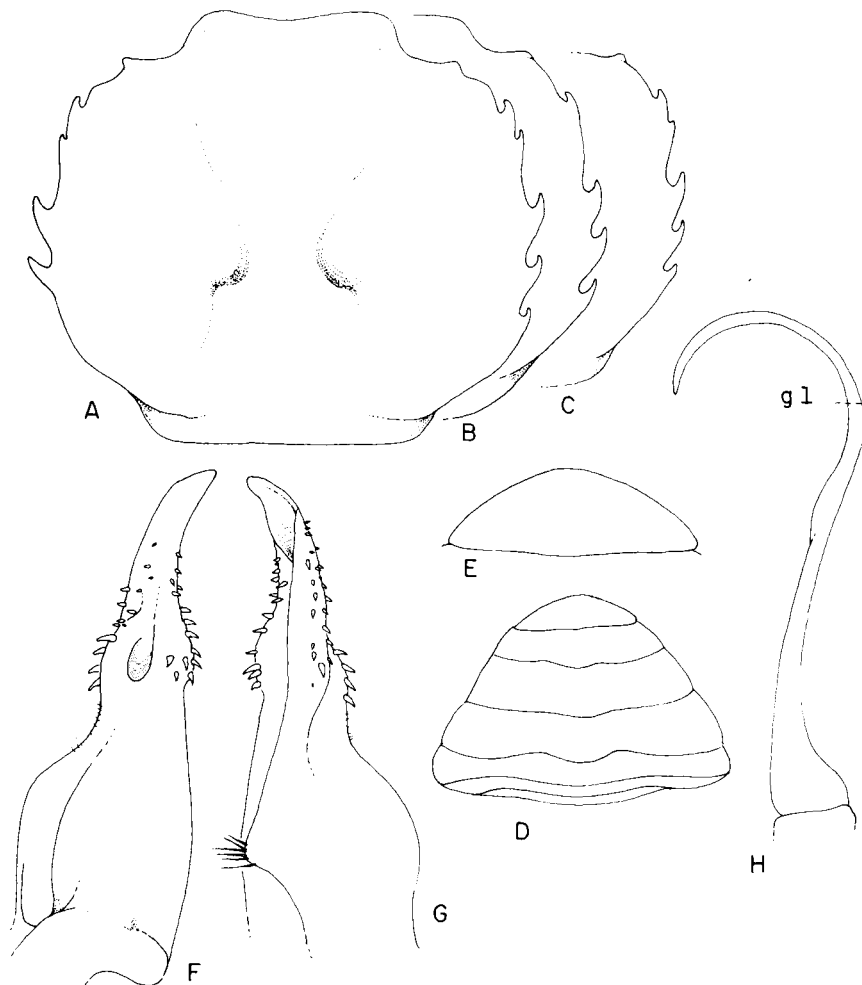


FIGURE 21

Mikrotrichodactylus borellianus Nobili: A, B, C, outline of carapace; D, abdomen; E, 7th abdominal segment; F, first male gonopod, left, cephalic; G, same, caudal; H, second male gonopod. A, F-H, male from Rio Paraguay (USNM) cl 11.9 mm; B, D, E, male from Arroyo Postillon (MH 3693), cl 11.3 mm; C, female from the same locality, 11.3 mm. gl, level of gonopore of first gonopod.

lateral border formed by two longitudinal subparallel lobes; apex linguiform, strongly bent mesially; strong spines on mesial and lateral surfaces of distal expansion, diminishing in size distally. Gonopore large, opening caudal. Second male pleopod longer than first, sickle-shaped.

Material examined

Paraguay. Rio Paraguay, Puerto Max, Arroyo Postillon; 3 males, 2 females (MH 3693). Rio Paraguay, between Puerto Casado and Puerto Sastre; KRIEG, Nr 1931; 2 females (ZSM 1097/2). Villarrica; 1901; SPEYER; 2 males (ZSM 1097/3). Partially flooded shipyard (San Isidro) on Rio Paraguay in NW Asuncion; Rio La Plata drainage; 1 June 1979; J. N. TAYLOR & T.W. GRIMSHAW; Lat/Long: 25° 17' S - 57° 39' W; Field Number P79-11A (USNM Accession No 341275); 3 specimens. Arroyo Gaguairesau at bridge on route 2, approximately 1.5 km E of toll booth (just beyond km 39) and approximately 13.5 km W of Caacupe; 6 June 1979; R. BAILEY & J. N. TAYLOR; Lat/Long: 25° 22' 42" S - 57° 15' 18" W; Field Number P79-21 (USNM Accession No 341275); 15 specimens. Paraguari, Arroyo Caanabe; 19 June 1979; R. BAILEY, J. N. TAYLOR & T.W. GRIMSHAW; Lat/Long: 25° 45' 18" S - 57° 11' 42" W; Field Number P79-24 (USNM Accession No 341275); 5 specimens. Caaguazu, Arroyo Tobatiry at bridge on dirt highway, near 22 km N of junction with route 2 in Coronel Oviedo; 29 July 1979; J. N. TAYLOR & T.W. GRIMSHAW; Lat/Long: 25° 16' 54" S - 56° 24' W; Field Number P79-69 (USNM Accession No 341275); 5 specimens. President Hayes Department, Rio Pilcomayo, overflow pools at bridge (= Puerto Falcón) to Argentina, approximately 12 km WSW Chaco-i; Rio Paraguay; 29 August 1979; J. N. TAYLOR, B. SMITH, E. KOON & R. MYERS; Lat/Long: 26° 24' 0" S - 57° 4' 48" W; Field Number P79-98 (USNM Accession No 341275); 4 specimens. San Pedro/Caaguazu Departments, Arroyo Pindo at bridge on dirt highway (route 3) approximately 9 km N of Mbutuy and approximately 67 km N of Coronel Oviedo; Rio Manduvira; 29 July 1979; J. N. TAYLOR, T. W. GRIMSHAW & J. K. CREIGHTON; Lat/Long: 24° 52' 54" S - 56° 19' 48" W; Field Number P79-68 (USNM Accession No 341275); 3 specimens. Concepcion Department, Rio Paraguay, flood pools at municipal airport, approximately 4 km S of Concepcion; Rio de la Plata drainage; 9 October 1979; J. N. TAYLOR & T. W. GRIMSHAW; Lat/Long: 23° 27' 18" S - 57° 27' 00" W; Field Number P79-109 (USNM Accession No 341275); 2 specimens. President Hayes Department, small stream approximately 33.7 km NW of toll booth on Puente Remanso bridge, Rio Confuso; 8 November 1979; J. N. TAYLOR, T. W. GRIMSHAW & B. SMITH; Lat/Long: 25° 04' 54" - 57° 26' W Field Number P79-79 (USNM Accession No 341275); 16 specimens. Argentina? Parana, near Romallo; July 1913; ELLENRIDER; 10 males, 17 females (ZSM 1097/1).

Type and distribution

The syntypes were collected by Alfredo BORELLI at the Colonia Risso, Rio Apa in the high Paraguay River basin, Paraguay. RATHBUN (1906) mentions cotypes in the USNM and MP. It is recorded in the literature from the following localities. Paraguay. Concepcion Department: Puerto Max. Boqueron Department: Puerto Casado and Puerto Sastre. Guaira Department: Villarrica (BOTT, 1969). Argentina. Santa Fe Province: Las Garzas, near Ocampo; Reconquista (RATHBUN, 1906); Rio Parana Mini (RINGUELET, 1949); Romallo (BOTT, 1969). Corrientes Province: Goya (RINGUELET, 1949). Chaco Province: Resistencia. Misiones Province: Posadas (RATHBUN, 1906). Brazil. Para State: Pindobal; Lago do Tostao; Rio Tapajos. Amazonas State: Igarape das 3 Casas (BOTT, 1969).

Remarks

In immature males the two lobes on the lateral surface of the distal bulbous expansion of gonopod are not clearly distinct, but even these specimens can be separated from *M. panoplus* by the shape of the apex which is more recurved mesially, and by the mesial border of the bulbous expansion which is more rounded.

The species display considerable variations in the anterior teeth of carapace. Thus, in 6 specimens examined from Rio Apa, Paraguay, all have the 1st tooth as a tiny spine, but 2nd tooth is present as a blunt projection, a lobe, or it is altogether absent (Fig. 21A-C).

Trichodactylus (Mikrotrichodactylus) borellianus brasiliensis, described by PRETZMANN (1968b) from Brazil (but precise locality unknown), is separated by this author from the typical *borellianus* because its carapace is more convex and less sculptured, the lateral teeth is not prominent, the 3rd not reduced (characters of *panoplus*), the lateral margin is more straight and the transversal groove of ischium of 3rd maxilliped is less transversely directed.

The small female reported by MOREIRA (1912) from Puerto Espiridiao, Rio Jaurús, Mato Grosso State, as *Trichodactylus (Trichodactylus) parvus* may be a specimen of *Mikrotrichodactylus borellianus* in which all lateral teeth, with the exception of the third, have become angled lobes. Reduction of the teeth occurs in both *M. borellianus* and *M. panoplus*. As will be mentioned below, the specimens of *M. panoplus* from Buenos Aires (Figure 22D, and the *aberratio* of *panoplus* reported by RINGUELET, 1949) also approach the condition found in *T. parvus*.

Mikrotrichodactylus panoplus (von Martens, 1869)

Fig. 3F; 4F; 6F; 10H; 22A-L

Sylviocarcinus panoplus von Martens, 1869a, p. 3, pl. 1, fig. 1.- GÖLDI, 1886, p. 34.- NOBILI, 1896, p. 3.

Orthostoma panoplus, NOBILI, 1898, p. 12 (part.).- ORTMANN, 1897, p. 326.

Dilocarcinus panoplus, ORTMANN, 1893, p. 492.- NOBILI, 1899a, p. 3.- ORTMANN, 1903, p. 311.

Trichodactylus (Valdivia) panoplus, RATHBUN, 1906, p. 52, pl. 17, fig. 5, text-fig. 114.- RINGUELET, 1949, p. 103, pl. 8, fig. 3, pl. 9, fig. 1.

Trichodactylus (Trichodactylus) panoplus, GARCIA, 1973, p. 97, fig. 1-5.- LOPRETTO, 1976, p. 79, fig. 10-13.

Dilocarcinus panoplus var. *marmorata* Nobili, 1901, p. 11.

Trichodactylus (Trichodactylus) panoplus panoplus, BOTT, 1969, p. 21, pl. 4, fig. 6a, b, pl. 18, fig. 37.- MANNING & HOBBS, 1977, p. 160.

Trichodactylus panoplus, RODRIGUEZ, 1981, p. 48.

Dilocarcinus armatus A. Milne Edwards, 1869, p. 177.

Trichodactylus (Valdivia) spec. [aberratio Trichodactylus (V.) panoplus (von Martens, 1869)], RINGUELET, 1949, p. 103, pl. 8, fig. 3, pl. 9, fig. 1.

Description

Carapace suborbicular; upper surface regularly convex; regions not delimited; wide depressions on protogastric, epibranchial and metabranchial regions, and on each side of protogastric regions. Branchio-cardiac, branchio-urogastric and urogastric grooves form wide depressions. Postgastric pits absent. Lateral margins angled; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace; spinulation of lateral margin variable (see under Remarks), but in more generalized condition margin has 5 spiniform teeth behind external orbital angle, first two placed closed together, second smaller than first, other teeth widely spaced, last one at level of cardiac region. Front bilobed more or less inclined downwards. Orbits small, suborbicular, eyes large and completely filling orbits; orbital suture absent; lower orbital margin smooth; inner orbital angle with strong acute spine directed mesially; occlusive orbital tooth small, attached to external orbital angle; outer orbital angle smooth, not projected; buccal angle smooth or faintly papillated. Front advanced, hiding epistome in dorsal view; anterior surface of front high in middle, thin on sides; 2 distinct middle pillars separated by U-shaped sinus, but without deep recess; antennular septum sunken; epistome high, directed forward, with thin transverse ridge across it.

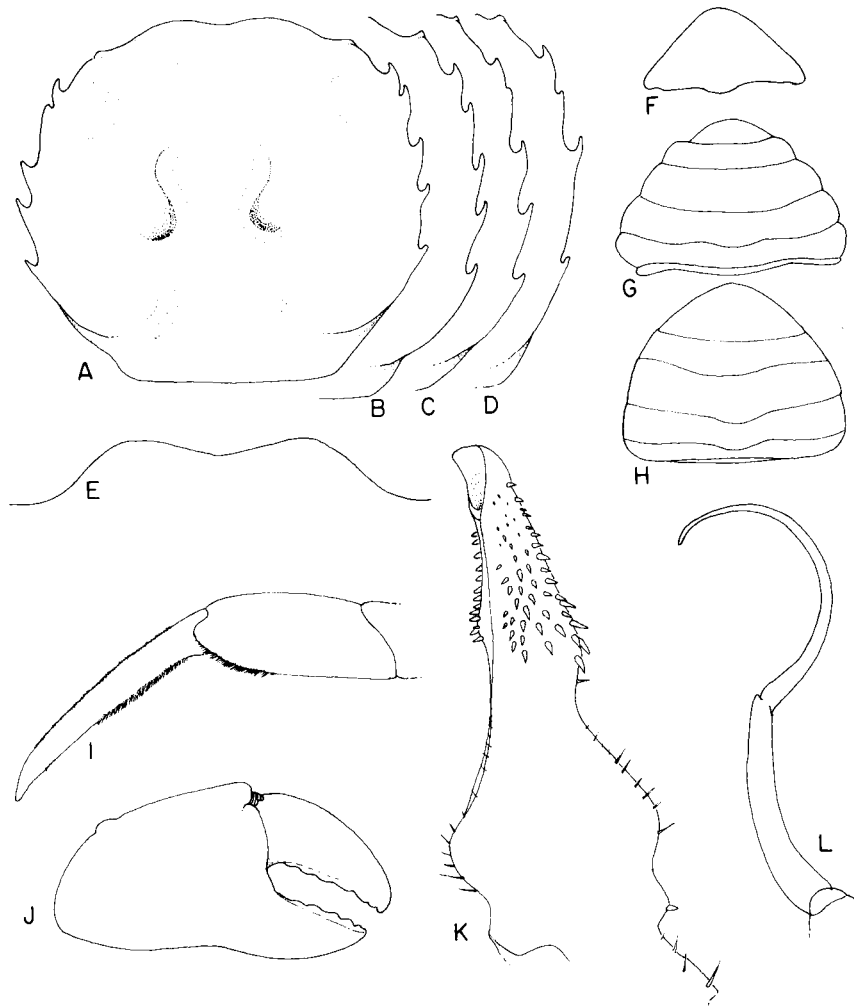


FIGURE 22

Mikrotrichodactylus panoplus (von Martens), specimens from Buenos Aires: A-D, outline of carapace; E, front; F, 7th abdominal segment; G, male abdomen; H, female abdomen; I, propodus and dactylus of 5th pereopod; J, larger chela; K, first male gonopod, left, caudal; L, second male gonopod. A, E-G, I-L, male, cl 13.6 mm; B, H, female, cl 11.0 mm; C, male, cl 8.8 mm; D, male cl 8.8 mm.

All abdominal sutures distinct in both male and female, but only last segment freely movable, segments 3-5 ankylosed; male abdomen wide, triangular; lateral margins of segments 3-6 form conspicuous lobes over general outline of abdomen; last segment widely rounded, approximately 0.55 as long as broad.

Shallow transverse depression across ischium of 3rd maxilliped. Chelipeds strongly unequal, largest strongly developed in mature males, fingers short and curved, widely gaping lower margin of movable finger sinuous; teeth small, subequal, regularly placed along the fingers; palm and fingers smooth, smaller chela with longitudinal ridge on each finger. Carpus with strong hooked spine; merus with small apical spine on upper border and large submedian spine on lateral margin. Legs long and slender; dactyli long, falciform, with short felt-like pubescence on sides and rows of short hairs on upper and lower margins, claws short without conspicuous carinae; lower margin of propodus with short hairs on distal quarter in 2nd and 3rd pair of pereopods, in distal half in 5th pair, and absent in 4th pair.

First male gonopods in normal position folded diagonally under abdomen; gonopod divided in two portions by strong middle constriction; basal portion expanded in mesial and lateral directions, flattened in caudal and cephalic directions, lateral border strongly sinuous, mesial border slightly concave; distal portion forms narrow acuminate tube, expanded at base; apex awl-shaped, bent mesiad; gonopore long, oval, open mesocaudally; strong conical spines arranged in irregular rows over mesial and latero-caudal surfaces. Second male gonopod longer than first, sickle-shaped.

Material examined

Brazil. Rio Grande do Sul; 1 male, 4 mature females, 1 immature female (VON MARTENS Nr 1130/254; ZSM 1100/1, ex. Museum Lübeck).- Argentina. Buenos Aires; 9 April 1920; Dr FRANK; 2 males, 1 female (MH K-5251).

Type and distribution

The type material was collected by Reinhardt HENSEL at Rio Cadea and Santa Cruz, above Rio Pardo, Guahyba, near Porto Alegre, Rio Grande do Sul, Brazil. Dr Reinhardt HENSEL (1826-1881), was a German zoologist and mammalogist, "ordentlicher Professor" of Zoology at the Academy of Proskau, Schleswig (1867-1881), and member of the Kaiserlich Leopold-Karolus Deutsche Akademie der Naturforschung. Under the patronage of the academy he undertook zoological studies in Southern Brazil, and from 1863-1866 he collected in Rio Grande do Sul, specially Porto Alegre and the German colonies to the north of that city (PAPAVERO, 1972). The specimens from Brazil mentioned above perhaps were part of the type material. RATHBUN (1906) mentions a male cotype in the collections of the USNM. Other records from the literature are the following. Brazil. Rio Grande do Sul State (NOBILI, 1899a; MOREIRA, 1901; BOTT, 1969): Guahyba, near Porto Alegre (type, VON MARTENS, 1869a); Sao Lourenço (ORTMANN, 1893). Rio de Janeiro State: near Rio de Janeiro (A. MILNE EDWARDS, 1869). Argentina. Buenos Aires Province (RATHBUN, 1906): Ensenada, Rio de la Plata (ORTMANN, 1893); Tigre, Rio de la Plata (type of *Dilocarcinus panoplus* var. *marmorata* Nobili, 1901). Uruguay. Paysandu Department: Santa Rita. Rio Negro Department: Arroyo Salsipuedes Grande. Treinta y tres Department: Rio Olimar; Laguna Merin. Durazno Department: Paso de la Cruz. Tucuarembó Department: Arroyo Yaguaron 29 km S of Ansina (GARCIA, 1973).

Remarks

The specimens I examined and those reported in the literature display a trend towards a reduction of the lateral spines which affects the first and second one, and secondarily the last two. Thus in the specimens from Rio Grande do Sul and Uruguay (GARCIA, 1973) the teeth are not reduced in number and only the last of the series is reduced in size. Fig. 22A-D shows some of the variations observed in a lot of 6 specimens from Buenos Aires. In this case, the 2nd spine is smaller in all specimens, in two it is very minute and in one it is replaced by

a lobe; in one specimen, in addition to the reduction of the 2nd and 5th spines, the 4th is absent. The last arrangement is also present in a small crab reported by RINGUELET (1949) as an *aberratio* of *panoplus* (2nd tooth represented by a lobe, 4th lacking) found in a locality in Northern Argentina where numerous "normal" specimens of *borellianus* were present.

***Rodriguezia* Bott, 1969**

Trichodactylus (Rodriguezia) Bott, 1969, p. 25.

Antero-lateral margin devoided of teeth; front slightly bilobed; all abdominal segments distinct in male and female; dactylus and propodus of legs covered by felt-like pubescence; first gonopod short, straight in dorsal and lateral views, divided into two portions by strong middle constriction as observed in caudal view, basal portion expanded in meso-lateral direction, with strong conical spines over distal portion, gonopore long, suboval; second gonopod considerably shorter (0.5) than first, terminal article shorter (0.5) than first, acuminate.

Type species.- *Trichodactylus villalobosi* Rodríguez & Manrique, 1967

Key to the species of *Rodriguezia*

1. Carapace and pereopods completely depigmented, eyes devoided of cornea, legs extremely long and slender....*mensabak*
- Carapace and pereopods not depigmented, eyes with developed cornea, legs not unusually elongated*villalobosi*

Distribution

The genus comprises only two closely related species, one epigean and another troglobious, both from the State of Chiapas, Mexico.

***Rodriguezia mensabak* (Cottarelli & Argano, 1977)**

Trichodactylus (Rodriguezia) mensabak Cottarelli & Argano, 1977, p. 207, fig. 1, 2.

Description

Carapace and pereopods completely depigmented. Carapace suborbicular, slightly convex; upper surface smooth with sparse pores; internal organs visible by transparency; gastric and hepatic regions prominent; postfrontal lobes slightly prominent; antero-lateral margin devoided of teeth. Front slightly bilobed, depressed and inclined downwards; postero-lateral and inferior margins of front bordered by small tubercles. Eyes devoided of cornea, eye-stalk short and stout, little mobile.

All abdominal segments distinct in male and female; male abdomen triangular, outer margin straight, last segment widely rounded, approximately 0.56 as long as broad.

Third maxilliped with distal margin of merus sinuous. Chelipeds subequal; fingers with inconspicuous tubercles. Legs extremely long and slender; dactylus covered with minute setae.

First gonopod straight, wider at basal portion, constricted at 2/3 of its length and slightly expanded in distal third; strong conical spines over distal portion, patch of spinules over basal mesial angle and few setae over lateral border; gonopore long, suboval. Second gonopod considerably shorter than first (approximately 1/2),