Taxonomy of the neotropical freshwater crab family Trichodactylidae
I. The generic system with description of some new genera

(Crustacea: Decapoda: Brachyura)

CÉLIO MAGALHÃES & MICHAEL TÜRKAY

With 50 figures and 2 tables

Abstract

In this first part of a monographic treatment of the neotropical freshwater crab family Trichodactylidae the generic system is revised on the basis of the morphologies of the endophragmal system, the male pleopods, and the segmentation of the male abdomen. The importance and morphology of taxonomic characters is discussed. In order to get homogeneous taxa the following three new genera are introduced: *Bottiella, Melocarcinus, Moreirocarcinus*. In the present classification the family contains 15 genera with 49 valid species and subspecies.

Introduction

Taxonomic studies of the South American freshwater crab family Trichodactylidae have been mainly concerned with descriptions of species. Three revisionary works of the Trichodactylidae have been published to date, the early monograph of RATHBUN (1906), the study of BOTT (1969), and the monograph of RODRIGUEZ (1992). The latter two taxonomic revisions contain a number of inaccuracies mainly caused by BOTT's misinterpretation of some species described by PRETZMANN (1968a,b) and SCHMITT & PRETZMANN (1968), as well as the non-availability of this type material. The descriptions of species in these last three publications were not definitive and lacked figures. Most of the taxonomic problems of this family arise from these anomalies. Another very serious problem with the revisions published to date is that all of them were compiled on the basis of totally inadequate Brazilian material. As the trichodactylids have their highest diversity in the Amazon region, some of the species have up to now only been known by single and partly damaged specimens. In the literature there are also few records from this area. Besides the material cited by BOTT (1969) and collected by H. SIOLI and E.-J. FITTKAU (both at that time at the „Max Planck Institut für Limnologie, Arbeitsgruppe Tropenökologie" in Plön, Germany), as well as the scattered specimens cited in PRETZMANN's and RODRIGUEZ's descriptions, the following papers contain some further information on Brazilian species: ADIS et al. (1985), GOULDING et al. (1988), TRAJANO (1987), and ZWINK (1990).

When we started our study, one of us (C. M.) had performed new sampling in the Amazon area and had examined the vast trichodactylid collections of the "Museu de Zoologia da Universidade de São Paulo". This exceptionally rich collection from all areas of Brazil included many specimens of species formerly regarded as rare. Subsequently all available collections in Brazil, Argentina, and Bolivia were checked, as well as North American and European museum holdings. All types of formerly enigmatic species could be reexamined and classified appropriately. We are therefore now in a position to present a monographic treatment of the family based on all this information.

The present paper is the first in a series dealing with our findings. It describes the systematic groupings by which we classify the species. Further publications on specific genera will follow subsequently in order to present the data in detail.

Authors' addresses:

Dr. CÉLIO MAGALHÃES, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, 69011-970 Manaus, Amazonas, Brazil. — Dr. MICHAEL TÜRKAY, Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt a. M., Germany.

Characters used for classification

Characters of the first male pleopods have been used for classifying freshwater crabs in recent times, because external characters have proved to be quite variable in this group of Brachyura. In trichodactylids, however, somatic characters have been helpful to a certain extent, especially the segmentation of the abdomen and the anterolateral dentition. RODRIGUEZ (1992) presented a new system using a number of characters, 40 of which were subjected to a cladistic analysis to determine overall similarity. These characters can be treated by grouping them to a number of units, which will be discussed here. For terminology refer to Figs. 5–7.

Carapacial structures: These include the shape and dentition of the anterolateral borders and the frontal margin as well as the distinctness of the furrows delimiting surface regions . This distinctness is related to the arching of the surface and, thus, not an independent character (characters 1–16 in RODRIGUEZ 1992). The characters related to the dentition and the shape of the carapace show a very high even intraspecific variability in a number of genera (e. g. Sylviocarcinus). In fact, they do not aid in the classification of the trichodactylids and are used as secondary characters in some species groups. This is a well known old issue and was the reason why most authors used other character groups for setting up a meaningful system of genera. In this respect we find it especially hard to believe that Carcinus maenas can be treated as the outgroup crab for assigning polarities to these characters. It is not at all clear if the anterolateral dentition and shape of the front corresponding to that crab have to be regarded as plesiomorphic within the trichodactylids. Because of this we prefer not to give such characters a high relevance in setting up natural groups.

Structures related to respiration: RODRIGUEZ (1992) correctly pointed out that there are some specific trends concerning the structure of the exhalant openings. In Trichodactylus and allied genera the efferent channels are restricted to the corners of the endostome by structures of the endopod of the first maxillipeds. This development is known also within other brachyuran families and may have evolved independently. In the Gecarcinidae the displacement of the exhalant openings towards a restricted zone of the lateral part of the endostome is clearly correlated with more terrestrial habits (TÜRKAY 1983b). The polarity in this whole set of characters seems to be clear. The well delimited exhalant openings in the genera related to Trichodactylus is evidently the apomorphic state, which seems to have evolved within the trichodactylids as is the case within other brachyuran groups. The suggestion of RODRIGUEZ, that the structure of the orbit and the morphology of the middle gutter of the epistome may be related to these different respiratory mechanisms, does not hold upon close examination of the character distribution, so that these character complexes have to be treated as separate concerning the specific evolutionary significance. In fact, there is no sound functional or physiological study which could help to correlate these structures to the respiratory system.

Segmentation of the abdomen: Within the trichodactylids the fusion of certain groups of segments has traditionally been used for delimiting genera. It seems clear that a regularly segmented abdomen, with all segment delimitations visible, is the plesiomorphic state within the Brachyura as a whole, and that the fusing is apomorphic. There is much evidence indicating, that these fusion processes have taken place independently in a number of families. Within the trichodactylids members of most genera related to Trichodactylus do not exhibit any fusion in the segments. However, this is not an exclusive state, as Avotrichodactylus has fused segments in the male abdomen and the one species of Goyazana is regularly segmented. Therefore the segmentation of the abdomen can be used as a character for delimiting genera, but it cannot be treated as a synapomorphy to define higher categories. This means that the polarity of the character is clear, but that the apomorphic state has most probably evolved independently several times within the family. To date we of course only know the external structure of the abdominal segments. Probably the question as to the specialization can only be solved by examining the morphology and function of the whole complex. Nothing is known, for example, about the disappearance of the abdominal musculature in genera where the fusion is complete.

Sternum and endophragmal system: The brachyuran body is constructed around the locomotory complex of the thorax. GUINOT (1979) has clearly demonstrated the importance of the endophragmal system in understanding the diversity of Brachyura. She also gave hints how to use these structures for the purpose of classification. It is very important to study the furrows on the sternum in order to get an idea of the morphology of the endophragmal system. This again is not only a complex structure on its own, but as stressed by TÜRKAY (1983b) the crests and apodemes are structures for the insertion of the musculature of the coxopodites and basipodites of the pereiopods. The balance of the crab when standing upright and walking is highly controlled by the Depressores Basipoditorum (as well as by the Depressores Meropoditorum), the size and diameter of which is a mechanically limiting factor in locomotory activity. Thus, the lines and crests on the sternum have an important functional significance regarding various types of locomotion. Broadly oval sterna are clearly apomorphic in relation to narrow ones, as the center of gravity is transferred to a posterior position between the walking legs (TÜRKAY 1983a). All highly evolved and terrestrial grapsoid crabs have very broad sterna in comparison to the more primitive families. Thus, the shape of the sternum is a primary character. As already pointed out by GUINOT (1979) the crests delimiting the individual thoracic sternites can meet at the midline of the sternum or they can be reduced mesially, leaving space between them. Another crest, which we call the median plate in this paper, can exist as a longitudinal structure in the midline of several thoracic segments. It also carries musculature, especially parts of the Promotor Coxae and Depressor Basipoditis in a number of the crabs examined. The reduction of this crest, therefore, means also a different implantation of the locomotory musculature and is quite a complex event. Therefore the characters of the endophragmal system have high evolutionary significance. For this study we have, wherever possible in commoner species, examined the endophragmal system by taking off the carapace. In all remaining species we have examined the sternal furrows and drawn conclusions from what we have seen in the anatomical preparations. Endophragmal and sternal structures have up to now never been used for the classification of

trichodactylids. We have found that they have proved to be particularly helpful.

Reproductive structures: The significance of the structure of the first male pleopods has been discussed by a number of authors. TÜRKAY (1975) pointed out that these structures are less affected by environmental changes, as their functionality is exclusively attached to the moment of sperm transfer when they have to function as a complex system which includes the female reproductive armature. Basic changes in the morphology of this organ can only occur if the female duct evolves in the same direction. This coevolution of two morphologically different structures is definitively slower than that of environmentally affected external characters. Relationships are, thus, better reflected by gonopodial morphology than by most external characters. Authors working in crab systematics have accepted this issue (see GUINOT 1979). Problems arise in groups with very homogeneous first gonopod architecture, as detailed characters (length of individual spines, specific angle, etc.) are subjected to the same variability as other characters. In the trichodactylids the male first pleopod is one of the primary characters for classification. For use in generic classification the construction of the organ has to be understood. This means that the position of the distal opening and the displacement of the sperm channel have to be detected, in order to get a sound basis for comparisons and homologies, rather than comparing the overall shape. For this reason we do not find it adequate to reduce the morphology of the first gonopod to three formal characters, as done by RODRIGUEZ (1992) for his cladistic analysis. In contrast, the length of the second gonopod in relation to the first one is not a well understood character. It is not easy to define the apomorphic stage in this without knowing anything about the function of the very long flagellae. Again, we do not believe that *Carcinus maenas* can be used as an outgroup concerning the gonopodial structures in order to determine the plesiomorphic state.

Conclusions: Comparing the sets of characters used in this study with those in the monograph by RODRIGUEZ (1992) there are no large differences as to the specific detail, except that we put major emphasis on the important features of the endophragmal system. The main difference is that we do not treat the single features as individual independent characters, but rather as functional complexes. As will be seen later, the high correlation of some characters evident in the data matrix of RODRIGUEZ (1992) leads to similar results, and shows that the listed 40 characters have not been evolved totally independent of each other.

Translating the character analysis into a system

As stated in the description of characters, we put major emphasis on the constructionally important endophragmal and sternal structures (Figs. 1–3, 7), and on the morphology of the first gonopod. We have also used abdomen segmentation as another key character. The general classificatory results can be described as follows:

1. The genera related to *Trichodactylus* are characterized by a broadly oval sternum, which is much broader than in other genera. All of the former genera have an en-

dophragmal system in which the endosternites IV/V, V/VI, and VI/VII approach the center of the sternum without meeting each other; the median plate is developed as a high crest in the thoracic somites VII–VIII. The male first pleopod is a simple tube without marked torsion of the sperm channel, and the distal opening is terminal. All abdominal segments are free in most of the genera, but there is a fusion in *Avotrichodactylus*. This group of genera share even more characters, such as the delimitation of the exhalant channels, the absence of postgastric pits, and the partial covering of the penial groove by the lobe of the VIIIth sternite and (sometimes) the VIIth episternite (see RODRIGUEZ 1992).

2. All remaining genera have a comparatively narrow sternal plastron, the endosternites V/VI and VI/VII do not nearly reach the midline of the sternum. The male first pleopods can have various forms. Some abdominal segments are fused in most genera, except in *Goyazana*. The remaining characters are opposite to the first grouping: no confinement of the exhalant channels to the lateral parts of endostome, the presence of postgastric pits, and uncovered penial grooves (see RODRIGUEZ 1992).

3. Within the second group two lineages are apparent. The first lineage has an endophragmal median plate only in the thoracic segments VII–VIII. In the second the median plate is present in the thoracic segments V–VIII. In addition the second group of genera has a clearly narrower sternal plastron than the first.

Consequently, the *Trichodactylus*-group is a well delimited, homogeneous unit with a number of derived characters. We agree with RODRIGUEZ (1992), that subfamilial rank should be assigned to this assemblage. The treatment of the remaining groups is more complicated. They could be grouped in another subfamily as proposed by RODRIGUEZ, but in this case they would share mainly plesiomorphic characters, the only positive feature being the existence of postgastric pits. The alternative treatment would be to split the family into three subfamilies on the basis of the sternal structures described above. This again has the disadvantage that most of the characters apart from the sternal structures would be negative ones. In translating this into a classification of the family we do not have a strong argument for either of the alternatives. We propose, therefore, to follow the subfamilial system of RODRIGUEZ for the sake of stability and because of the results of his similarity matrix. We stress, however, that this must not reflect an evolutionary homogeneity within the second subfamily.

We propose some changes concerning the generic system within the two subfamilies. This applies especially to the second subfamily in which we do not recognize the tribe Holthuisiini which only contains the genus *Sylviocarcinus*, as it was split off by a very formal interpretation of the male gonopod shape. All other characters allow the grouping of this genus with the Valdiviini and this is also clearly shown in the cladogram published by RODRIGUEZ (1992) (Fig. 4). As to the genera, we have dismembered all heterogeneous assemblages by introducing some new genera or by not treating others as inclusive, as has been done by RODRIGUEZ. Only the genus *Zilchiopsis* had to be redefined on the basis of its type species and, after having removed all artificial groupings, transferred
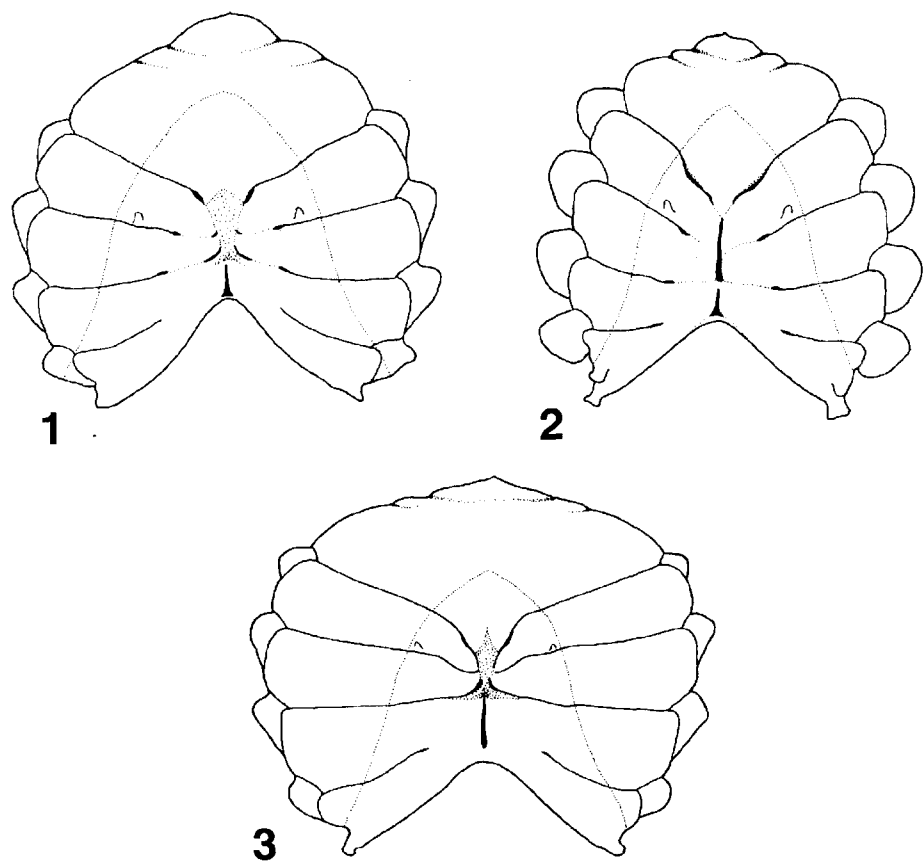
Figs. 1–3. Sternal plates of subfamilies and tribes of Trichodactylidae. — 1) Dilocarcininae — Valdiviini (*Sylviocarcinus pictus*); 2) Dilocarcininae — Dilocarcinini (*Dilocarcinus pagei*); 3) Trichodactylinae (*Trichodactylus fluviatilis*).
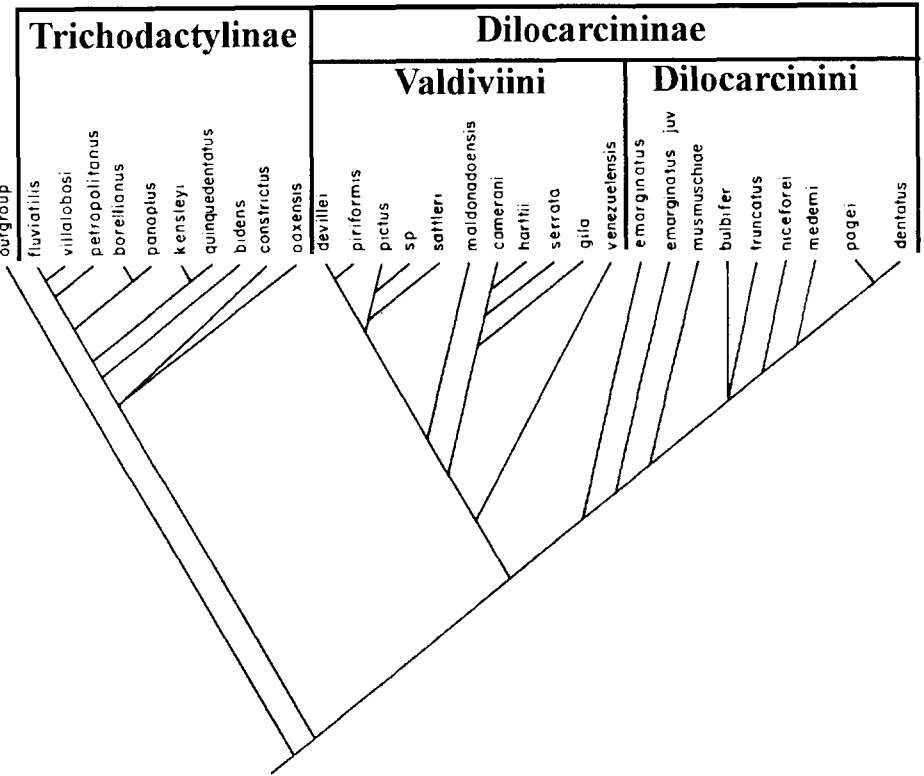

Fig. 4. Cladogram of RODRIGUEZ (1992) with superposition of the groupings introduced in the present paper showing the general similarity of proposed relationships.

Table 1. System of the family Trichodactylidae as presented in this paper.

Trichodactylinae H. MILNE-EDWARDS 1853

Avotrichodactylus PRETZMANN 1968
  constrictus (PEARSE 1911)
  oaxensis RODRIGUEZ 1992
Rodriguezia BOTT 1969
  mensabak (COTTARELLI & ARGANO 1977)
  villalobosi (RODRIGUEZ & MANRIQUE 1966)

Trichodactylus LATREILLE 1828
  borellianus NOBILI 1896
  crassus A. MILNE-EDWARDS 1869
  dentatus H. MILNE-EDWARDS 1853
  ehrhardti BOTT 1969
  faxoni RATHBUN 1906
  fluviatilis LATREILLE 1828
  kensleyi RODRIGUEZ 1992
  panoplus (VON MARTENS 1869)
  parvus MOREIRA 1912
  petropolitanus (GÖLDI 1886)
  quinquedentatus RATHBUN 1893

Dilocarcininae PRETZMANN 1978

Dilocarcinini PRETZMANN 1978

Bottiella n. gen.
  cucutensis (PRETZMANN 1968)
  medemi (SMALLEY & RODRIGUEZ 1972)
  niceforei (SCHMITT & PRETZMANN 1968)
Dilocarcinus H. MILNE-EDWARDS 1853
  pagei pagei STIMPSON 1861
  pagei enriquei PRETZMANN 1978
  septemdentatus (HERBST 1783)
  truncatus RODRIGUEZ 1992
Fredilocarcinus PRETZMANN 1978
  musmuschiae (PRETZMANN & MAYTA 1980)
  raddai (PRETZMANN 1978)
  apyratii MAGALHÃES & TÜRKAY 1995
Goyazana BOTT 1969
  castelnaui (H. MILNE-EDWARDS 1853)
  rotundicauda MAGALHÃES & TÜRKAY 1995
Moreirocarcinus n. gen.
  chacei (PRETZMANN 1968)
  emarginata (H. MILNE-EDWARDS 1853)
  laevifrons (MOREIRA 1901)
Poppiana BOTT 1969
  argentiniana (RATHBUN 1906)
  bulbifer (RODRIGUEZ 1992)
  dentata (RANDALL 1839)

Valdiviini PRETZMANN 1978

Forsteria BOTT 1969
  venezuelensis (RATHBUN 1905)
Melocarcinus n. gen.
  meekei (PRETZMANN 1968)
Rotundovaldivia PRETZMANN 1968
  latidens (A. MILNE-EDWARDS 1869)
Sylviocarcinus H. MILNE-EDWARDS 1853
  australis MAGALHÃES & TÜRKAY 1995
  devillei H. MILNE-EDWARDS 1853
  maldonadoensis (PRETZMANN 1978)
  pictus (H. MILNE-EDWARDS 1853)
  piriformis (PRETZMANN 1968)
Valdivia WHITE 1847
  camerani (NOBILI 1896)
  haraldi BOTT 1969
  novemdentata (PRETZMANN 1968)
  serrata serrata WHITE 1847
  serrata harttii (RATHBUN 1905)
Zilchiopsis BOTT 1969
  collastinensis (PRETZMANN 1968)
  cryptodus (ORTMANN 1893)
  oronensis (PRETZMANN 1968)

Table 2. Generic classification of trichodactylid species and subspecies by Rodriguez (1992) and in the present paper. Valid species and subspecies are printed in bold characters in the first column. Synonymies can be detected by referring to the relative genus in this paper.

Species or subspecies	Genus in RODRIGUEZ (1992)	Genus in present paper
acutidens PRETZMANN	*Trichodactlylus*	*Trichodactylus*
apaluensis PRETZMANN	*Dilocarcinus*	*Poppiana*
apyratii MAGALHÃES & TÜRKAY	- - - - -	*Fredilocarcinus*
argentiniana RATHBUN	*Dilocarcinus*	*Poppiana*
armatus A MILNE-EDWARDS	*Mikrotrichodactylus*	*Trichodactylus*
australis MAGALHÃES & TÜRKAY	- - - - -	*Sylviocarcinus*
bachmayeri PRETZMANN	*Dilocarcinus*	*Poppiana*
bidens BOTT	*Avotrichodactylus*	*Avotrichodactylus*
boliviensis PARISI	*? Zilchiopsis*	*Poppiana*
borellianus NOBIL!	*Mikrotrichodactylus*	*Trichodactylus*
bourgueti RATHBUN	*? Valdivia*	*Rotundovaldivia*
brasiliensis PRETZMANN	*Mikrotrichodactylus*	*Trichodactylus*
bulbifer RODRIGUEZ	*Dilocarcinus*	*Poppiana*
camerani NOBILI	*Valdivia*	*Valdivia*
castelnaui H. MILNE-EDWARDS	*Dilocarcinus*	*Goyazana*
cayennensis PRETZMANN	*Dilocarcinus*	*Poppiana*
chacei PRETZMANN	*Zilchiopsis*	*Moreirocarcinus*
collastinensis PRETZMANN	*Sylviocarcinus*	*Zilchiopsis*
constrictus PEARSE	*Avotrichodactylus*	*Avotrichodactylus*
crassus A. MILNE-EDWARDS	*Trichodactylus*	*Trichodactylus*
cristatus BOTT	*Dilocarcinus*	*Dilocarcinus*
cryptodus ORTMANN	*Zilchiopsis*	*Zilchiopsis*
cucutensis PRETZMANN	*Dilocarcinus*	*Bottiella*
cunninghami BATE	*Trichodactylus*	*Trichodactylus*
cururuensis BOTT	*Valdivia*	*Valdivia*
dentata RANDALL	*Dilocarcinus*	*Poppiana*
dentatus H. MILNE-EDWARDS	*Trichodactylus*	*Trichodactylus*
devillei H. MILNE-EDWARDS	*Sylviocarcinus*	*Sylviocarcinus*
ecuadoriensis PRETZMANN	*Zilchiopsis*	*Moreirocarcinus*
ecuadoroides PRETZMANN	*Zilchiopsis*	*Moreirocarcinus*
edentata BOTT	*Forsteria*	*Forsteria*
edwardsi RATHBUN	*Trichodactylus*	*Trichodactylus*
ehrhardti BOTT	*Trichodactylus*	*Trichodactylus*
emarginatus H. MILNE-EDWARDS	*Zilchiopsis*	*Moreirocacinus*
enriquei PRETZMANN	*Dilocarcinus*	*Dilocarcinus*
falcipenis PRETZMANN	*Valdivia*	*Rotundavaldivia*
faxoni RATHBUN	Incertae sedis	*Trichodactylus*
fluviatilis LATREILLE	*Trichodactylus*	*Trichodactylus*
gigas SMALLEY & RODRIGUEZ	*Sylviocarcinus*	*Sylviocarcinus*
gila PRETZMANN	*Valdivia*	*Valdivia*
glaber PRETZMANN	*Trichodactylus*	*Trichodactylus*
guayanensis PRETZMANN	- - - - -	Incertae sedis
gurupensis RATHBUN	Incertae sedis	*? Sylviocarcinus*
haraldi BOTT	*Valdivia*	*Valdivia*
harttii RATHBUN	*Valdivia*	*Valdivia*
kensleyi RODRIGUEZ	*Trichodactylus*	*Trichodactylus*
laevifrons MOREIRA	*Dilocarcinus*	*Moreirocacinus*

Table 2. (continued).

| Species or subspecies	Genus in RODRIGUEZ (1992)	Genus in present paper
latidens A. MILNE-EDWARDS	*Valdivia*	*Rotundovaldivia*
maldonadoensis PRETZMANN	*Sylviocarcinus*	*Sylviocarcinus*
margaritifrons ORTMANN	*Sylviocarcinus*	*Sylviocarcinus*
marmorata NOBILI	*Mikrotrichodactylus*	*Trichodactylus*
maytai PRETZMANN	*Trichodactylus*	*Trichodactylus*
medemi SMALLEY & RODRIGUEZ	*Dilocarcinus*	*Bottiella*
meekei PRETZMANN	? *Forsteria*	*Melocarcinus*
mensabak COTTARELLI & ARGANO	*Rodriguezia*	*Rodriguezia*
multidentatus VON MARTENS	*Dilocarcinus*	*Poppiana*
musmuschiae PRETZMANN & MAYTA	*Fredilocarcinus*	*Fredilocarcinus*
niceforei SCHMITT & PRETZMANN	*Dilocarcinus*	*Bottiella*
novemdentata PRETZMANN	*Valdivia*	*Valdivia*
oaxensis RODRIGUEZ	*Avotrichodactylus*	*Avotrichodactylus*
orbicularis MEUSCHEN	*Dilocarcinus*	*Dilocarcinus*
ornatifrons PRETZMANN	*Forsteria*	*Forsteria*
oronensis PRETZMANN	? *Zilchiopsis*	*Zilchiopsis*
pagei STIMPSON	*Dilocarcinus*	*Dilocarcinus*
panoplus VON MARTENS	*Mikrotrichodactylus*	*Trichodactylus*
paranensis BOTT	Incertae sedis	*Trichodactylus*
pardalinus GERSTÄCKER	*Sylviocarcinus*	*Sylviocarcinus*
parvus MOREIRA	? *Mikrotrichodactus*	*Trichodactylus*
peruvianus A. MILNE-EDWARDS	*Sylviocarcinus*	*Sylviocarcinus*
petropolitanus GÖLDI	*Trichodactylus*	*Trichodactylus*
pictus H. MILNE-EDWARDS	*Sylviocarcinus*	*Sylviocarcinus*
piriformis PRETZMANN	*Sylviocarcinus*	*Sylviocarcinus*
punctatus EYDOUX & SOLEYET	*Trichodactylus*	*Trichodactylus*
quadrata H. MILNE-EDWARDS	*Trichodactylus*	*Trichodactylus*
quinquedentatus RATHBUN	*Trichodactylus*	*Trichodactylus*
raddai PRETZMANN	*Fredilocarcinus*	*Fredilocarcinus*
rionegrensis PRETZMANN	*Sylviocarcinus*	*Sylviocarcinus*
rionovoensis BOTT	*Trichodactylus*	*Trichodactylus*
rotundicauda MAGALHÃES & TÜRKAY	- - - - -	*Goyazana*
sattleri BOTT	*Zilchiopsis*	*Zilchiopsis*
septemdentatus HERBST	*Dilocarcinus*	*Dilocarcinus*
serrata WHITE	*Valdivia*	*Valdivia*
spinifer H. MILNE-EDWARDS	*Dilocarcinus*	*Dilocarcinus*
spinifrons KINGSLEY	*Sylviocarcinus*	*Sylviocarcinus*
surinamensis PRETZMANN	*Valdivia*	*Valdivia*
thayeri RATHBUN	*Trichodactylus*	*Trichodactylus*
theresiopoliensis PRETZMANN	*Trichodactylus*	*Trichodactylus*
tifucanus RATHBUN	*Trichodactylus*	*Trichodactylus*
torresi PRETZMANN	*Sylviocarcinus*	*Sylviocarcinus*
trinidadensis PRETZMANN	*Dilocarcinus*	*Poppiana*
truncatus RODRIGUEZ	*Dilocarcinus*	*Dilocarcinus*
venezuelensis RATHBUN	*Forsteria*	*Forsteria*
villalobosi RODRIGUEZ & MANRIQUE	*Rodriguezia*	*Rodriguezia*
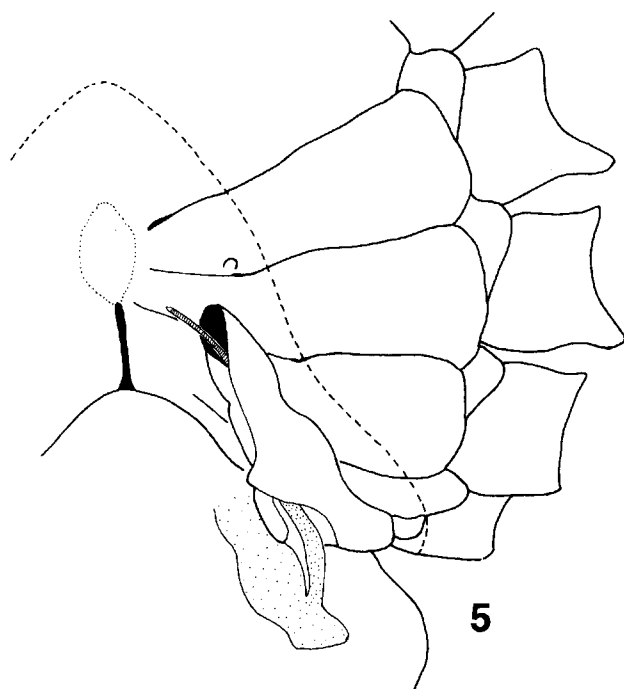
Fig. 5. Position of male Plp 1 in the sterno-abdominal cavity of *Trichodactylus*. The visible face of the limb is the ventral one, the opposite side the dorsal.

from the Dilocarcinini to the Valdiviini. By this, both tribes become homogeneous with reference to sternal and endophragmal structures.

The system used in our study is presented in Table 1; Table 2 lists the classification into genera as proposed by RODRIGUEZ (1992) and ourselves.

Terminology and presentation

One of the main characters used for classification of the freshwater crabs is the morphology of the male first pleopod (plp 1). The terminology used for the description of this appendage is explained in Figs. 5-6 and is based on the orientation of the first pleopod with the crab. The face showing towards the dorsal side (i.e. towards the sternum) is termed dorsal; the one facing ventral (towards the abdomen) is termed ventral; the direction towards the middle of the sternum is mesial; the one towards the outer side is lateral. The terms distal (terminal) and proximal (basal) are used to describe a position on the pleopod.

The description of the endophragmal system follows GUINOT (1979) (Fig. 7). Endosternites are the plates originating from the separation lines between thoracic segments. The median line is oriented fronto-caudally in the middle of the sternum and may be the base of a high crest in the endophragmal system. The presence of the median line does not necessarily indicate that the crest is high. The endophragmal system must be properly prepared in order to confirm this character state, which is impossible in type material or rare species. Therefore in some instances the formula "endophragmal system, as judged from the external view, identical with..." has been used. All segment identifications in the thorax and abdomen are given in Roman numbers.

The locality lists are grouped by countries and provinces (or states). In case of repetition of localities we have used "idem". This
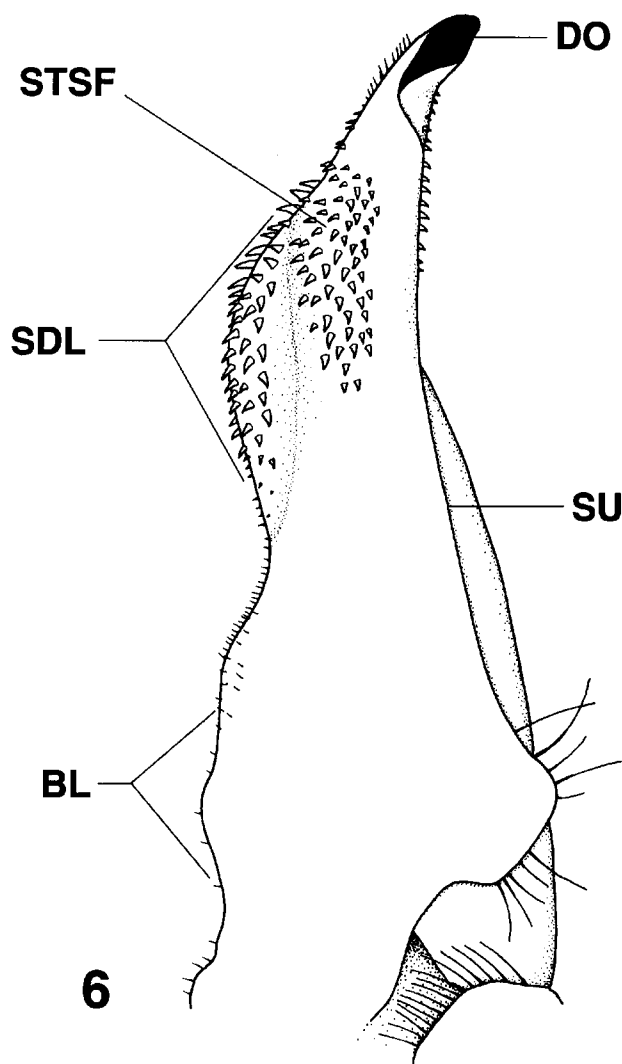

Fig. 6. Right Plp 1 of *Sylviocarcinus devillei* with an explanation of the structures used in the keys and descriptions. — BL = Basal lobe, DO = distal opening, SDL = subdistal lobe, STSF = subterminal spine field, SU = suture.

means that all the information in front of the date and/or collector are identical with the previous sample.

The synonymy lists cover the literature published after BOTT's (1969) revision and prior to this date only synonyms are listed.
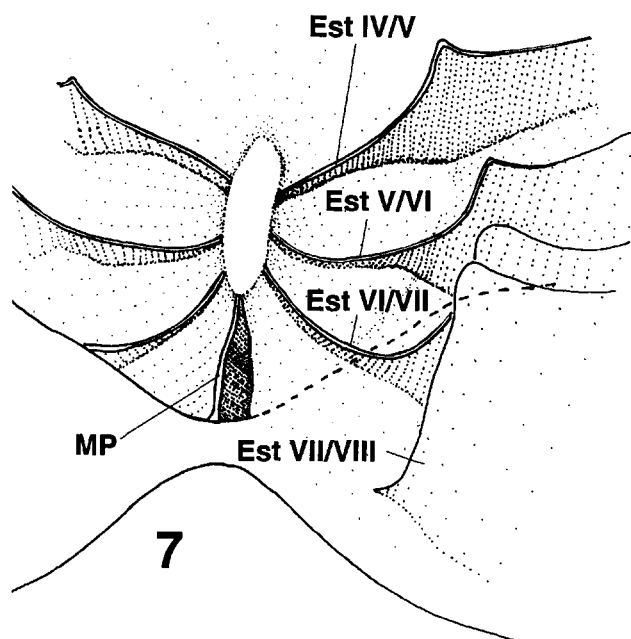
Fig. 7. Schematic drawing of the endophragmal system of *Trichodactylus*. Est = Endosternite, MP = median plate, the Roman figures signify the thoracal segments.

List of the museums and institutions with examined trichodactylid collections including the abbreviations that have been used throughout the paper to mark the repositories of specimens:

AMNH = American Museum of Natural History, New York; ANSP = Museum of the Academy of Natural Sciences of Philadelphia; EPA = Expedição Permanente na Amazônia; FCEyN = Facultad de Ciências Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires; FMNH = Field Museum of Natural History, Chicago; FZB = Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre; INPA-CR = Coleção Sistematica de Invertebrados, Seção Crustacea, Instituto Nacional de Pesquisas da Amazônia; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles; MACN = Museo Argentino de Ciencias Naturales "BERNARDINO RIVADAVIA", Buenos Aires; MCSNG = Museo Civico di Storia Naturale "GIACCOMO DORIA", Genova; MCSNM = Museo Civico di Storia Naturale de Milano; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MLP = Museo de La Plata, La Plata; MNHN = Muséum National d'Histoire Naturelle, Paris; MNRJ = Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MPEG = Museu Paraense EMILIO GOELDI, Belém; MZUSP = Museu de Zoologia da Universidade de São Paulo, São Paulo; MZUT = Museo ed Istituto di Zoologia Sistematica dell'Universitá di Torino; MZVS = Musée Zoologique de l'Université LOUIS PASTEUR et de la Ville de Strasbourg, Strasbourg; NHMB = Naturhistorisches Museum Basel, Basel; NHML = The Natural History Museum, London; NHMW = Naturhistorisches Museum Wien, Wien; NNHM = Nationaal Natuurhistorisch Museum, Leiden; NRMSt = Naturhistoriska Riksmuseet, Stockholm; Plp 1 = First male pleopod; SMF = Senckenberg Museum, Frankfurt a. M.; UFPB = Coleção de Crustacea da Universidade Federal da Paraiba, João Pessoa; UFPE = Coleção Zoológica do Departamento de Oceanografia da Universidade Federal de Pernambuco, Recife; UFRGS = Coleção Zoológica do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul, Porto Alegre; UNAM = Colleción de Carcinologia del Instituto de Biologia, Universidad Nacional Autónoma de México, México, D. F.; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D. C.; UZM = Universitetets Zoologiske Museum, København; ZMB = Zoologisches Museum der Humboldt-Universität, Berlin; ZMH = Zoologisches Institut und Museum, Hamburg; ZSM = Zoologische Staatssammlung, München.

Key to trichodactylid genera

This key should be used with great care. The segmentation of the abdomen is not always typical, as in younger specimens the borders between the somites may still be present, fading away in larger specimens. The same applies to the anterolateral teeth. Therefore, after a specimen is identified the first male pleopod (plp 1) should be compared to the figures illustrated in this paper to confirm the determination.

1. All abdominal segments free 2
— At least abdominal segments III–V fused (in female *Goyazana* the abdominal segments III–VI can be largely fused) 4
2. Median line of thoracic sternum present in somites V–VIII. Male plp 1 with distal half tapering, distal opening small and facing caudo-laterally; plp 2 longer than plp 1 .. *Goyazana*
— Median line of thoracic sternum present in somites VII and VIII. Male plp 1 with distal half subcylindrical, distal opening large and facing caudo-mesially. Male plp 2 various 3
3. Male plp 2 longer than plp 1 .... *Trichodactylus*
— Male plp 2 much shorter than plp 1 .... *Rodriguezia*
4. Segment VI of abdomen free 5

— Segment VI of abdomen fused with the proximal ones . 10
5. Subterminal spine field of male plp 1 arranged on mesio-ventral and dorsal faces of the stem in one continuous patch 6
— Subterminal spine field of male plp 1 developed only on mesio-ventral face of stem; if on both sides, strong basal lobe present 8
6. Male plp 1 strongly curved towards ventral side, regularly tapering, with tip very sharply pointed . *Avotrichodactylus*
— Male plp 1 straight or slightly bent towards mesio-dorsal side, either with strong subdistal lobe or subcylindrical tip .. 7
7. Stem of male plp 1 with a very prominent basal lobe .... *Melocarcinus*
— Stem of male plp 1 without prominent basal lobe .... *Sylviocarcinus*
8. Spine field situated on an evidently bulged subdistal lobe . ... *Forsteria*
— Subdistal lobe faint or absent; basal lobe usually present; stem tapering 9
9. Male plp 1 with a well developed spine field; basal lobe rectangular, sometimes (as in *V. novemdentata*) hardly visible .... *Valdivia*
— Male plp 1 with a poorly developed spine field; basal lobe rounded .... *Rotundovaldivia*

10. Median line of thoracic sternum present in somites VII–VIII only 11

— Median line of thoracic sternum present in somites V–VIII 12

11. Male plp 1 with subdistal lobe bearing a spine field; distal part of appendage slightly bent in a mesio-dorsal direction .... *Sylviocarcinus*

— Male plp 1 without distinct subdistal lobe; spine field poorly developed; distal part of limb strongly bent in a latero-ventral direction .... *Zilchiopsis*

12. Male plp 1 with marginal suture twisted in a ventro-lateral direction very near to the apex; apex flattened; distal part showing a strong torsion in a clockwise direction on right pleopods (anti-clockwise on left ones) 13

— Male plp 1 with marginal suture straight or twisted in a mesio-dorsal direction near to the apex; apex subcylindrical; distal part without torsion 14

13. Male abdomen narrowly triangular, its lateral margins concave. Ventral border of male plp 1 following a regular curve, subterminal spine field forming a more or less continuous patch 15

— Male abdomen broadly triangular, its lateral margins convex. Ventral border of male plp 1 clearly bulging proximally, subterminal spine field composed of two discontinuous patches .... *Fredilocarcinus*

14. Male plp 1 with distal opening simple, V-shaped or slit-like 15

— Male plp 1 with distal opening circular to broadly oval, its margins rolled up .... *Poppiana*

15. Male plp 1 tapering, straight or slightly bent in a mesio-dorsal direction; lateral and mesial borders following a regular curve .... *Moreirocarcinus*

— Male plp 1 with distal part subcylindrical, slightly or strongly bent in a ventral direction; mesial border bulging subdistally .... *Bottiella*

Systematic account

Trichodactylidae H. MILNE-EDWARDS 1853

1853 Trichodactylacea H. MILNE-EDWARDS, Ann. Sci. nat., (3)20: 213.

Trichodactylinae s. str.

Type genus: *Trichodactylus* LATREILLE 1828.

Diagnosis: Sternal plastron broadly oval; endosternites IV/V, V/VI, and VI/VII and corresponding sutures on sternum nearly reaching midline; median plate well developed in thoracic somites VII–VIII. Sternal lobe of VIIIth thoracic somite and sometimes also episternite VII partly covering penial groove of male. Male plp 1 a simple tube with terminal distal opening; subdistal spine fields on both sides of the stem. Generally (with the exception of *Avotrichodactylus*) all abdominal segments free. Postgastric pits of carapace missing.

Avotrichodactylus PRETZMANN 1968

(Figs. 8, 11, 12)

1968 Trichodactylus (Avotrichodactylus) PRETZMANN, Entom. Nachrbl., 15(7/8): 71.

Type species: *Trichodactylus constrictus* PEARSE 1911 [by monotypy].

Diagnosis: Carapace with 2–3 anterolateral teeth. Abdominal segments III–V fused. Thoracic sternum relatively long and narrow, endosternites IV/V and VI/VII reach midline (judged by external view); median line present in somites VII–VIII. Male plp 1 strongly curved towards the ventral side, regularly tapering, tip sharply pointed; subterminal spine field arranged in a continuous patch on the mesio-ventral and dorsal faces of the stem; suture following general curve of the limb, no torsion visible. Plp 2 shorter than plp 1.

Distribution: Restricted to Mexico.

Remarks: Three species have been recognized in this genus, *A. constrictus, A. bidens,* and *A. oaxensis* by RODRIGUEZ (1992). After examining a good number of specimens, we found that the number of the anterolateral teeth in *A. constrictus* is variable. Even the female paratype of *A. bidens* (SMF 4888) has an accessory lobe on the left anterolateral border between the two teeth, situated exactly like the third tooth in *A. constrictus,* the right anterolateral border has only two teeth. Similar observations on other specimens lead us to believe, that *A. constrictus* and *A. bidens* are unseparable and, thus, we treat them as synonyms.

Species included: *constrictus* (PEARSE 1911) [= *bidens* Bott 1969], *oaxensis* RODRIGUEZ 1992.

Rodriguezia BOTT 1969

(Figs. 9, 13)

1969 Trichodactylus (Rodriguezia) BOTT, Abh. senckenb. naturf. Ges., 518: 25.

Type species: *Trichodactylus villalobosi* RODRIGUEZ & MANRIQUE 1967 [by original designation].

Diagnosis: Lateral (including antero- and postero-lateral) teeth absent. Thoracic sternum broadly oval; endosternites IV/V, V/VI, and VI/VII crest-shaped mesially and meeting the midline; median plate crest-shaped and present only in somites VII–VIII. All abdominal segments free. Male plp 1 straight, with subterminal spine fields arranged in two discontinuous patches on the lateral and dorsal sides of the stem; suture straight (i.e. pleopod not torded); distal opening broad. Male plp 2 markedly shorter than plp 1.

Distribution: Mexico.

Species included: *mensabak* COTTARELLI & ARGANO 1977, *villalobosi* RODRIGUEZ & MANRIQUE 1966.
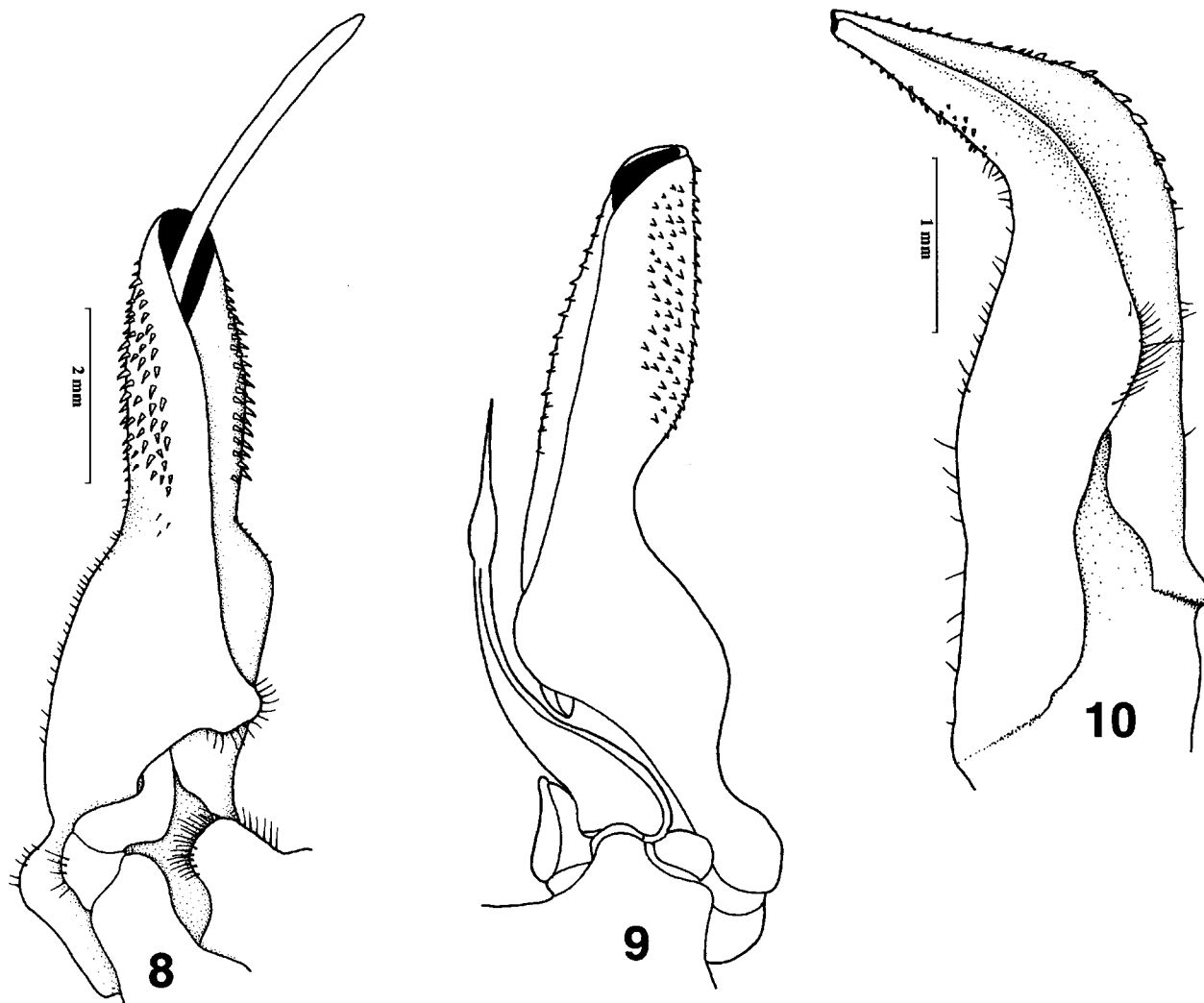
Figs. 8–10. Male pleopods of type species of trichodactyline genera [8, 10 right limb; 9 left limb]. — 8) *Avotrichodactylus constrictus* (USNM 189307); 9) *Rodriguezia villalobosi* (after Rodriguez & Manrique 1966); 10) *Trichodactylus fluviatilis* (SMF 1825).

Trichodactylus Latreille 1828

(Figs. 10, 14, 15)

1828 *Trichodactylus* Latreille, Encycl. méth. Hist. nat., 10: 705.
1968 *Trichodactylus (Mikrotrichodactylus)* Pretzmann, Entom. Nachrbl., 15(7/8): 71 [Type species by original designation: *Trichodactylus borellianus* Nobili 1896].

Type species: *Trichodactylus fluviatilis* Latreille 1828 [by monotypy].

Diagnosis: Lateral (including antero- and postero-lateral) teeth absent or up to five. Thoracic sternum broadly oval; endosternites IV/V, V/VI, and VI/VII crest-shaped mesially and meeting the midline in most species (except *T. borellianus* and *T. parvus*); median plate crest-shaped and present only in somites VII–VIII. All abdominal segments free. Male plp 1 straight, with subterminal spine fields arranged in two discontinuous patches

on lateral and dorsal sides of the stem; suture straight (i.e. pleopod not torded); distal opening broad. Male plp 2 longer than plp 1.

Distribution: Nearly the whole of tropical/subtropical South America, most species in Brazil.

Remarks: Pretzmann (1968: 71) established the subgenus *Trichodactylus (Mikrotrichodactylus)* and cited *T. borellianus* as the type of the taxon. Rodriguez (1992) assigned generic rank to it. In this study the subgenus of Pretzmann is not recognised as a separate taxon because, without making artificial divisions in *Trichodactylus*, there are no characters that distinguish *T. borellianus*. This species has an endophragmal system like *T. parvus*, but the male pleopods are different. Alternatively, *T. panoplus* and *T. borellianus* have similar male pleopods but different endophragmal systems. The peculiarities of the pleopod shape exhibited by *T. borellianus* are not sufficient to
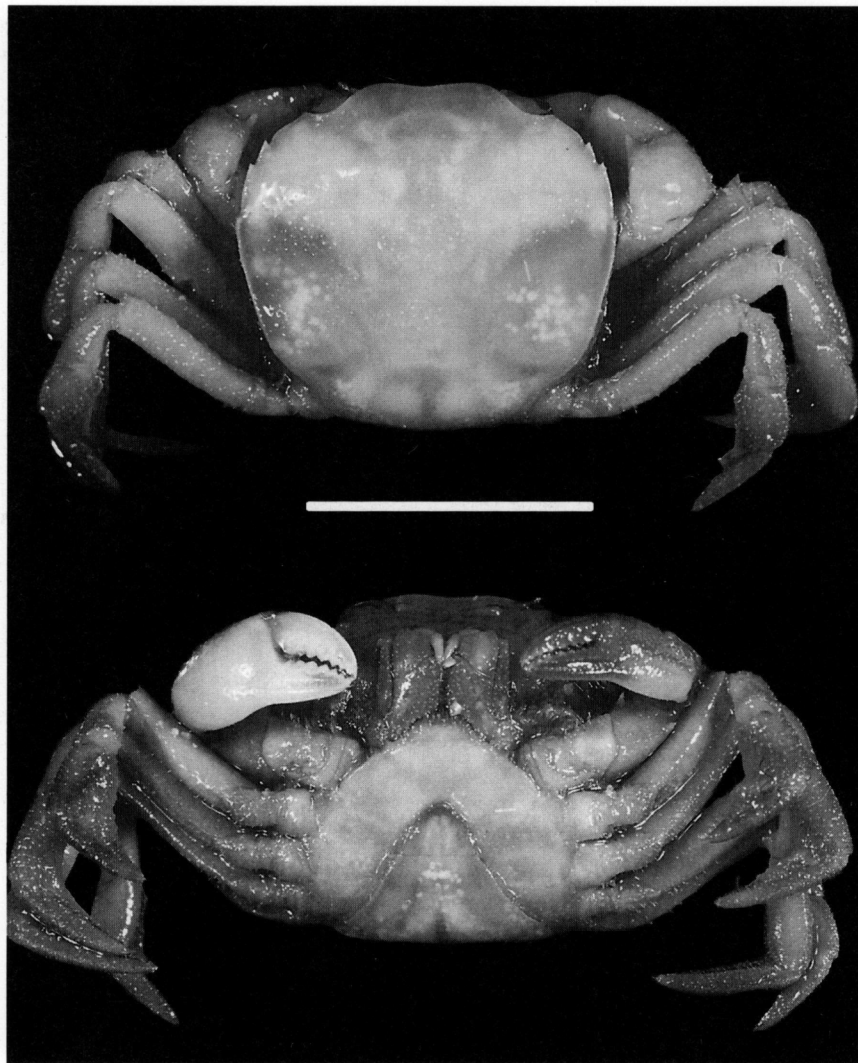
Fig. 11. *Avotrichodactylus constrictus* (NHML 1907.5.15.5-9), dorsal and ventral aspect. — Scale 10 mm.

justify a separate genus. The differences described by RODRIGUEZ (1992) in his key to the genera do not hold upon closer examination. The diagonal folding of male first pleopods is a common character not only to the species included by him in *Mikrotrichodactylus,* but occurs also in all the smaller species of the Amazon drainage, which, however, have not the "apex bent mesiad". A full treatment of this genus will be given in a subsequent paper.

Fig. 12. *Avotrichodactylus constrictus* (NHML 1907.5.15.5-9), X-Ray picture of endophragmal system.
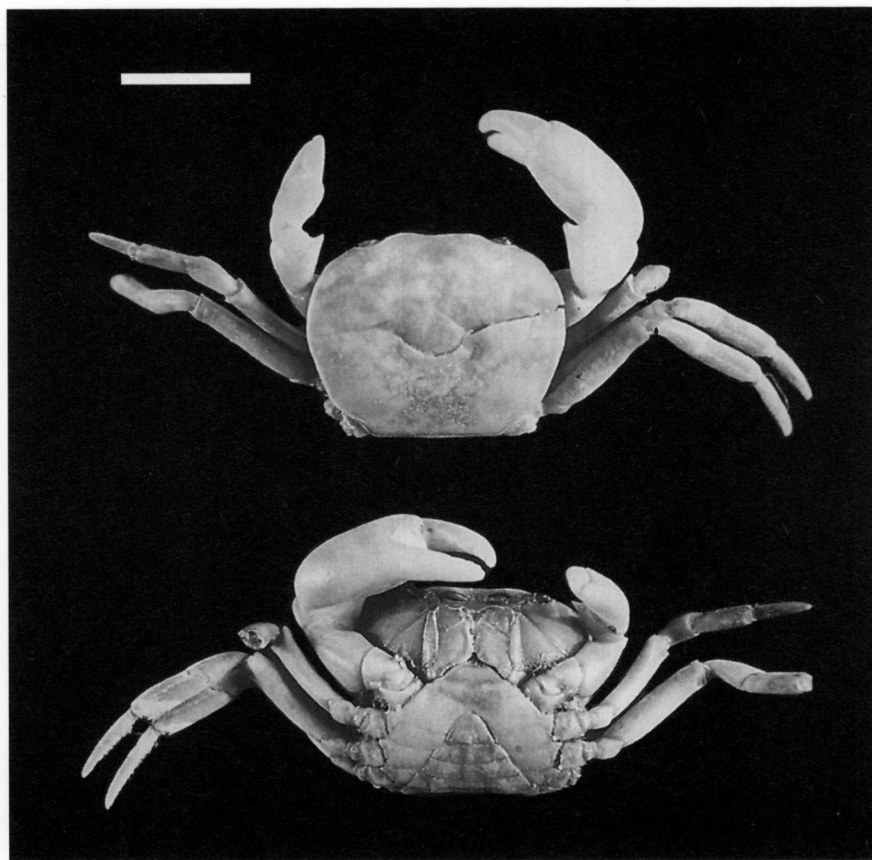
Fig. 13. *Rodriguezia villalobosi* (holotype, UNAM EM-7832), dorsal and ventral aspect. — Scale 10 mm.

Concerning the taxonomy there are still problems in clearly separating the Brazilian forms around *T. fluviatilis.* Therefore the species list presented here is preliminary as to this species group.

Most species of this genus occur in Brazil, which appears to be the centre of distribution for this group. However, this fact may be due to poor collecting because members of this genus are widely distributed throughout South America.

Species included: *borellianus* NOBILI 1896, *crassus* A. MILNE-EDWARDS 1869, *dentatus* H. MILNE-EDWARDS 1853, *ehrhardti* BOTT 1969, *faxoni* RATHBUN 1905 [= *maytai* PRETZMANN 1978], *fluviatilis* LATREILLE 1828 [= *tifucanus theresiopoliensis* PRETZMANN 1968], *kensleyi* RODRIGUEZ 1992, *panoplus* (VON MARTENS 1869) [= *borellianus brasiliensis* PRETZMANN 1968], *parvus* MOREIRA 1912, *petropolitanus* GÖLDI 1886 [= *petropolitanus paranensis* BOTT 1969, *thayeri glaber* PRETZMANN 1968, *tifucanus acutidens* PRETZMANN 1968], *quinquedentatus* RATHBUN 1893.

Dilocarcininae PRETZMANN 1978

1978 Dilocarcininae PRETZMANN, Sitz.-Ber. österr. Akad. Wiss., **187**(2): 170.

Type genus: *Dilocarcinus* H. MILNE-EDWARDS 1853.
Diagnosis: Sternal plastron relatively narrow; endosternites IV/V, V/VI, and VI/VII and corresponding sutures of the sternum not nearly reaching the midline; median plate well developed either in thoracic somites V–VIII or VII–VIII. Penial grove of male totally open, not even partly covered by any sternal lobe. Male plp 1 various. Generally (with exception of *Goyazana*) some abdominal segments fused. Postgastric pits of carapace present.

Dilocarcinini s. str.

Diagnosis: Endophragmal system with median plate well developed in thoracic somites V–VIII. Generally (with exception of *Goyazana*) some abdominal segments fused.
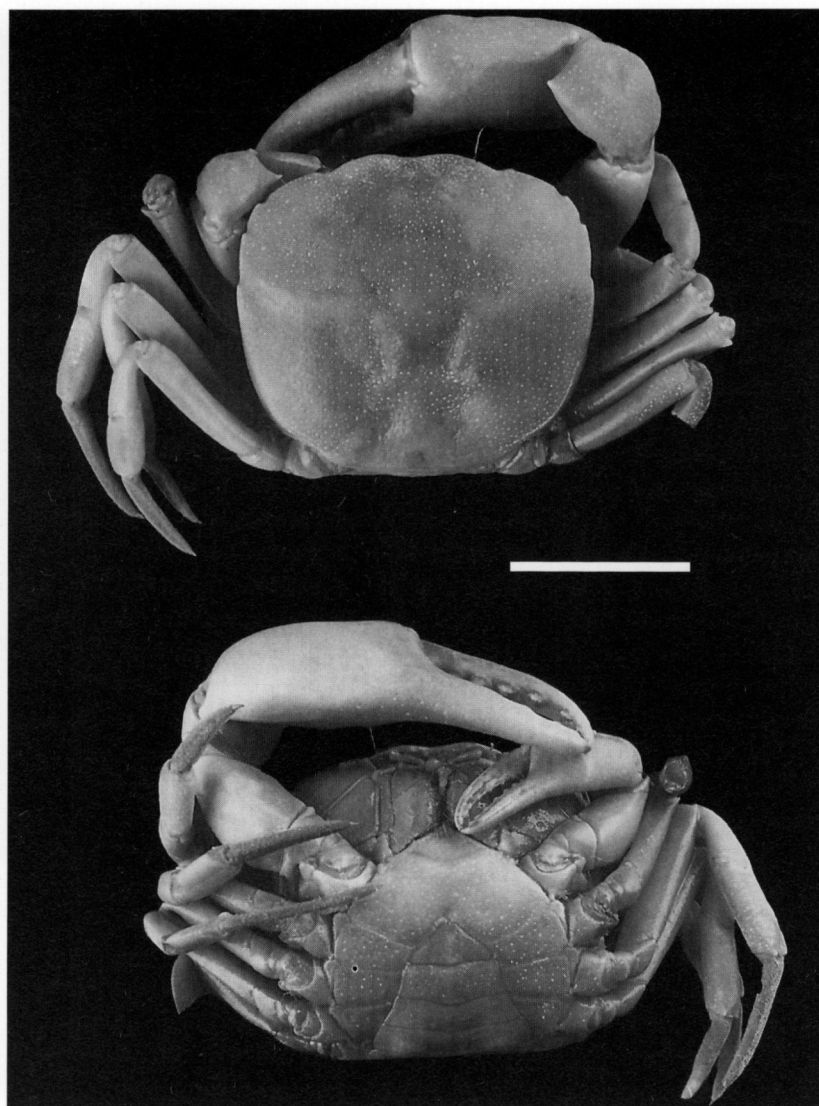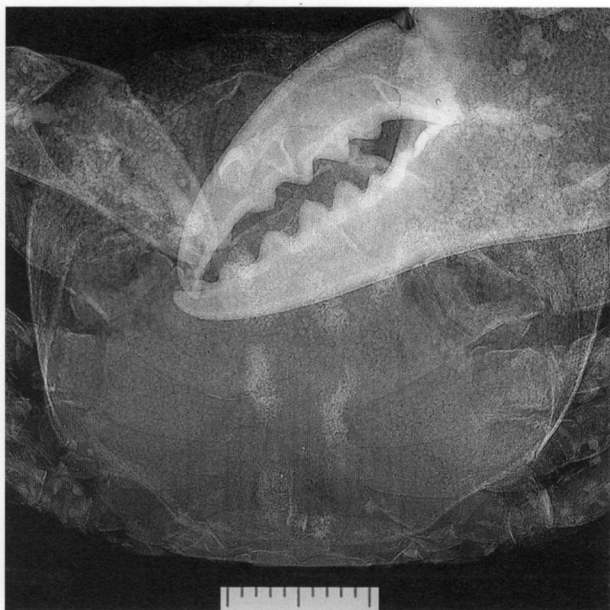
Fig. 14. *Trichodactylus fluviatilis* (SMF 4319), dorsal and ventral aspect. — Scale 20 mm.

Bottiella n. gen.
(Figs. 16, 22)

Type species: *Dilocarcinus* (*Dilocarcinus*) *medemi* SMALLEY & RODRIGUEZ 1972.

Etymology: This genus is named for RICHARD BOTT, who was the first modern author having revised the Trichodactylidae.

Fig. 15. *Trichodactylus fluviatilis* (SMF 4319), X-Ray picture of endophragmal system.
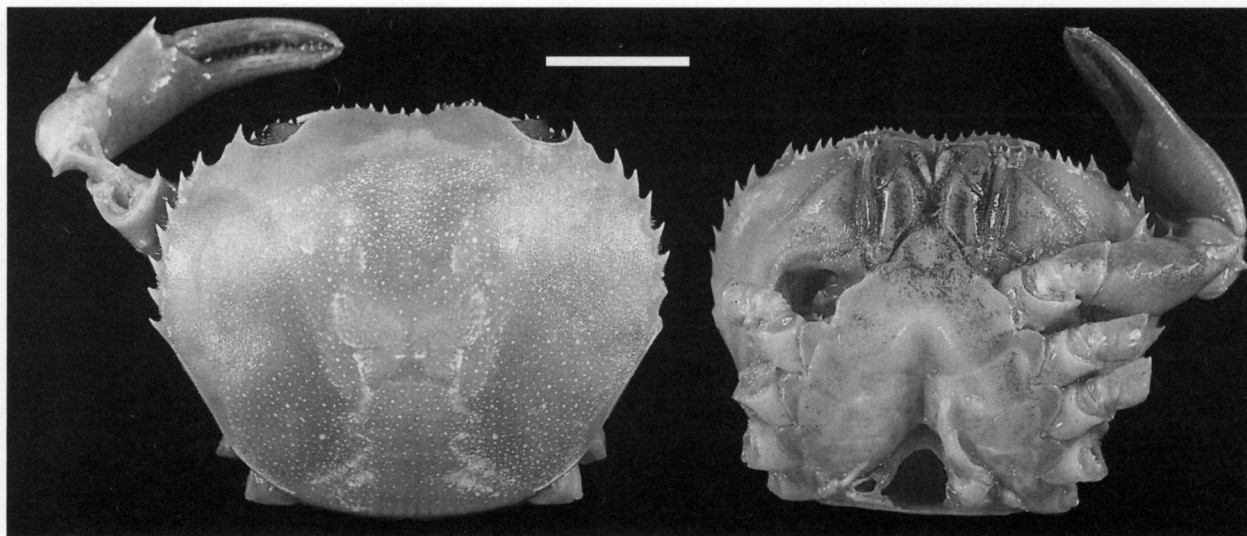
Fig. 22. *Bottiella medemi* (holotype, USNM 139122), dorsal and ventral aspect. — Scale 10 mm.

Dilocarcinus H. MILNE-EDWARDS 1853
(Figs. 17, 23, 24)

1853 *Dilocarcinus* H. MILNE-EDWARDS, Ann. Sci. nat., (3)**20**: 215.

Type species: *Dilocarcinus spinifer* H. MILNE-ED-
WARDS 1853 [by subsequent designation: PRETZMANN 1968].

Diagnosis: Carapace with 6 or more anterolateral
teeth. Abdominal segments III–VI fused. Thoracic ster-
num relatively long and narrow, only endosternites IV/V
reaching the midline; median plate crest-shaped and pre-
sent in somites V–VIII. Male abdomen narrowly
triangular, its margins concave. Ventral border of male plp
1 following a regular curve; distal end of the appendage
flattened, with a clear subdistal lobe at least on the ventral
face; subterminal spine field more or less continuous on
the ventral, lateral, and sometimes also dorsal faces; suture
following the general line of plp 1 along the major part of
the stem, and twisted in a ventro-lateral direction very near
to the apex, thus, the strong torsion (clockwise in the right
plp 1, anti-clockwise in the left) is confined to the distal
part. Plp 2 longer than plp 1.

Distribution: All South American lowlands from
Guyana to Argentina.

Remarks: In our opinion this genus includes only
three species. We have excluded a number of species which
RODRIGUEZ (1992) included in this genus making it to a
highly heterogeneous group with respect to the mor-
phology of male plp 1. We believe that by our action
Dilocarcinus becomes a more natural group than it has
been before.

Of the species included, *D. pagei* can easily be separated
from *D. septemdentatus* by the distinctly crested third ab-
dominal segment. We agree with LOPRETTO (1981) in not
recognizing *D. pagei cristatus* BOTT 1969 as a valid
subspecies, because homo- and heterochely were observed
within one population. After having examined the
holotype of *D. pagei enriquei*, we propose, in contrast to
RODRIGUEZ (1992), to keep the subspecies separate for the
time being on the basis of its very long and slender

helipeds, which are quite peculiar, until more specimens
can be examined in order to determine the variability of
this character. A full treatment of the problems involved
in separating the species of this genus will be published in
a separate paper.

Species included: *pagei pagei* STIMPSON 1861 [=
pagei cristatus BOTT 1969], *pagei enriquei* PRETZMANN
1978, *septemdentatus* (HERBST 1783) [= *spinifer* H. MILNE-
EDWARDS 1853], *truncatus* RODRIGUEZ 1992.

Fredilocarcinus PRETZMANN 1978
(Figs. 18, 25, 26)

1978 *Dilocarcinus (Fredilocarcinus)* PRETZMANN, Sitz.-Ber. österr.
Akad. Wiss. math. naturw. Kl., (I) **187**(6–10): 168.

Type species: *Dilocarcinus (Fredilocarcinus) raddai*
PRETZMANN 1978 [by monotypy].

Diagnosis: Carapace with 6 or more anterolateral
teeth. Abdominal segments III–VI fused. Thoracic ster-
num relatively long and narrow, only endosternites IV/V
reaching midline; median plate crest-shaped and present in
somites V–VIII. Male abdomen broadly triangular, its
margins convex. Ventral border of male plp 1 clearly bul-
ging proximally; tip of appendage asymmetrical, subdistal
lobe weak, only on ventral face; subterminal spine field
composed of two discontinuous patches; suture following
the general line of plp 1 along the major part of stem, and
twisted in a ventro-lateral direction very near to the apex,
thus, the strong torsion (clockwise in the right plp 1, anti-
clockwise in the left) is confined to the distal part. Plp 2
longer than plp 1.

Distribution: Amazon drainage of Peru and
Brazilian western Amazon region.

Remarks: We agree with RODRIGUEZ (1992), that
this genus should be treated as separate in relation to
Dilocarcinus. The species included have only rarely been
collected, which reflects the lack of information on the
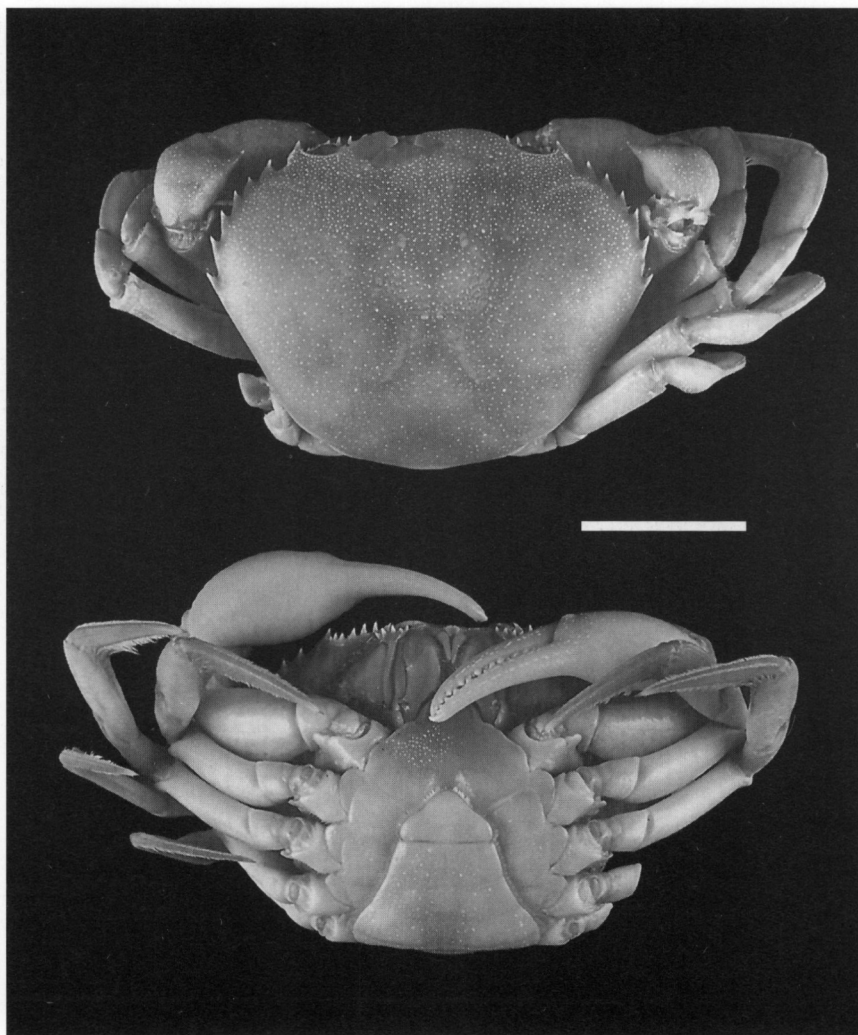fauna of the western Amazon system. We will treat the

Fig. 23. *Dilocarcinus septemdentatus* (SMF 2718), dorsal and ventral aspect. — Scale 20 mm.

species and associated problems in detail in a separate paper (MAGALHÃES & TÜRKAY 1996b).

Species included: *musmuschiae* (PRETZMANN & MAYTA 1980), *raddai* (PRETZMANN 1978), *apyratii* MAGALHÃES & TÜRKAY 1996.
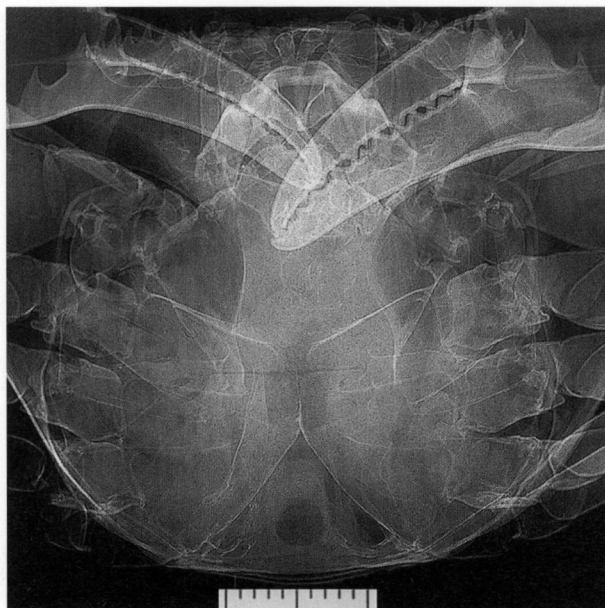

Fig. 24. *Dilocarcinus septemdentatus* (SMF 2718), X-ray picture of endophragmal system.

Fig. 25. *Fredilocarcinus raddai* (NHML 1883.26), dorsal and ventral aspect. — Scale 10 mm.
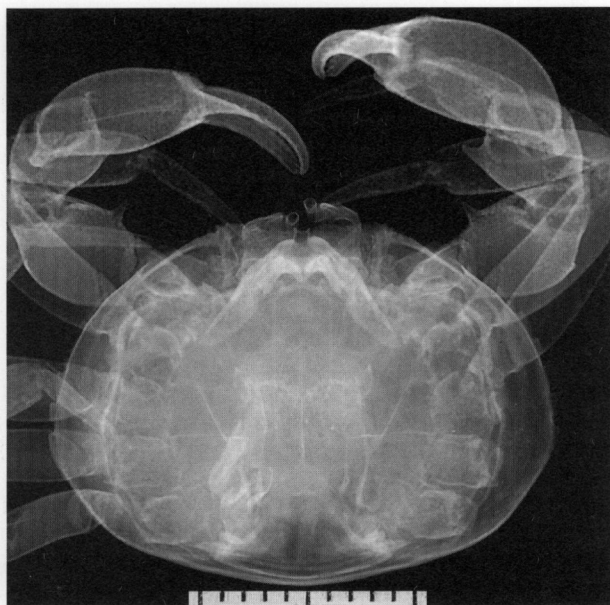

Fig. 26. *Fredilocarcinus musmuschiae* (SMF 22353), X-ray picture of endophragmal system.

Fig. 27. *Goyazana castelnaui* (SMF 22263), dorsal and ventral aspect. — Scale 20 mm.

Goyazana Bott 1969
(Figs. 19, 27, 28)

1969 *Dilocarcinus* (*Goyazana*) Bott, Abh. senckenb. naturf. Ges., **518**: 47.

Type species: *Dilocarcinus castelnaui* H. Milne-Edwards 1853 [by monotypy].

Diagnosis: Carapace with 6 or less anterolateral teeth. All abdominal segments free. Thoracic sternum long
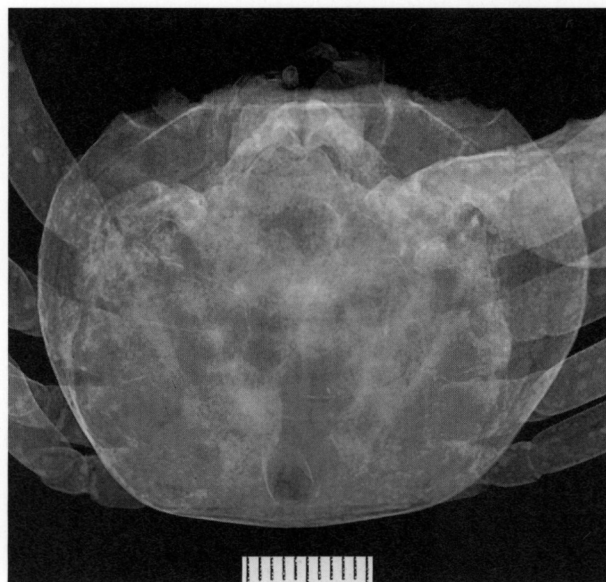

Fig. 28. *Goyazana castelnaui* (SMF 22263), X-ray picture of endophragmal system.

Fig. 29. *Moreirocarcinus chacei* (NHML 1883.26), dorsal and ventral aspect. — Scale 10 mm.

Fig. 30. *Moreirocarcinus emarginatus* (SMF 22271), X-ray picture of endophragmal system.

and narrow. Endophragmal system only with endosternite IV/V reaching the midline as a high crest, the following two endosternites do so only as very low elevations in the central part of the sternum; median plate crest shaped and present in somites V–VIII, however, relatively low in somite V, getting higher towards caudal end of sternum. Male plp 1 without a subterminal lobe, development of spine fields at both sides of the distal part of the stem variable; suture straight (means following the general line of plp 1 and in reality s-shaped like the limb) in the major part of stem, displaced laterally at the extreme tip and meeting the caudally oriented distal opening. Plp 2 longer than plp 1.

Distribution: Brazil, Amazon lowlands of Peru and Ecuador.

Remarks: *Goyazana* was attributed subgeneric rank by BOTT (1969: 47), *Dilocarcinus* (*Goyazana*). Recently RODRIGUEZ (1992) synonymized it with *Dilocarcinus*. As stated before, we do not agree with this very inclusive treatment of *Dilocarcinus*. As *Goyazana* appeared to have no more morphological affinities with *Dilocarcinus* proper than with any other genus, it is assigned to the rank of genus by us.

Species included: *castelnaui* H. MILNE-EDWARDS 1853, *rotundicauda* MAGALHÃES & TÜRKAY 1996.

Moreirocarcinus n. gen.
(Figs. 20, 29, 30)

Type species: *Trichodactylus* (*Trichodactylus*) *chacei* PRETZMANN 1968.

Etymology: This genus is named for CARLOS MOREIRA, who was the only older Brazilian autor having done pioneer work on trichodactylids. He also described one of the species included in this genus.

Diagnosis: Carapace with 2–6 anterolateral teeth. Abdominal segments III–VI fused. Thoracic sternum and endophragmal system (as judged by external view for most species) identical with those of *Poppiana*. Male plp 1 tapering, straight or slightly bent in mesio-dorsal direction; lateral and mesial borders follow a regular curve; subterminal spine field fairly well developed; suture straight (means following the general curve of plp 1), not torded; distal opening simple, V-shaped. Plp 2 longer than plp 1.

Distribution: Orinoco drainage of Colombia and Venezuela; Amazon drainages of Brazil, Peru, and Ecuador.

Remarks: Members of this new genus *Moreirocarcinus* were included in *Dilocarcinus* and *Zilchiopsis* by RODRIGUEZ (1992). The reasons for not treating *Dilocarcinus* as inclusive have been given under the remarks to *Bottiella*. The three species included in our new genus are closely related and form a homogeneous group inhabiting lowlands of big river drainages.

For recognizing individual species some confusion concerning the identity of *Zilchiopsis chacei ecuadoroides*, treated hereafter as synonym of *Moreirocarcinus chacei*, may arise by the fact, that PRETZMANN (1983b: 330) claimed to have figured it on Pl. 13–14. Reexamination of the original specimens showed that the figures on the named plates represented *Z. ecuadoriensis*, as stated by PRETZMANN on page 328, and not *Z. chacei ecuadoroides*. This last subspecies was in fact not figured by PRETZMANN (1983b).

Species included: *chacei* (PRETZMANN 1968) [= *chacei ecuadoroides* (PRETZMANN 1978)] *emarginatus* (H. MILNE-EDWARDS 1853) [= *ecuadoriensis* PRETZMANN 1968], *laevifrons* (MOREIRA 1901).

Poppiana BOTT 1969
(Figs. 21, 31, 32)

1840 *Orthostoma* RANDALL, J. Acad. nat. Sci. Philadelphia, 8: 122. [Type species by monotypy *Orthostoma dentata* RANDALL 1840.] [Nomen praeoccupatum: *Orthostoma* EHRENBERG 1837.]
1969 *Poppiana* BOTT, Abh. senckenb. naturf. Ges., 518: 49.

Type species: *Orthostoma dentata* RANDALL 1840 [by original designation].

Diagnosis: Carapace with 6 or more (up to 12) anterolateral teeth. Abdominal segments III–VI fused. Thoracic sternum relatively long and narrow; only endosternites IV/V of endophragmal system reaching the midline; somite-borderlines V/VI and VI/VII only slightly elevated; median plate crest-shaped and present in somites V–VIII, lowest in somite V highest in somite VIII. Male plp 1 regularly curved with or without a subdistal lobe on its ventral face; subterminal spine field fairly well developed; suture gradually displaced to the mesiodorsal face near distal end of the appendage where it meets the cylindrical to broadly oval distal opening; margins of the latter clearly rolled up. Plp 2 longer than plp 1.

Distribution: The three species, which we include in *Poppiana* were recorded from the northern (Venezuela, Trinidad, Surinam, Guyana) and southern — central (Brazil, Bolivia, Peru, Paraguay, Argentina) South America.

Remarks: BOTT (1969: 51) included *Dilocarcinus laevifrons* MOREIRA 1901 in his new genus *Poppiana*. With respect to the morphology of the male pleopod, this made the genus a heterogeneous taxon and so we decided to assign it to our new genus *Moreirocarcinus*.

SMALLEY & RODRIGUEZ (1972) did not recognize *Poppiana*, they included the type species *Orthostoma dentata* in *Dilocarcinus* and thus both genera were synonymized. PRETZMANN (1979) considered *Poppiana* valid and he included *Trichodactylus* (*Dilocarcinus*) *bachmayeri* in this genus. RODRIGUEZ (1992) synonymized *Poppiana* with *Dilocarcinus*. We recognize BOTT's genus and separate it from *Dilocarcinus* on the basis of the specific structure of the male plp 1 tip and the torsion of the suture.

Species included: *bulbifer* RODRIGUEZ 1992, *dentata* (RANDALL 1840) [= *dentatus cayennensis* (PRETZMANN 1968), *dentatus trinidadensis* (PRETZMANN 1968), *multidentatus* (VON MARTENS 1869)], *argentiniana* (RATHBUN 1905) [= *argentinianus apaluensis* (PRETZMANN 1968), *bachmayeri* (PRETZMANN 1968), *boliviensis* (PARISI 1923)].

Valdiviini PRETZMANN 1978

1978 *Valdiviini* PRETZMANN, Sitz.- Ber. österr. Akad. Wiss., 187(2): 170.

Type genus: *Valdivia* WHITE 1847.

Diagnosis: Endophragmal system with the median plate well developed in thoracic somites VII–VIII. Always with some abdominal segments fused.
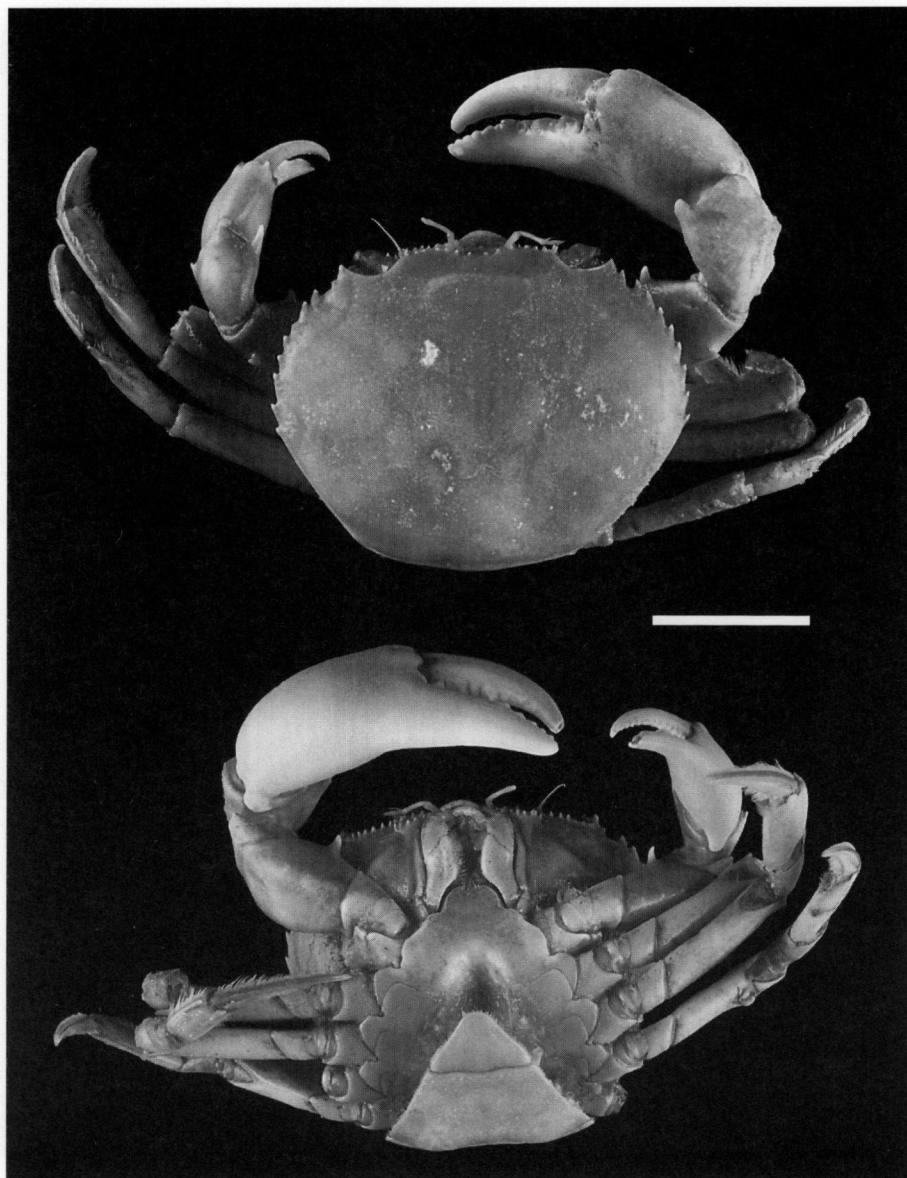
Fig. 31. *Poppiana dentata* (SMF 22245), dorsal and ventral aspect. — Scale 20 mm.
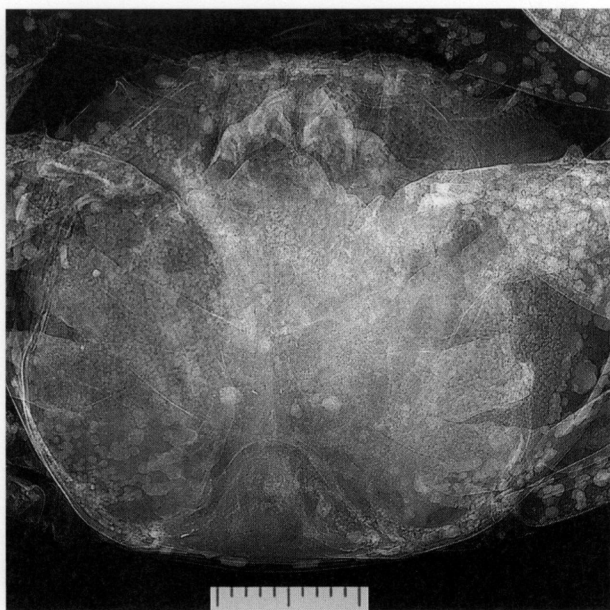
Forsteria BOTT 1969

(Figs. 33, 39, 40)

1969 *Valdivia* (*Forsteria*) BOTT, Abh. senckenb. naturf. Ges., **518**: 37.

Type species: *Valdivia* (*Forsteria*) *venezuelensis edentata* BOTT 1969 [by original designation].

Diagnosis: Carapace with 3–4 anterolateral teeth, fading away in large specimens. Abdominal segments III–V fused. Thoracic sternum and endophragmal system as in

Fig. 32. *Poppiana dentata* (SMF 4296), X-ray picture of endophragmal system.

Fig. 39. *Forsteria venezuelensis* (holotype of *V. (F.) venezuelensis edentata*, ZSM 1102/1), dorsal and ventral aspect. — Scale 20 mm.
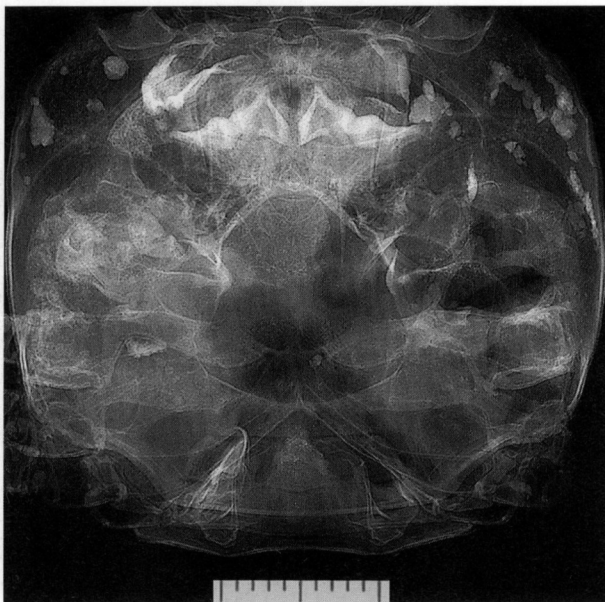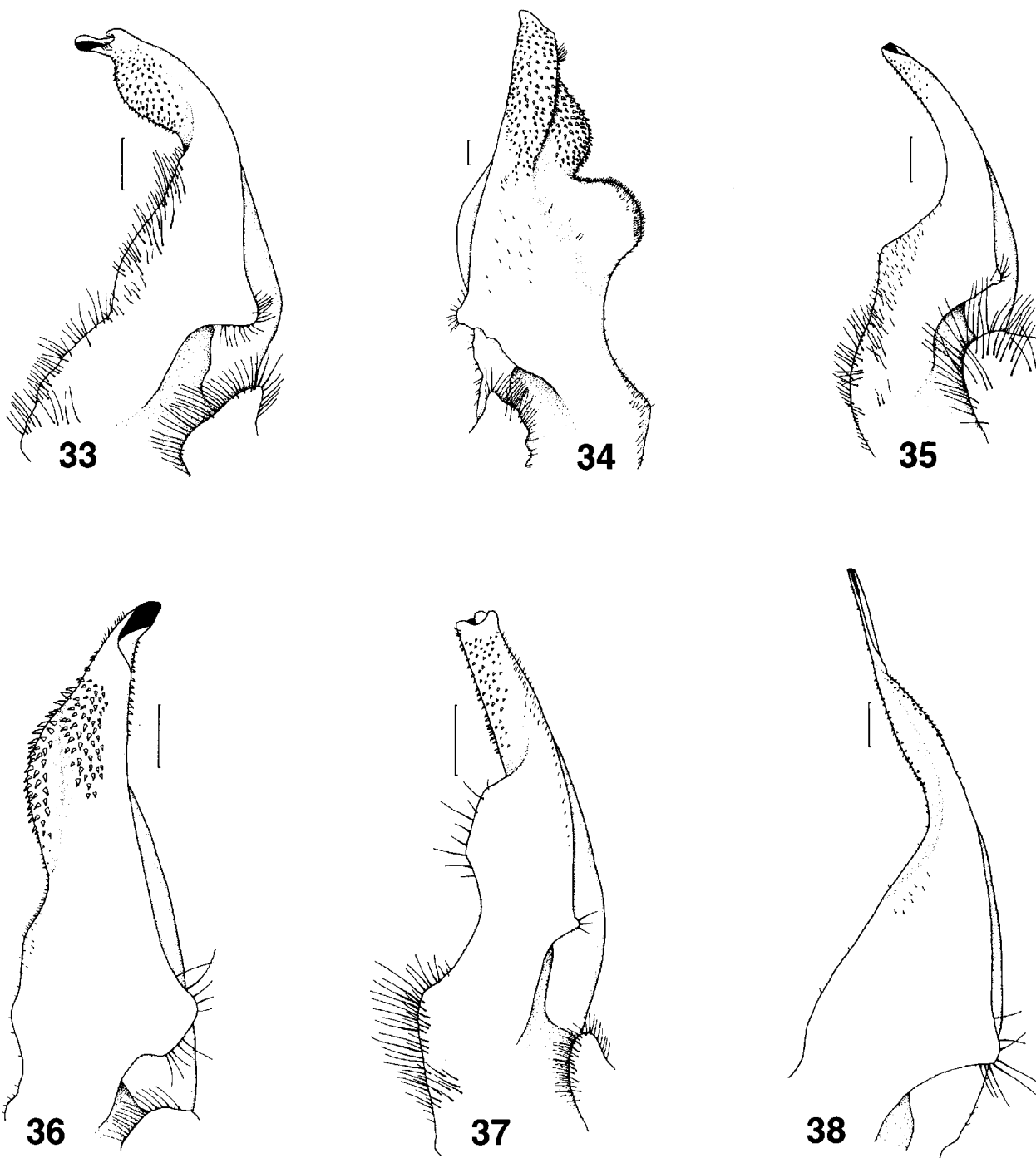
fully agree with this action, as it retains *Valdivia* as a relatively homogeneous taxon with respect to the shape of male pleopod.

Species included: Monotypic for *venezuelensis* (RATHBUN 1905) [= *edentata* BOTT 1969, *ornatifrons* PRETZMANN 1968].

Fig. 40. *Forsteria venezuelensis* (holotype of *V. (F.) venezuelensis edentata*, ZSM 1102/1), X-ray picture of endophragmal system.

Figs. 33–38. Male pleopods of type species of the genera of Valdiviini, ventro-mesial aspect except 35 [mesial aspect] [34 left limb; all others right limb]; scales 1 mm. — 33) *Forsteria venezuelensis* (USNM 234450); 34) *Melocarcinus meekei* (holotype, USNM 59345); 35) *Rotundovaldivia latidens* (USNM 231776); 36) *Sylviocarcinus devillei* (SMF 12705); 37) *Valdivia serrata serrata* (MZUSP 6310); 38) *Zilchiopsis collastinensis* (ZMH K-5255).

Valdivia. Male plp 1 with a distinctly bulged subdistal lobe on its latero-ventral side; spine field well developed, confined to the subdistal lobe; basal lobe inconspicuous. Suture displaced to the dorsal side in the distal third of the limb, returning to the ventral side at the extreme tip where it meets the terminally situated distal opening. Plp 2 longer than plp 1.

Distribution: Orinoco drainage system of Venezuela and Colombia.

Remarks: BOTT (1969: 37) established *Forsteria* at subgeneric level, *Valdivia* (*Forsteria*). This subgenus was subsequently synonymised with *Valdivia* by SMALLEY & RODRIGUEZ (1972) and RODRIGUEZ (1981). Recently RODRIGUEZ (1992) assigned *Forsteria* to generic level. We

Fig. 39. *Forsteria venezuelensis* (holotype of *V. (F.) venezuelensis edentata*, ZSM 1102/1), dorsal and ventral aspect. — Scale 20 mm.

fully agree with this action, as it retains *Valdivia* as a relatively homogeneous taxon with respect to the shape of male pleopod.

Species included: Monotypic for *venezuelensis* (RATHBUN 1905) [= *edentata* BOTT 1969, *ornatifrons* PRETZMANN 1968].
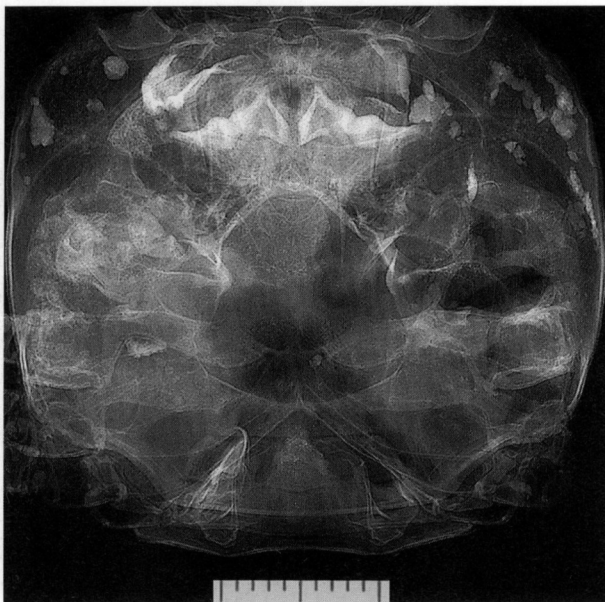

Fig. 40. *Forsteria venezuelensis* (holotype of *V. (F.) venezuelensis edentata*, ZSM 1102/1), X-ray picture of endophragmal system.

Fig. 41. *Melocarcinus meekei* (holotype, USNM 59345), dorsal and ventral aspect. — Scale 20 mm.

Melocarcinus n. gen.

(Figs. 34, 41, 42)

Type species: *Trichodactylus* (*Valdivia*) *meekei* PRETZMANN 1968.

Etymology: This genus is dedicated to Dr. GUSTAVO SCHMIDT DE MELO, carcinologist at the Museu de Zoologia in São Paulo, in appreciation for his work on Brazilian crabs.
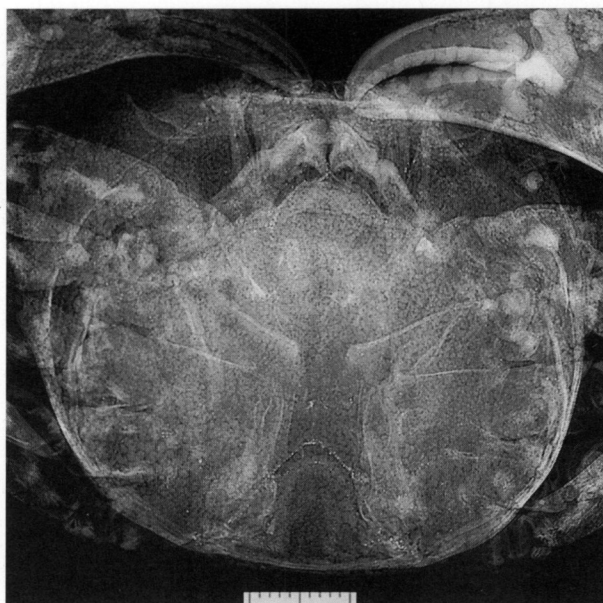

Fig. 42. *Melocarcinus meekei* (holotype, USNM 59345), X-ray picture of endophragmal system.

Diagnosis: Carapace with 4 anterolateral teeth. Abdominal segments III–V fused. Sternal plate and endophragmal system (judged by external view) as in *Sylviocarcinus*. Male plp 1 with a subdistal lobe, subterminal spine field well developed, arranged in one longitudinal area, which is split proximally on the dorsolateral face; stem with a prominent basal lobe on its ventral border; suture begins at ventro-mesial side, in the distal half it is more or less displaced towards the dorsal side, where it meets the similarly directed distal opening. Plp 2 longer than plp 1.

Distribution: Southern Panama.

Remarks: *Melocarcinus* is distinguished by the very peculiar shape of its male plp 1 and cannot be grouped with other species without creating heterogeneous assemblages. The suggestion of RODRIGUEZ (1992), that *M. meekei* might be closely related to *Forsteria venezuelensis*, thus, cannot be supported. The morphological peculiarity of the present genus matches with its far northern range. To our knowledge it is the only trichodactylid occurring in Panama.

Species included: Monotypic for *meekei* (PRETZMANN 1968).

Rotundovaldivia PRETZMANN 1968

(Figs. 35, 43, 44)

1968 *Valdivia (Rotundovaldivia)* PRETZMANN, Entom. Nachrbl., 15(7/8): 73.

Type species: *Trichodactylus (Valdivia) bourgeti* RATHBUN 1905 [by original designation].

Diagnosis: Carapace with 5–6 anterolateral teeth. Abdominal segments III–V fused. Sternal plate and endophragmal system as in *Valdivia*. Male plp 1 with stem regularly tapering to tip, subdistal lobe absent; subterminal spine field poorly developed, situated on the latero-ventral face; basal lobe rounded, knob-shaped; suture displaced to the dorsal side in the distal third of the appendage, returning to ventral side at the extreme tip where it meets the terminally situated distal opening. Plp 2 longer than plp 1.

Distribution: Restricted to the western Amazon basin, to date known from Peru and Brazil.

Remarks: *Rotundovaldivia* was originally given subgenus status by PRETZMANN (1968: 73) and he designated *Trichodactylus (Valdivia) bourgeti* as the type species of the subgenus. Later PRETZMANN (1983b: 326) raised this subgenus to generic level and named, as the type species of the genus, *Trichodactylus (Valdivia) latidens* A. MILNE-EDWARDS 1869. This action is not permitted under the rules of the International Code and the species of RATHBUN remains the type species of *Rotundovaldivia* as originally designated by PRETZMANN. In spite of this formally incorrect statement, the identity of the genus remained the same, as we found out by reexamining the type material that *T. (V.) bourgeti* was indeed a synonym of *R. latidens*. RODRIGUEZ (1992) suggested, that the present genus may be included in *Valdivia*, because of the morphologically intermediate male plp 1 of *R. harttii gila* PRETZMANN. This statement has been made on the basis of PRETZMANN's figures of *R. latidens*, which do not show much detail. However, the proportions of the basal lobe of

the male plp 1 differ so clearly from that of all *Valdivia* species proper, that we propose keeping *R. latidens* in a separate genus. By this action *Valdivia* remains homogeneous.

Species included: Monotypic for *latidens* (A. MILNE-EDWARDS 1869) [= *bourgeti* (RATHBUN 1905), *bourgueti* (sic!) *falcipenis* (PRETZMANN 1968)].

Sylviocarcinus H. MILNE-EDWARDS 1853

(Figs. 36, 45, 46)

1853 *Sylviocarcinus* H.MILNE-EDWARDS, Ann. Sci. nat., (3)20: 215.

1968 *Holthuisia* PRETZMANN, Entom. Nachr.-Bl. Wien, 15(7/8): 74. [Type species by original designation: *Dilocarcinus pictus* H. MILNE-EDWARDS 1853].

Type species: *Sylviocarcinus devillei* H. MILNE-EDWARDS 1853 [by monotypy].

Diagnosis: Carapace with four or less (exceptionally up to five) anterolateral teeth, fading away in large specimens. Abdominal segments III–V or III–VI fused. Thoracic sternum relatively long and narrow. Endophragmal system with endosternites IV/V and VI/VII reaching the midline, latter very low towards the center of the sternum; median plate only evident and crest-shaped in somites VII–VIII. Male plp 1 with or without a subdistal lobe, subterminal spine fields well developed, mostly arranged in three parallel longitudinal areas, which, however, can be more or less fused; suture begins on the ventromesial side, in the distal half it is more or less displaced towards the dorsal side and returns at the tip again to the ventro-mesial side where it meets the similarly directed distal opening.

Distribution: All larger river drainage systems of South America (Amazon, Magdalena, Maracaibo, Paraguay, Paraná), recorded from Colombia, Venezuela, Guyana, Suriname, Brazil, Ecuador, Peru, Bolivia, Paraguay, and Argentina.

Remarks: There has been some discussion in the past as to the name of the genus including *S. devillei* and *S. pictus*. BOTT (1969) used *Sylviocarcinus* and treated *Holthuisia* PRETZMANN 1968 as a synonym. PRETZMANN & MAYTA (1980:5) and PRETZMANN (1983b: 321) in contrary used *Holthuisia* stating, that *S. devillei*, the type species of *Sylviocarcinus*, is a female and no males were known (we agree with this formal statement after reexamination of the series SMF 4334 in which the males belong to other species. — See MAGALHÃES & TÜRKAY 1996a for more details). They prefer therefore, to leave *S. devillei* in *Valdivia* where RATHBUN (1906) placed it. After our reexamination of the type specimen of this species, and examination of male specimens recently collected from the lower Amazon basin, we can say that *S. devillei* is not a *Valdivia* and, thus, *Sylviocarcinus* is a valid genus. Consequently we continue to use this name and treat *Holthuisia* as a younger subjective synonym, because we consider *S. pictus* congeneric with *S. devillei*. The only reason for using *Holthuisia* in the future could be the generic separation of *S. pictus* from *S. devillei* and allies, which we do not think to be adequate. In this case forms like *S. maldona-*

Fig. 43. *Rotundovaldivia latidens* (holotype of *Trichodactylus* (*Valdivia*) *bourgeti*, MCZ 6727), dorsal and ventral aspect. — Scale 10 mm.

doensis or probably also *S. piriformis* should have to be separated. We do not advocate this "atomizing" of the genus into mostly monotypic units. In our treatment we, thus, agree with the results of RODRIGUEZ (1992).

Concerning the generic name *Holthuisia* PRETZMANN 1968, BOTT (1969) pointed out, that it was introduced in the original description with two spellings *"Holthuisisia"* and *"Holthuisia"*. As he synonymized the genus with *Sylviocarcinus*, he did not give one spelling precedence
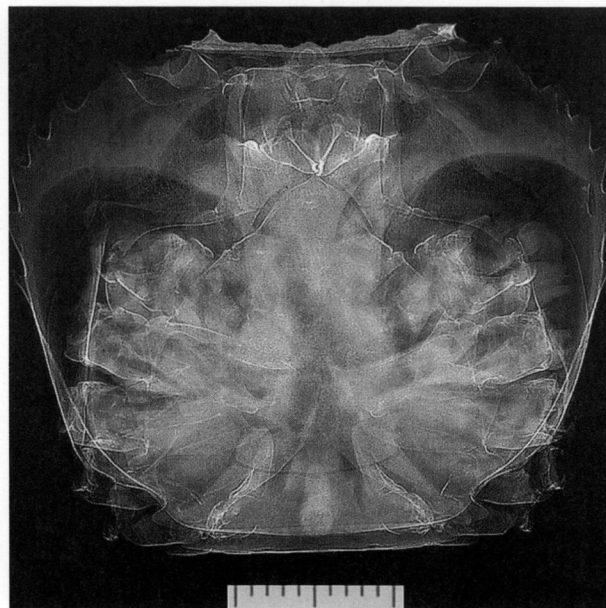

Fig. 44. *Rotundovaldivia latidens* (SMF 22620), X-ray picture of endophragmal system.
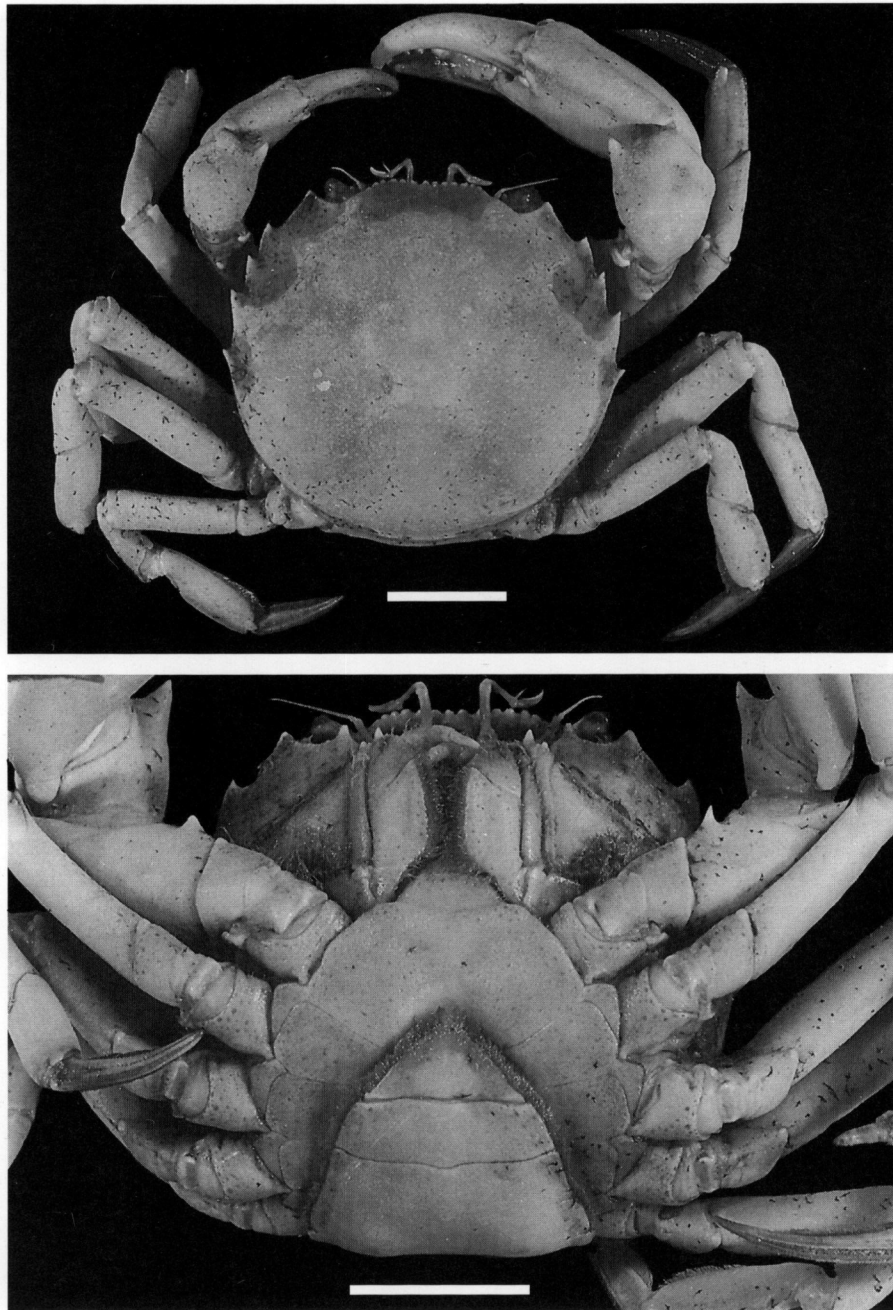
Fig. 45. *Sylviocarcinus devillei* (SMF 12705), dorsal and ventral aspect. — Scale 20 mm.

over the other. PRETZMANN (1983b) definitively declared, that *Holthuisisia* has to be treated as a primary incorrect spelling and thus, acted as first revising author in the sense of Art. 24(b) of the International Code. By his action the spelling *Holthuisia* takes precedence over *Holthuisisia*.

Species included: *australis* MAGALHÃES & TÜRKAY 1996, *devillei* H. MILNE-EDWARDS 1853 [= *gigas* SMALLEY & RODRIGUEZ 1972, *margaritifrons* (ORTMANN 1893), *peruvianus* A. MILNE-EDWARDS 1869, *spinifrons* (KINGSLEY 1880)], *maldonadoensis* (PRETZMANN 1978) [= ? *gurupensis* (RATHBUN 1905)], *pictus* (H. MILNE-EDWARDS 1853) [= ? *pardalinus* (GERSTÄCKER 1856), *picta rionegrensis* (PRETZMANN 1968)], *piriformis* (PRETZMANN 1968) [= *torresi* (PRETZMANN 1968)].
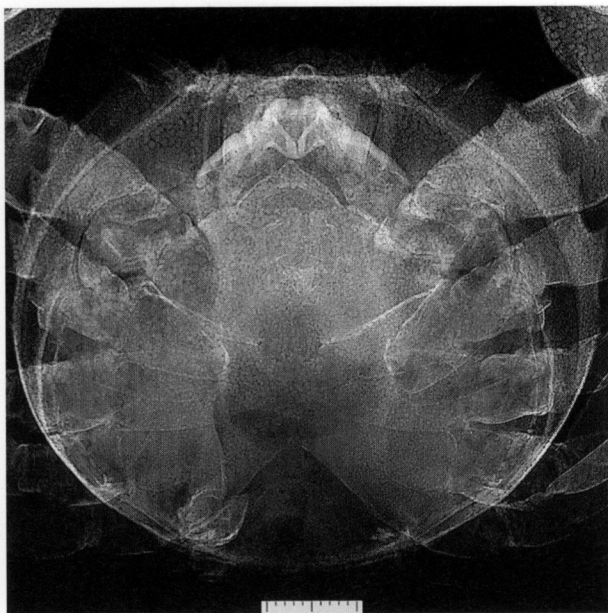
Fig. 46. *Sylviocarcinus devillei* (SMF 18704), X-ray picture of endophragmal system.

Valdivia WHITE 1847

(Figs. 37, 47, 48)

1847 *Valdivia* WHITE, Ann. Mag. nat. Hist., **20**: 206.

Type species: *Valdivia serrata* WHITE 1847 [by monotypy].

Diagnosis: Carapace with two or more anterolateral teeth. Abdominal segments III–V fused. Thoracic sternum relatively long and narrow. Endophragmal system with endosternite IV/V reaching the midline, V/VI and VI/VII do so only as low elevations; median plate present as a relatively low crest only in somites VII–VIII. Male plp 1 with the subdistal lobe faint or absent, subterminal spine field always well developed; rectangular basal lobe present, more or less developed, hardly visible in *V. novemdentata;* suture begins at the ventro-mesial side, in the last third of the appendage it is displaced dorsally, returning to the ventral side at the extreme tip where it meets the terminally situated distal opening (this distal part of the suture is sometimes hidden by terminal lobes at the mesio-ventral corner of the tip). Plp 2 longer than plp 1.

Distribution: Tropical and temperate South America from Venezuela to northern Argentina.

Remarks: *Valdivia* is broadly related to *Sylviocarcinus* and one of the species, *V. novemdentata,* has a male pleopod quite similar in shape to that of *S. australis.* In *Valdivia* the carapace is always flat and has an angular appearance; the male pleopod has a basal lobe and no subdistal one. In *Sylviocarcinus* the carapace of most species is clearly convex and the male pleopod lacks the basal lobe while it has usually a subdistal one. The two genera appear to represent two evolutionary lines with the species *V. novemdentata* and *S. australis* forming a link between the two lineages, as mentioned above. However, in any case those species can be grouped within one of the genera. This means of course, that both genera are closely related.

Following this definition of *Valdivia,* the species *V. camerani* has clearly to be included. For a long time it was treated as a species of *Trichodactylus,* because to date only subadult and young specimens were studied. RODRIGUEZ (1992) classified it with *Valdivia,* stating that it exhibits some peculiarities linking it with *Sylviocarcinus* and the Trichodactylinae. In fact, the pleopods figured in his paper are those of the immature form, as are those figured by LOPRETTO (1976). Therefore, the discussion on relationships in the former paper was misleading. After our examination of adult males (INPA-CR 363), we have no doubt about its proper classification into *Valdivia.* A full treatment of this problem will be given in a subsequent paper on the genus.

Species included: *camerani* (NOBILI 1896), *haraldi* BOTT 1969, *novemdentata* (PRETZMANN 1968), *serrata serrata* WHITE 1847 [= *serrata surinamensis* PRETZMANN 1968, *serrata cururuensis* BOTT 1969, *hartii gila* (PRETZMANN 1978)], *serrata harttii* (RATHBUN 1905).

Zilchiopsis BOTT 1969

(Figs. 38, 49, 50)

1969 *Zilchiopsis* BOTT, Abh. senckenb. naturf. Ges., **518**: 34.

Type species: *Zilchiopsis sattleri* BOTT 1969 [by original designation].

Diagnosis: Carapace with 4 (exceptionally 5) or less anterolateral teeth, usually fading away in large specimens. Abdominal segments III–VI fused. Thoracic sternum relatively long and narrow, the furrows marking the endosternites do not reach the midline; median plate present exclusively in somites VII and VIII. Male plp 1 without a distinct subdistal lobe; its distal part strongly bent in a latero-ventral direction; subterminal spine field poorly developed and situated along the mesial and ventrolateral margins of the bent terminal part, respectively; suture displaced towards the dorsal side at the beginning of the mentioned bent terminal part of the appendage, torded back again at the end of the spine field, and running along the ventral face, where it meets the terminally situated distal opening, thus, the suture shows a 3/4 torsion. Plp 2 longer than plp 1.

Distribution: Southern Amazon drainage of Brazil, Bolivia and Peru; Paraguay-Paraná drainage of Paraguay and northern Argentina.

Remarks: Identifying *Zilchiopsis* female specimens, on the base of carapace and abdomen morphology, is difficult because these characters are similar to those found in the *Sylviocarcinus pictus*-complex. However, the form of the female genital ducts appears to be a distinctive character for both genera. The duct of *Zilchiopsis* is cup-shaped and elevated above the sternal surface so that the opening can hardly be seen in a perpendicular view. In *Sylviocarcinus,* because the duct is relatively flat, the opening is freely visible in a perpendicular view. The posterior border of the duct can be elevated in large specimens of this genus, therefore approaching the shape of the *Zilchiopsis* duct. Even in this situation the duct opening remains visible and the separation of both genera remains possible.

Species included: *collastinensis* (PRETZMANN 1968) [= *sattleri* BOTT 1969], *cryptodus* (ORTMANN 1893), *oronensis* (PRETZMANN 1968).
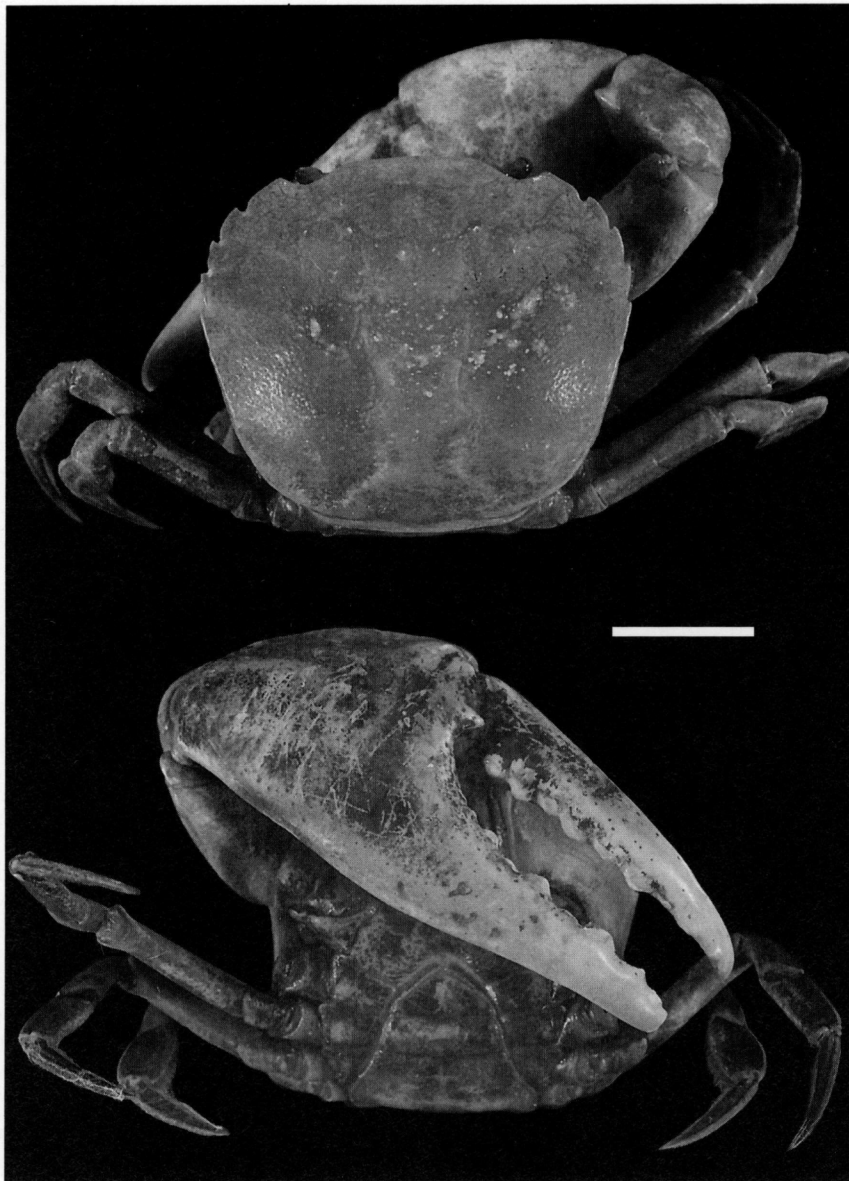
Fig. 47. *Valdivia serrata serrata* (holotype of *Rotundovaldivia harttii gila*, NHMW 4174), dorsal and ventral aspect. — Scale 20 mm.
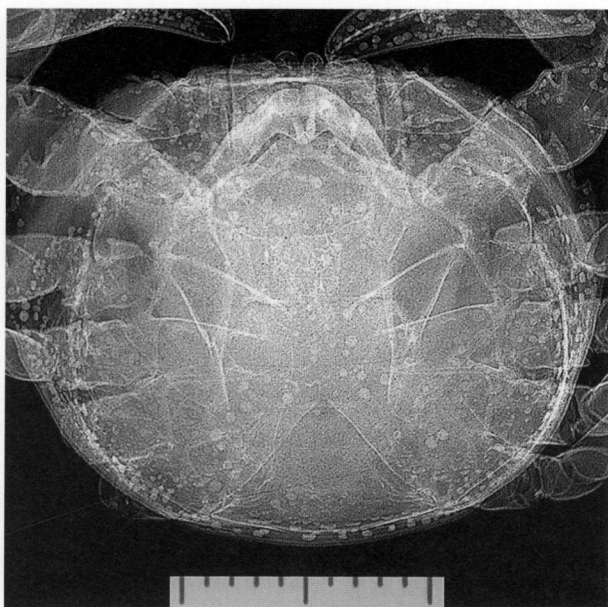

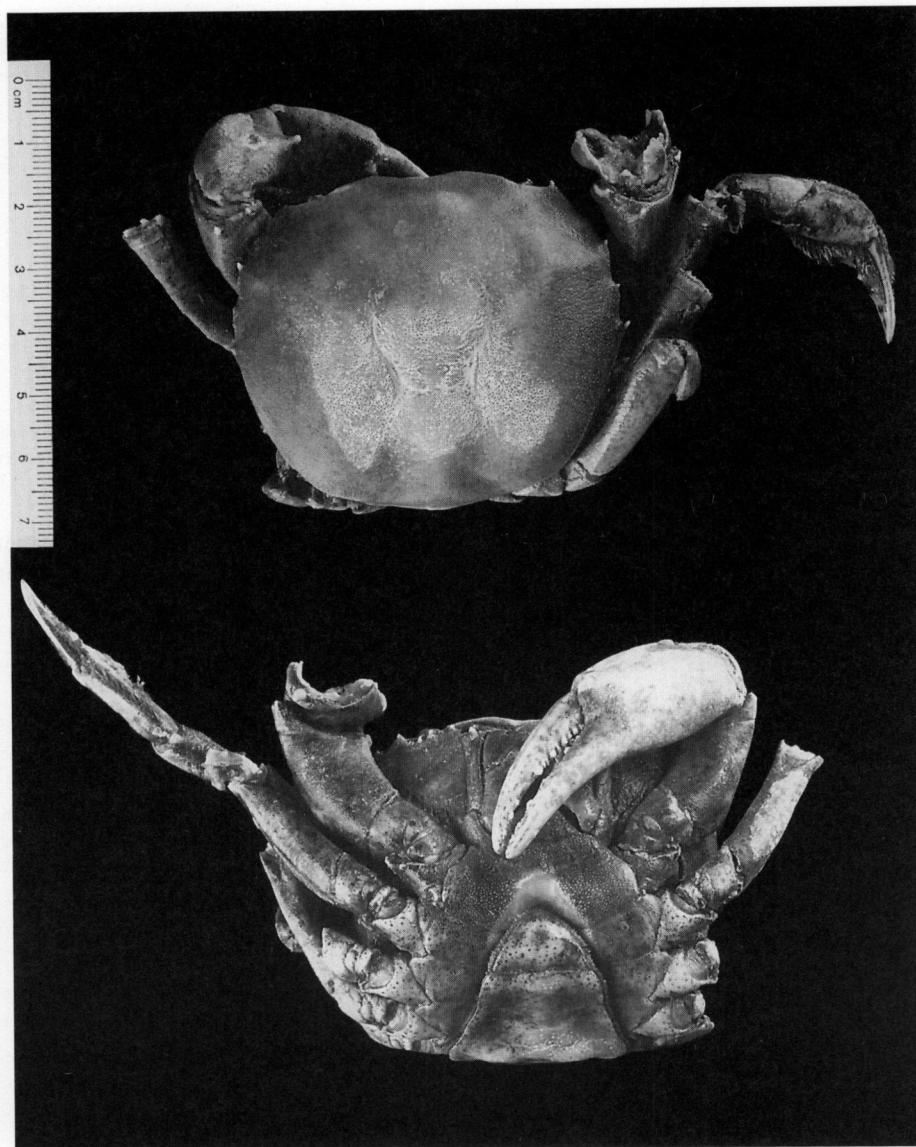Fig. 48. *Valdivia serrata serrata* (SMF 4137), X-ray picture of endophragmal system.

Fig. 49. *Zilchiopsis collastinensis* (holotype of *Zilchiopsis sattleri*, SMF 4365), dorsal and ventral aspect.

Fig. 50. *Zilchiopsis collastinensis* (SMF 4337), X-ray picture of endophragmal system.

References

ADIS, J., JUNK, W. J. & PENNY, N. D. (1985): Material zoológico depositado nas coleções sistemáticas de entomologia do INPA, resultante do "Projeto INPA/Max Planck" (Convênio CNPq/MPG). — Acta Amazonica, 15 (3–4): 481–504; Manaus.

BOTT, R. (1969): Die Süßwasserkrabben Südamerikas und ihre Stammesgeschichte. — Abh. senckenb. naturf. Ges., 518: 1–94, Taf. 1–24; Frankfurt a. M.

COTTARELLI, V. & ARGANO, R. (1977): Trichodactylus (Rodriguezia) mensabak n. sp. (Crustacea, Decapoda, Brachyura), granchio cieco delle acque sotterranee del Chiapas (Messico). — Quad. Probl. attuali Sci. Cult., Acad. naz. Lincei, 171(3): 207–212, figs. 1–4; Roma.

GERSTÄCKER, A. (1856): Carcinologische Beiträge. — Arch. Naturgesch., 22(1): 101–162; Berlin.

GÖLDI, E. A. (1886): Studien über neue und wenig bekannte Podophthalmen Brasiliens. — Arch. Naturgesch., 52(1): 19–46, Taf. 2–3; Berlin.

GOULDING, M. G., CARVALHO, M. L. & FERREIRA, E. G. (1988): Rio Negro, rich life in poor water. Amazonian diversity and foodchain ecology as seen through fish communities, xi + 200 pp.; Den Haag (SPB Academic Publishing).

GUINOT, D. (1979): Morphologie et phylogenèse des Brachyoures. — Mém. Mus. nation. Hist. nat., (N.S.)(A)112: 1–354, text-figs. 1–70, Pls. 1–27; Paris.

HERBST, J. F. W. (1782–1804): Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten, 1–3; Berlin & Stralsund.

KINGSLEY, J. S. (1880): Carcinological notes, no. 1. — Proc. Acad. nat. Sci. Philadelphia, 1880: 34–37; Philadelphia.

LATREILLE, P. A. (1828): Trichodactyle, Trichodactylus. — In: Encyclopédie Méthodique. Histoire naturelle. Entomologie, ou histoire naturelle des Crustacés, des Arachnides et des Insectes, 10: 705; Paris (Agasse).

LOPRETTO, E. C. (1976): Morfologia comparada de los pleopodos sexuales masculinos en los Trichodactylidae de la Argentina (Decapoda, Brachyura). — Limnobios, 1(3): 67–94, figs. 1–30; Berisso, Argentina.

— — — (1981): Discusion sobre las presuntas subspecies de Dilocarcinus (D.) pagei (Crustacea, Brachyura, Trichodactylidae). Redescripcion y referencia a su polifenismo. — Physis, (B)39(97): 21–31, figs. 1–41; Buenos Aires.

MAGALHÃES, C. & TÜRKAY, M. (1996a): Taxonomy of the neotropical freshwater crab family Trichodactylidae. II. The genera Forsteria, Melocarcinus, Sylviocarcinus, and Zilchiopsis. — Senckenbergiana biol., 75(1/2): 97–130, figs. 1–57; Frankfurt a. M.

— & — (1996b): Taxonomy of the neotropical freshwater crab family Trichodactylidae. III. The genera Fredilocarcinus and Goyazana. — Senckenbergiana biol., 75(1/2): 131–142, figs. 1–11; Frankfurt a. M.

MARTENS, E. VON (1869): Südbrasilianische Süss- und Brackwasser-Crustaceen nach den Sammlungen des Dr. REINH. HENSEL. — Arch. Naturgesch., 35(1): 1–37, Taf. 1–2; Berlin.

MILNE-EDWARDS, A. (1869): Révision des genres Trichodactylus, Sylviocarcinus et Dilocarcinus et description de quelques espèces nouvelles qui s'y rattachent. — Ann. Soc. entom. France, (4)9: 170–178; Paris.

MILNE-EDWARDS, H. (1853): Mémoire sur la famille des Ocypodiens. — Ann. Sci. nat., (3)20: 163–226; Paris.

MOREIRA, C. (1901): Contribuições para o conhecimento de fauna brazileira. Crustaceos do Brazil. — Archos. Mus. nac. Rio de Janeiro, 11: 1–152, pls. 1–5; Rio de Janeiro.

— — — (1912): Crustacés du Brésil. — Mém. Soc. zool. France, 25: 145–154, pls. 3–6; Paris.

NOBILI, G. (1896): Crostacei decapodi. Viaggio del Dott. A. BORELLI nella Republica Argentina e nel Paraguay. — Boll. Mus. Zool. Anat. comp. Univ. Torino, 11(222): 1–4; Torino.

ORTMANN, A. (1893): Die Decapoden-Krebse des Straßburger Museums, VII. Abtheilung: Brachyura, II. Unterabtheilung: Cancroidea, 2. Section: Cancrinae, 1. Gruppe: Cyclometopa. — Zool. Jb. Syst., 7(3): 411–495, Taf. 17; Jena.

PARISI, B. (1923): Un nuovo Potamonide americano. — Ann. Mus. civ. Stor. nat. Genova, 51: 29–30; Genova.

PEARSE, A. S. (1911): Report on the Crustacea collected by the University of Michigan — WALKER Expedition to the state of Veracruz, Mexico. — Rep. Michigan Acad. Sci., 13: 108–113; Lansing, Crawford.

PRETZMANN, G. (1968a): Weitere neue südamerikanische Süßwasserkrabben. (Vorläufige Mitteilung). — Entom. Nachrbl., 15(Sonderheft 2): 1–6; Wien.

— — — (1968b): Die Familie Trichodactylidae (MILNE-EDWARDS 1853) SMITH 1870 (Vorläufige Mitteilung). — Entom. Nachrbl., 15(7–8): 70–76; Wien.

— — — (1978): Neue Süßwasserkrabben aus den Anden. — Sitz.-Ber. österr. Akad. Wiss. math. naturw. Kl., (1)187(6–10): 163–170, Abb. 1–13; Wien.

— — — (1979): Poppiana bachmayeri nov. comb. — Ann. naturhist. Mus. Wien, 82: 591–593, Taf. 1–3; Wien.

— — — (1983a): Ergebnisse einiger Sammelreisen in Peru und Ecuador 1976/77. 2. Teil: Neue Trichodactylidae. — Ann. naturhist. Mus. Wien. 84(B): 307–311, Taf. 1–6; Wien.

— — — (1983b): Die Trichodactylidae von Peru und Ecuador. — Ann. naturhist. Mus. Wien, 84(B): 317–330, Taf. 1–14; Wien.

PRETZMANN, G. & MAYTA, R. (1980): Über einige Süßwasserkrabben aus Peru. — Anz. österr Akad. Wiss. math.-naturw. Kl., 1980(9): 137–144, Abb. 1–14; Wien.

RANDALL, J. W. (1840): Catalogue of the Crustacea brought by THOMAS NUTTALL and J. K. TOWNSEND, from the west coast of North America and the Sandwich Islands, with descriptions of such species as are apparently new, among which are included several species of different localities, previously existing in the collection of the Academy. — J. Acad. nat. Sci. Philadelphia, 8(1): 106–147, pls. 3–7; Philadelphia.

RATHBUN, M. J. (1893): Descriptions of new species of American fresh-water crabs. — Proc. U. S. nation. Mus., 16(959): 649–661, pls. 73–77; Washington, D. C.

— — — (1904–1906): Les crabes d'eau douce (Potamonidae). — Nouv. Arch. Mus. Hist. nat. Paris, 6(4): 225–312; 7(4): 159–321, pls. I–XXII; 8(4): 33–122. Paris.

RODRIGUEZ, G. (1981): Decapoda. — In: HURLBERT, S. H., RODRIGUEZ, G. & SANTOS, N. D. [Eds.]: Aquatic biota of tropical South America, 1 (Arthropoda): 41–51; San Diego, California (San Diego State University).

— — — (1992): The freshwater crabs of America. Family Trichodactylidae and supplement to the family Pseudothelphusidae. — Faune tropicale, **31**: 1–189, figs. 1–51; Paris (ORSTOM).

RODRIGUEZ, G. & MANRIQUE, F. (1967): El genero *Trichodactylus* en Mexico (Brachyura, Potamonidae). — An. Inst. Biol., **37**(1/2): 183–186, fig. 1, pl. 1; Mexico, D. F.

SCHMITT, W. L. & PRETZMANN, G. (1968): Eine neue *Trichodactylus*-Art aus Kolumbien (Vorläufige Mitteilung). — Entom. Nachrbl., **15**(Sonderheft 2): 6; Wien.

SMALLEY, A. E. & RODRIGUEZ, G. (1972): Trichodactylidae from Venezuela, Colombia, and Ecuador (Crustacea: Brachyura). — Tulane Stud. Zool. Bot. **17**(3/4): 41–55, figs. 1–23; New Orleans.

STIMPSON, W. M. (1861): Notes on certain decapod Crustacea. — Proc. Acad. nat. Sci. Philadelphia, **13**: 372–375; Philadelphia.

TRAJANO, E. (1987): Fauna cavernícola brasileira: composição preliminar. — Revta. bras. Zool., **3**(8): 503–531; São Paulo.

TÜRKAY, M. (1975): Statement: Die Bedeutung des Gonopodenaufbaus für die Aufklärung verwandtschaftlicher Beziehungen bei dekapoden Crustaceen. — Aufs. Red. senckenb. naturf. Ges., **27**: 114–115; Frankfurt a. M.

— — — (1983a): On the systematic position of the Australian mangrove crab *Heloecius cordiformis* (Crustacea: Decapoda: Brachyura). — Mem. austral. Mus., **18**: 107–111, figs. 1–3; Sydney.

— — — (1983b): Morphologisch-taxonomische Monographie der Gecarcinidae. Ein Beitrag zur vergleichenden Morphologie der Brachyura (Crustacea: Decapoda). — Dissertation Univ. Frankfurt a. M., iv + 111 pp., 106 figs.; Frankfurt a. M.

WHITE, A. (1847): Short descriptions of some new species of Crustacea in the collection of the British Museum. — Ann. Mag. nat. Hist., **20**: 205–207; London.

ZWINK, W. (1990): Fauna de Crustáceos. — In: Universidade Federal Do Rio De Janeiro, Museu Nacional: Levantamento faunístico da área sob influência da BR-364 (Cuiabá-Porto Velho): 102–103. — Rio de Janeiro (Museu Nacional)(Programa Polonoroeste. Relatório de Pesquisas n 13).