

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 pereopods. 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:

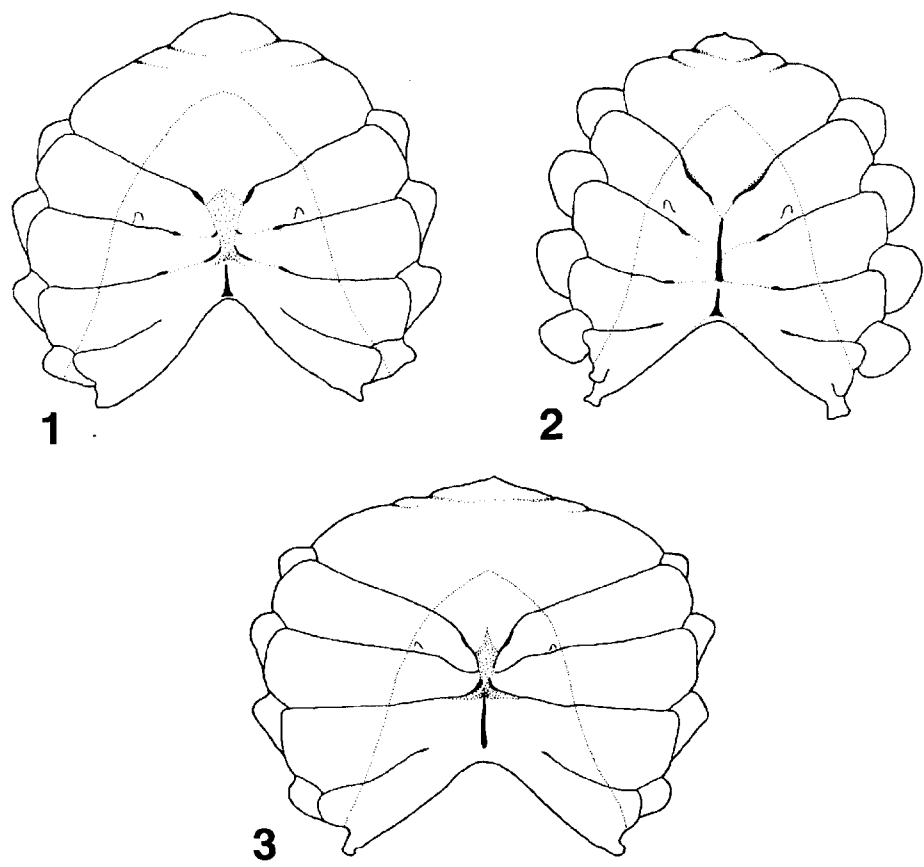
1. The genera related to *Trichodactylus* are characterized by a broadly oval sternum, which is much broader than in other genera. All of the former genera have an en-

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*).

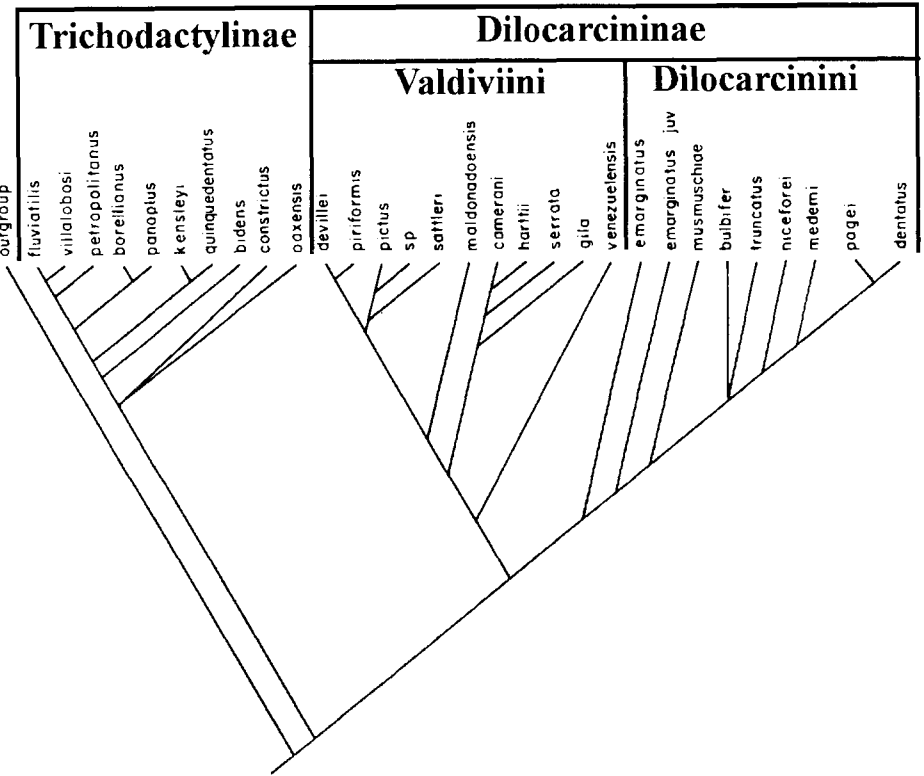


Fig. 4. Cladogram of RODRIGUEZ (1992) with superposition of the groupings introduced in the present paper showing the general similarity of proposed relationships.

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

Trichodactylinae H. MILNE-EDWARDS 1853

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| <i>Avotrichodactylus</i> PRETZMANN 1968 | <i>Trichodactylus</i> LATREILLE 1828 |
| <i>constrictus</i> (PEARSE 1911) | <i>borellianus</i> NOBILI 1896 |
| <i>oaxensis</i> RODRIGUEZ 1992 | <i>crassus</i> A. MILNE-EDWARDS 1869 |
| <i>Rodriguezia</i> BOTT 1969 | <i>dentatus</i> H. MILNE-EDWARDS 1853 |
| <i>mensabak</i> (COTTARELLI & ARGANO 1977) | <i>ehrharti</i> BOTT 1969 |
| <i>villalobosi</i> (RODRIGUEZ & MANRIQUE 1966) | <i>faxoni</i> RATHBUN 1906 |
| | <i>fluviatilis</i> LATREILLE 1828 |
| | <i>kensleyi</i> RODRIGUEZ 1992 |
| | <i>panoplus</i> (VON MARTENS 1869) |
| | <i>parvus</i> MOREIRA 1912 |
| | <i>petropolitanus</i> (GÖLDI 1886) |
| | <i>quinquedentatus</i> RATHBUN 1893 |

Dilocarcininae PRETZMANN 1978

- | | |
|---|---|
| Dilocarcinini PRETZMANN 1978 | Valdiviini PRETZMANN 1978 |
| <i>Bottiella</i> n. gen. | <i>Forsteria</i> BOTT 1969 |
| <i>cucutensis</i> (PRETZMANN 1968) | <i>venezuelensis</i> (RATHBUN 1905) |
| <i>medemi</i> (SMALLEY & RODRIGUEZ 1972) | <i>Melocarcinus</i> n. gen. |
| <i>niceforei</i> (SCHMITT & PRETZMANN 1968) | <i>meekei</i> (PRETZMANN 1968) |
| <i>Dilocarcinus</i> H. MILNE-EDWARDS 1853 | <i>Rotundovaldivia</i> PRETZMANN 1968 |
| <i>pagei pagei</i> STIMPSON 1861 | <i>latidens</i> (A. MILNE-EDWARDS 1869) |
| <i>pagei enriquei</i> PRETZMANN 1978 | <i>Sylviocarcinus</i> H. MILNE-EDWARDS 1853 |
| <i>septemdentatus</i> (HERBST 1783) | <i>australis</i> MAGALHÃES & TÜRKAY 1995 |
| <i>truncatus</i> RODRIGUEZ 1992 | <i>devillei</i> H. MILNE-EDWARDS 1853 |
| <i>Fredilocarcinus</i> PRETZMANN 1978 | <i>maldonadoensis</i> (PRETZMANN 1978) |
| <i>musmuschiae</i> (PRETZMANN & MAYTA 1980) | <i>pictus</i> (H. MILNE-EDWARDS 1853) |
| <i>raddai</i> (PRETZMANN 1978) | <i>piriformis</i> (PRETZMANN 1968) |
| <i>apyratii</i> MAGALHÃES & TÜRKAY 1995 | <i>Valdivia</i> WHITE 1847 |
| <i>Goyazana</i> BOTT 1969 | <i>camerani</i> (NOBILI 1896) |
| <i>castelnaui</i> (H. MILNE-EDWARDS 1853) | <i>haraldi</i> BOTT 1969 |
| <i>rotundicauda</i> MAGALHÃES & TÜRKAY 1995 | <i>novemdentata</i> (PRETZMANN 1968) |
| <i>Moreirocarcinus</i> n. gen. | <i>serrata serrata</i> WHITE 1847 |
| <i>chacei</i> (PRETZMANN 1968) | <i>serrata harttii</i> (RATHBUN 1905) |
| <i>emarginata</i> (H. MILNE-EDWARDS 1853) | <i>Zilchiopsis</i> BOTT 1969 |
| <i>laevifrons</i> (MOREIRA 1901) | <i>collastinensis</i> (PRETZMANN 1968) |
| <i>Poppiana</i> BOTT 1969 | <i>cryptodus</i> (ORTMANN 1893) |
| <i>argentiniana</i> (RATHBUN 1906) | <i>oronensis</i> (PRETZMANN 1968) |
| <i>bulbifer</i> (RODRIGUEZ 1992) | |
| <i>dentata</i> (RANDALL 1839) | |

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
<i>acutidens</i> PRETZMANN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>apaluensis</i> PRETZMANN	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>apyratii</i> MAGALHÃES & TÜRKAY	-----	<i>Fredilocarcinus</i>
<i>argentiniana</i> RATHBUN	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>armatus</i> A. MILNE-EDWARDS	<i>Mikrotrichodactylus</i>	<i>Trichodactylus</i>
<i>australis</i> MAGALHÃES & TÜRKAY	-----	<i>Sylviocarcinus</i>
<i>bachmayeri</i> PRETZMANN	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>bidens</i> BOTT	<i>Avotrichodactylus</i>	<i>Avotrichodactylus</i>
<i>boliviensis</i> PARISI	? <i>Zilchiopsis</i>	<i>Poppiana</i>
<i>borellianus</i> NOBILI	<i>Mikrotrichodactylus</i>	<i>Trichodactylus</i>
<i>bourgueti</i> RATHBUN	? <i>Valdivia</i>	<i>Rotundovaldivia</i>
<i>brasilensis</i> PRETZMANN	<i>Mikrotrichodactylus</i>	<i>Trichodactylus</i>
<i>bulbifer</i> RODRIGUEZ	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>camerani</i> NOBILI	<i>Valdivia</i>	<i>Valdivia</i>
<i>castelnaui</i> H. MILNE-EDWARDS	<i>Dilocarcinus</i>	<i>Goyazana</i>
<i>cayennensis</i> PRETZMANN	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>chacei</i> PRETZMANN	<i>Zilchiopsis</i>	<i>Moreirocarcinus</i>
<i>collastinensis</i> PRETZMANN	<i>Sylviocarcinus</i>	<i>Zilchiopsis</i>
<i>constrictus</i> PEARSE	<i>Avotrichodactylus</i>	<i>Avotrichodactylus</i>
<i>crassus</i> A. MILNE-EDWARDS	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>cristatus</i> BOTT	<i>Dilocarcinus</i>	<i>Dilocarcinus</i>
<i>cryptodus</i> ORTMANN	<i>Zilchiopsis</i>	<i>Zilchiopsis</i>
<i>cucutensis</i> PRETZMANN	<i>Dilocarcinus</i>	<i>Bottiella</i>
<i>cunninghami</i> BATE	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>cururuensis</i> BOTT	<i>Valdivia</i>	<i>Valdivia</i>
<i>dentata</i> RANDALL	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>dentatus</i> H. MILNE-EDWARDS	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>devillei</i> H. MILNE-EDWARDS	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>ecuadoriensis</i> PRETZMANN	<i>Zilchiopsis</i>	<i>Moreirocarcinus</i>
<i>ecuadoroides</i> PRETZMANN	<i>Zilchiopsis</i>	<i>Moreirocarcinus</i>
<i>edentata</i> BOTT	<i>Forsteria</i>	<i>Forsteria</i>
<i>edwardsi</i> RATHBUN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>ehrharti</i> BOTT	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>emarginatus</i> H. MILNE-EDWARDS	<i>Zilchiopsis</i>	<i>Moreirocacinus</i>
<i>enriquei</i> PRETZMANN	<i>Dilocarcinus</i>	<i>Dilocarcinus</i>
<i>falcipenis</i> PRETZMANN	<i>Valdivia</i>	<i>Rotundavaldivia</i>
<i>faxoni</i> RATHBUN	<i>Incertae sedis</i>	<i>Trichodactylus</i>
<i>fluviatilis</i> LATREILLE	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>gigas</i> SMALLEY & RODRIGUEZ	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>gila</i> PRETZMANN	<i>Valdivia</i>	<i>Valdivia</i>
<i>glaber</i> PRETZMANN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>guayanensis</i> PRETZMANN	-----	<i>Incertae sedis</i>
<i>gurupensis</i> RATHBUN	<i>Incertae sedis</i>	? <i>Sylviocarcinus</i>
<i>haraldi</i> BOTT	<i>Valdivia</i>	<i>Valdivia</i>
<i>harttii</i> RATHBUN	<i>Valdivia</i>	<i>Valdivia</i>
<i>kensleyi</i> RODRIGUEZ	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>laevifrons</i> MOREIRA	<i>Dilocarcinus</i>	<i>Moreirocacinus</i>

Table 2. (continued).

Species or subspecies	Genus in RODRIGUEZ (1992)	Genus in present paper
<i>latidens</i> A. MILNE-EDWARDS	<i>Valdivia</i>	<i>Rotundovaldivia</i>
<i>maldonadoensis</i> PRETZMANN	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>margaritifrons</i> ORTMANN	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>marmorata</i> NOBILI	<i>Mikrotrichodactylus</i>	<i>Trichodactylus</i>
<i>maytai</i> PRETZMANN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>medemi</i> SMALLEY & RODRIGUEZ	<i>Dilocarcinus</i>	<i>Bottiella</i>
<i>meekei</i> PRETZMANN	? <i>Forsteria</i>	<i>Melocarcinus</i>
<i>mensabak</i> COTTARELLI & ARGANO	<i>Rodriguezia</i>	<i>Rodriguezia</i>
<i>multidentatus</i> VON MARTENS	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>musmuschiae</i> PRETZMANN & MAYTA	<i>Fredilocarcinus</i>	<i>Fredilocarcinus</i>
<i>niceforei</i> SCHMITT & PRETZMANN	<i>Dilocarcinus</i>	<i>Bottiella</i>
<i>novemdentata</i> PRETZMANN	<i>Valdivia</i>	<i>Valdivia</i>
<i>oaxensis</i> RODRIGUEZ	<i>Avotrichodactylus</i>	<i>Avotrichodactylus</i>
<i>orbicularis</i> MEUSCHEN	<i>Dilocarcinus</i>	<i>Dilocarcinus</i>
<i>ornatifrons</i> PRETZMANN	<i>Forsteria</i>	<i>Forsteria</i>
<i>oronensis</i> PRETZMANN	? <i>Zilchiopsis</i>	<i>Zilchiopsis</i>
<i>pagei</i> STIMPSON	<i>Dilocarcinus</i>	<i>Dilocarcinus</i>
<i>panoplus</i> VON MARTENS	<i>Mikrotrichodactylus</i>	<i>Trichodactylus</i>
<i>paranensis</i> BOTT	<i>Incertae sedis</i>	<i>Trichodactylus</i>
<i>pardalinus</i> GERSTÄCKER	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>parvus</i> MOREIRA	? <i>Mikrotrichodactylus</i>	<i>Trichodactylus</i>
<i>peruvianus</i> A. MILNE-EDWARDS	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>petropolitanus</i> GÖLDI	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>pictus</i> H. MILNE-EDWARDS	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>piriformis</i> PRETZMANN	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>punctatus</i> EYDOUX & SOLEYET	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>quadrata</i> H. MILNE-EDWARDS	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>quinquedentatus</i> RATHBUN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>raddai</i> PRETZMANN	<i>Fredilocarcinus</i>	<i>Fredilocarcinus</i>
<i>rionegrensis</i> PRETZMANN	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>rionovoensis</i> BOTT	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>rotundicauda</i> MAGALHÃES & TÜRKAY	-----	<i>Goyazana</i>
<i>sattleri</i> BOTT	<i>Zilchiopsis</i>	<i>Zilchiopsis</i>
<i>septemdentatus</i> HERBST	<i>Dilocarcinus</i>	<i>Dilocarcinus</i>
<i>serrata</i> WHITE	<i>Valdivia</i>	<i>Valdivia</i>
<i>spinifer</i> H. MILNE-EDWARDS	<i>Dilocarcinus</i>	<i>Dilocarcinus</i>
<i>spinifrons</i> KINGSLEY	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>surinamensis</i> PRETZMANN	<i>Valdivia</i>	<i>Valdivia</i>
<i>thayeri</i> RATHBUN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>theresiopoliensis</i> PRETZMANN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>tifucanus</i> RATHBUN	<i>Trichodactylus</i>	<i>Trichodactylus</i>
<i>torresi</i> PRETZMANN	<i>Sylviocarcinus</i>	<i>Sylviocarcinus</i>
<i>trinidadensis</i> PRETZMANN	<i>Dilocarcinus</i>	<i>Poppiana</i>
<i>truncatus</i> RODRIGUEZ	<i>Dilocarcinus</i>	<i>Dilocarcinus</i>
<i>venezuelensis</i> RATHBUN	<i>Forsteria</i>	<i>Forsteria</i>
<i>villalobosi</i> RODRIGUEZ & MANRIQUE	<i>Rodriguezia</i>	<i>Rodriguezia</i>

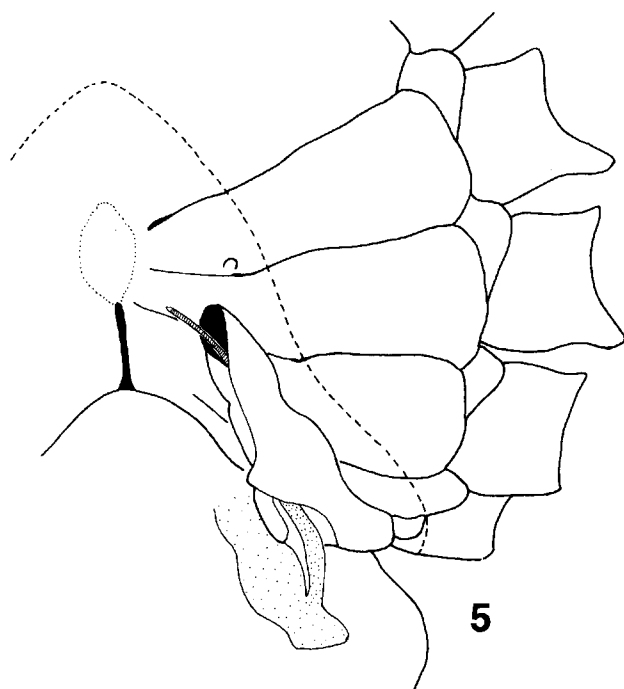


Fig. 5. Position of male Plp 1 in the sterno-abdominal cavity of *Trichodactylus*. The visible face of the limb is the ventral one, the opposite side the dorsal.

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

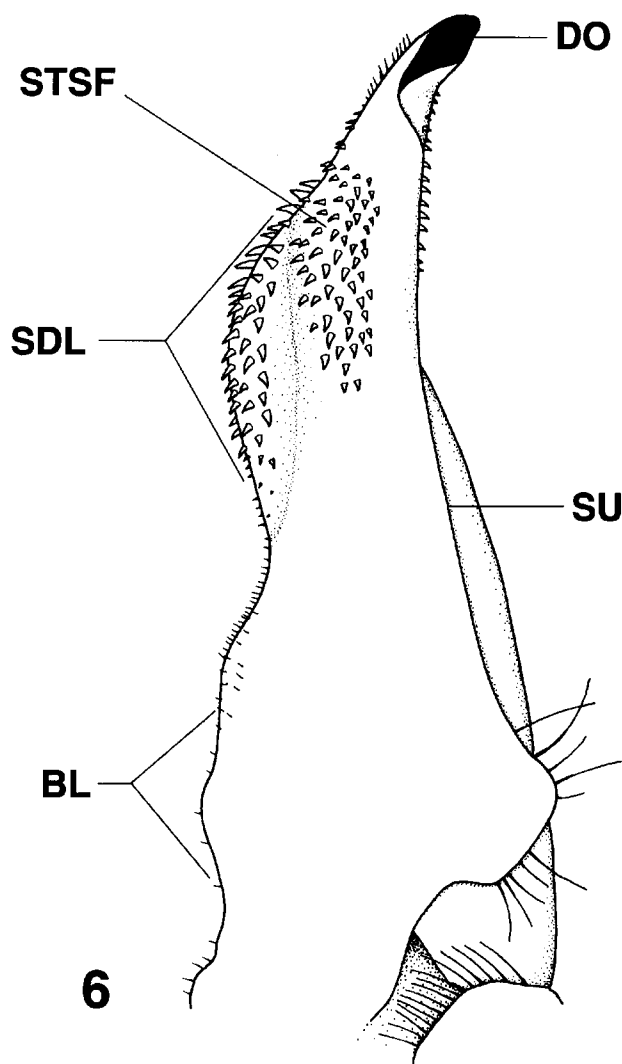


Fig. 6. Right Plp 1 of *Sylviocarcinus devillei* with an explanation of the structures used in the keys and descriptions. — BL = Basal lobe, DO = distal opening, SDL = subdistal lobe, STSF = subterminal spine field, SU = suture.

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.

Acknowledgements

We are very much indebted to our colleagues at the institutes listed below for allowing us to examine the trichodactylid material under their care. Special thanks are due to G. A. S. DE MELO (Museu de Zoologia da Universidade de São Paulo) for his unselfish support of our work and the loan of the whole trichodactylid collection of his museum. We are very grateful to G. PRETZMANN (Naturhistorisches Museum, Wien) for allowing us access to his type material. The x-rays were taken and processed by J. HABERSETZER and M. SIMON (both at the Senckenberg-Museum, Frankfurt a. M.) and we thank them for the amount of time they put into this endeavour. Special thanks are due to P.

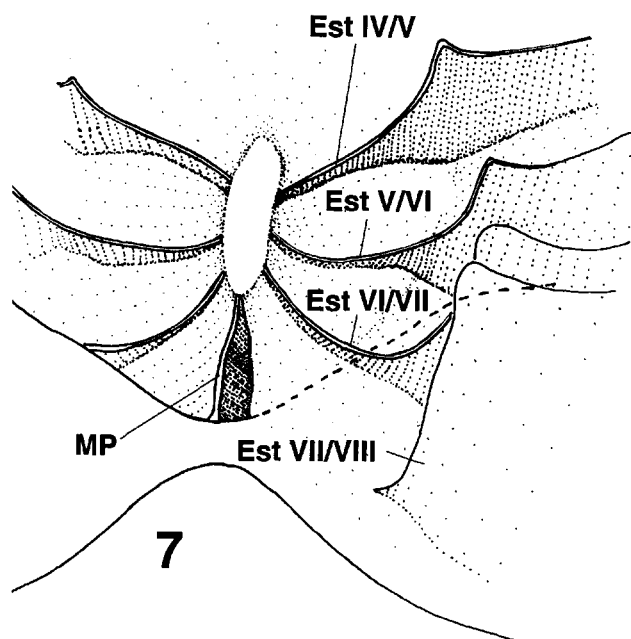


Fig. 7. Schematic drawing of the endophragmal system of *Trichodactylus*. Est = Endosternite, MP = median plate, the Roman figures signify the thoracic segments.

CLARK (The Natural History Museum, London) and D. JONES (Western Australian Museum, Perth) who streamlined our English and made many valuable suggestions. In spite of their huge work, there may still remain linguistic and other inaccuracies for which, of course, only we are responsible. We gratefully acknowledge the "Max Planck Gesellschaft", particularly the "Arbeitsgruppe Tropenökologie" and its chairman W. JUNK at the "Max Planck Institut für Limnologie" at Plön for assisting our studies by sponsoring two visits of C. MAGALHÃES to Frankfurt. Financial aid from the CNPq/INPA/ORSTOM cooperation programme to one of us (C. M.) is also gratefully acknowledged.

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

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 Ciencias 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 Sistemática 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 di 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 Sistemática dell'Università 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 Paraíba, 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 = Colección de Carcinología del Instituto de Biología, 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.

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

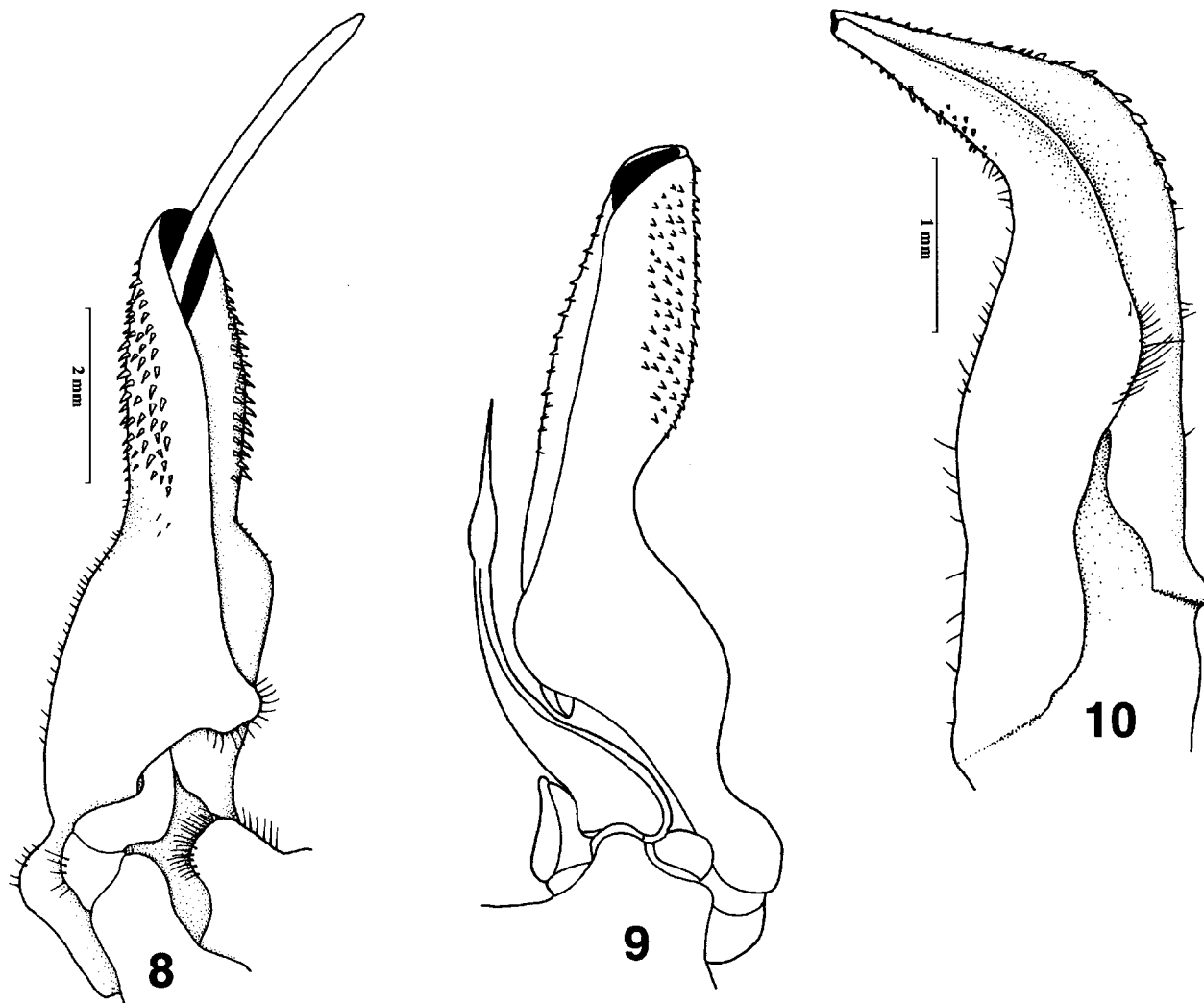
1969 *Trichodactylus* (*Rodriguezia*) BOTT, Abh. senckenb. naturf. Ges., 518: 25.

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 torqued); 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 torted); distal opening broad. Male plp 2 longer than plp 1.

Distribution: Nearly the whole of tropical/sub-tropical 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

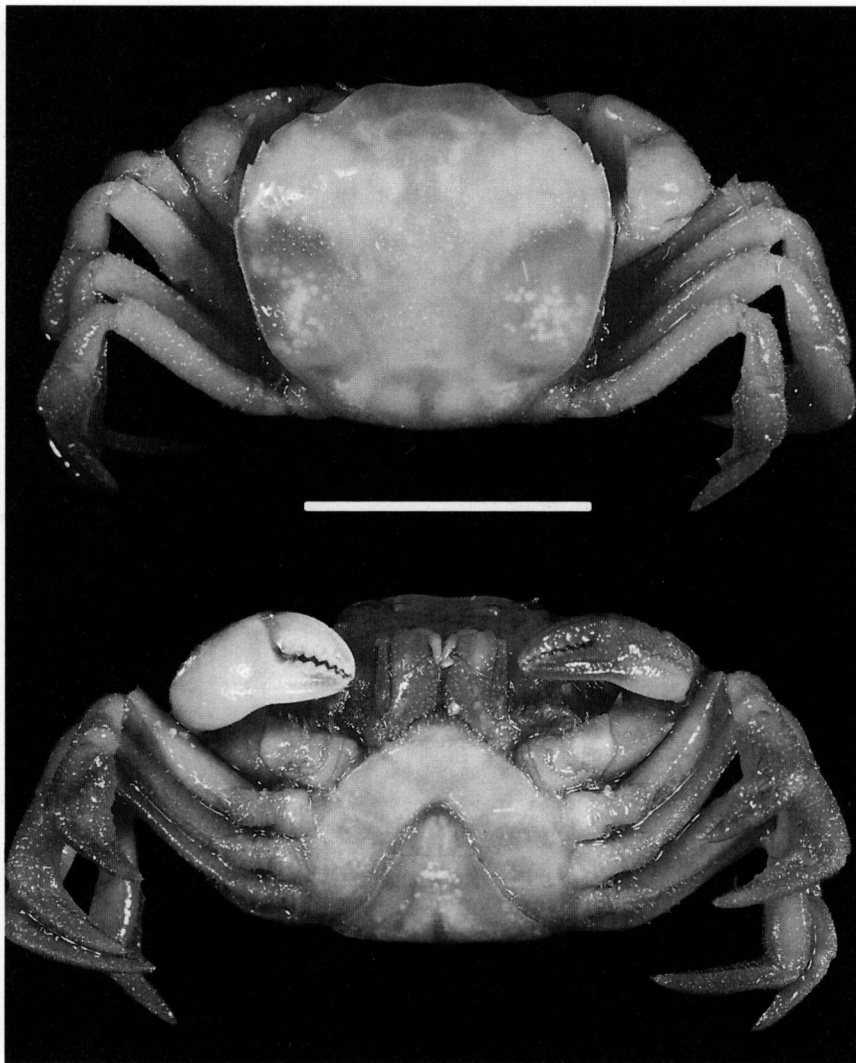


Fig. 11. *Avotrichodactylus constrictus* (NHML 1907.5.15.5-9), dorsal and ventral aspect. — Scale 10 mm.



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.

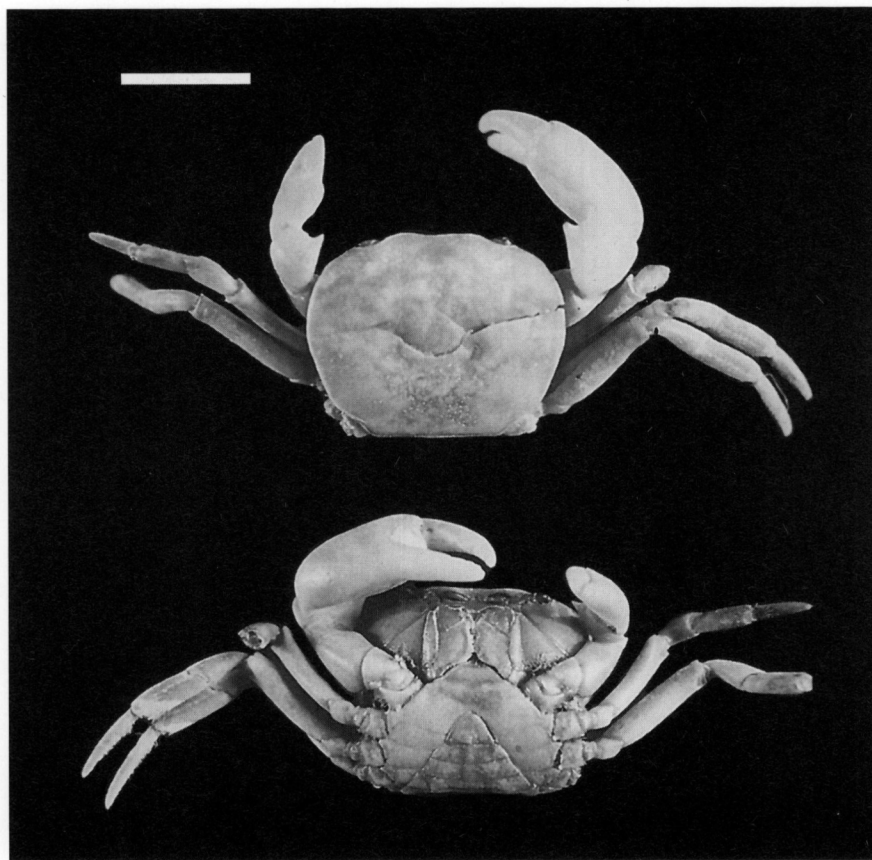


Fig. 13. *Rodriguezia villalobosi* (holotype, UNAM EM-7832), dorsal and ventral aspect. — Scale 10 mm.

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, *ehrbardi* 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 groove 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.